SPATIAL ECOLOGY, HABITAT SELECTION, AND OVERWINTERING OF THE EASTERN KINGSNAKE (*LAMPROPELTIS GETULA*) AT THE NORTHERN EXTENT OF ITS RANGE

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Cover photo:
Female eastern kingsnake (*Lampropeltis getula*) identified as KS2019.06 that was tracked for four years as part of this radio telemetry study.

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SPATIAL ECOLOGY, HABITAT SELECTION, AND OVERWINTERING OF THE EASTERN KINGSNAKE (*LAMPROPELTIS GETULA*) AT THE NORTHERN EXTENT OF ITS RANGE

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EXECUTIVE SUMMARY

We used radio telemetry to track 24 male and 22 female eastern kingsnakes (*Lampropeltis getula*) in the New Jersey Pinelands National Reserve. Snakes were tracked every 48 – 72 hours for one to four years. Body length and weight were positively correlated, and males were longer and heavier than females. Nine females laid eggs during the study, and the average clutch size was 12.5 ± 3.3 eggs and ranged from 6 – 17 eggs. Longer and heavier females laid more eggs.

We observed kingsnakes totally concealed 66% of the time, partially concealed 15% of the time, and fully exposed 19% of the time. Kingsnakes were seen least often in the morning and evening compared to during the day. We observed four peaks in shedding activity: mid spring (mid-May), early summer (mid-June), mid-summer (late July-early August), and early autumn (late September). All mating activity occurred between 27 April and 7 June, with a peak in mid-May.

Kingsnakes emerged from hibernacula from mid-March to mid-May and entered hibernacula to overwinter from late September to late December. About 63% of the snakes left hibernacula in April and about 53% of the snakes entered hibernacula in November. Kingsnakes were active from 156 - 265 d in a season. The mean number of active days was similar for males (199 ± 24 d) and females (200 ± 28 d). The number of active days among the four years of the study was similar.

Most of the 3,587 kingsnake telemetry relocations occurred within wetlands (83.5%). Increasing the size of an upland buffer to wetlands gradually increased the proportion of kingsnake observations contained, with the 300-ft (91.4-m) maximum buffer for wetland protection under the Pinelands Comprehensive Management Plan containing 93.0% of all telemetry relocations and the 600-ft (182.9 m) extended buffer in the Toms River Corridor portion of the Pinelands containing 96.0% of all observed kingsnake locations.

Kingsnakes moved an average of 114.8 ± 44.0 ft (35.0 ± 13.4 m) per day and 3.8 ± 1.4 mi (6.1 ± 2.3 km) per season. Home ranges tended to be elongated in one direction and averaged roughly twice as long as wide. We found no differences between males and females in total distance, mean daily distance, or maximum distance moved, or home range length and width, although males averaged slightly larger than females across all movement metrics.

We distilled the GIS-based New Jersey Department of Environmental Protection land use-land cover categories into six macrohabitat types: upland forest, upland field, herbaceous wetland, deciduous wetland, coniferous wetland, and cedar swamp. In a second order analysis, we compared these macrohabitat types within home ranges and core areas that kingsnakes used to potential available home ranges and core areas simulated in the vicinity of each snake. Kingsnakes selected home ranges with more coniferous wetlands and herbaceous wetlands and less upland forest than available home ranges. Core area selection was similar with respect to avoidance of upland forest and selection for herbaceous wetlands, but unlike home ranges, observed core areas contained significantly more deciduous wetland than available core areas.

We separated the kingsnake active season into a transitional period (stationary at or near its den or actively traveling to or from its summer habitat) and an active period (the warmer part of the year when kingsnakes were focused on foraging) and analyzed second order macrohabitat selection within kingsnake home ranges. During transitional periods, females selected deciduous wetlands and herbaceous wetlands and avoided coniferous wetlands. Males also selected deciduous wetlands, but unlike females, they avoided herbaceous wetlands and upland forest, and used coniferous wetlands roughly in proportion to their availability. During active periods, females again selected deciduous wetlands and avoided coniferous wetlands, but showed no responses to any other land cover categories. Active males selected upland fields and herbaceous wetlands and avoided cedar swamps.

We tested whether the amount of preferred or avoided macrohabitats influenced home range size. Home ranges composed of greater amounts of preferred cover (coniferous wetland and herbaceous wetland) were smaller, whereas home ranges containing more avoided cover (upland forest) were larger. This indicated that kingsnakes traveled further to access preferred habitat types.

When we collected data on each kingsnake location in the field, we also collected the same data on a nearby random point where the snake could have been. Comparing these paired points showed that kingsnakes occurred in association with deeper leaf litter and a higher availability of woody debris than random points, regardless of sex or transitional or active period. When the dataset was divided into males and females in their transitional and active periods, results showed kingsnakes preferred to be in habitats with warmer soil temperatures, lower surface temperatures, more open canopy forest, and with some means to conceal themselves, such as thick and tall shrubs, larger diameter trees, and large diameter logs.

Most kingsnakes overwintered singly, but we observed instances of communal denning. Fidelity to hibernacula was variable, but relatively low. Snakes spent more time in hibernacula over the 2019 - 2020 winter compared to 2020 - 2021 winter, but all other year-to-year comparisons were the same. We identified 51 hibernacula in seven different habitat types. Although snakes used six types of features to access hibernacula for overwintering, most snakes used the base of live or dead trees or shrubs for access. We observed no differences in habitat types or hibernacula access features between males and females.

Most (77%) of the hibernacula were located in pine/maple swamps, pine lowlands, and pine uplands. Hibernacula in pine/maple swamps and pine lowlands were primarily underlain by Atsion sand, which is a hydric mineral or sandy soil, whereas hibernacula in pine uplands were mostly associated with drier sands classified as upland or transitional soils. Fewer hibernacula were in maple swamps, which were all underlain by the hydric mineral soil Berryland, and cedar swamps, which primarily grow in organic soils with a deep layer of peat.

INTRODUCTION

The eastern kingsnake (*Lampropeltus getula*) is a large, glossy, black snake with thin white or cream lines that form a chain-like pattern along its body (Figure 1). This species is distributed along the Atlantic Coastal Plain of the United States from southern New Jersey to northern Florida (Krysko et al. 2017). Although considered globally secure, the eastern kingsnake has shown enigmatic declines in the southern portions of its range, especially in Florida (Krysko and Smith 2005, Stapleton et al. 2008, Winne et al. 2007, Godley et al. 2017).

Radio telemetry studies on eastern kingsnakes are limited, the number of snakes tracked in the studies was low (from 9 – 12 individuals), and results with respect to habitat selection varied by scale. At fine scales, kingsnakes in Georgia and New Jersey selected microhabitats associated with concealment, such as greater shrub density and coarse woody debris (Steen et al. 2010) and greater shrub foliage and litter depth (Wund et al. 2007). Although anecdotal accounts have associated kingsnakes with wetlands (Kauffeld 1957, Gibbons 1977, Conant and Collins 1998), at the home range or landscape scale, kingsnakes in Georgia selected hardwood and natural pine habitats over wetlands and other habitats (Steen et al. 2010) and kingsnakes in New Jersey occupied a variety of upland and wetland habitats and were characterized as macrohabitat generalists (Wund et al. 2007). Therefore, the association between kingsnakes and wetlands has not been demonstrated empirically.

Since 1980, Pinelands wetlands have been granted a high degree of protection by the Comprehensive Management Plan (CMP), which is administered by the Pinelands Commission (Pinelands Commission 1980, Collins and Russell 1988). The CMP requires that a 300-ft (91.4-m) upland buffer be established between a wetland and any proposed development. The 300-ft buffer may be reduced if it can be demonstrated that a development project will not result in a significant adverse impact to the wetland. In the Toms River Corridor located in the northern portion of the Pinelands, the upland buffer was increased to 600 ft (182.9 m) to better protect species that utilize both uplands and wetlands (Pinelands Commission 2004). The ability of wetlands and surrounding buffers to protect kingsnakes has significant conservation implications because the Pinelands represents the northernmost extent of their range and they are listed as special concern in the state (DiLeo 2016).

Little information exists regarding overwintering in eastern kingsnakes. Although brumation was not addressed in the Georgia study (Steen et al. 2010), New Jersey kingsnakes were found to overwinter in the root system of trees or shrubs in forested wetlands or in habitats adjacent to wetlands (Wund et al. 2007). The full suite of habitat types used for overwintering, features used to access hibernacula, underlying geology, timing of ingress and egress, and hibernacula fidelity have not been described for eastern kingsnakes. Because of the use of heavy machinery, the timing of kingsnake surface activity and overwintering can help determine when to conduct timber harvests, habitat restoration activities, and electric transmission line vegetation management to better protect such species of conservation concern.

Figure 1. Examples of adult eastern kingsnakes (*Lampropeltis getula getula*) showing typical coloration and pattern.

In this study, we used radio telemetry data from four years of tracking eastern kingsnakes to: (1) describe seasonal and daily activity, (2) determine the extent to which wetlands and associated upland buffers may protect kingsnakes, (3) compare home ranges, core areas, and movement metrics, (4) quantify habitat selection at multiple scales, and (5) describe the habitats, features, geology, timing, and fidelity associated with overwintering. We discuss our results in relation to other eastern kingsnake studies.

MATERIAL AND METHODS

Study Area

We conducted this study in the Pinelands National Reserve, which is an approximately 1.1 million-acre (4,450 km^2), fire-prone, acid-water, sandy soil ecosystem that lies on the outer coastal plain of southern New Jersey (Figure 2). Based on New Jersey Department of Environmental Protection (NJDEP) land use-land cover data (NJDEP 2024a), approximately 16% of the Reserve is composed of developed land and upland agriculture and the remaining 84% is covered by a variety of upland (44%) and wetland (40%) habitats. Upland habitat types in the Pinelands are primarily pine (*Pinus* species) and oak (*Quercus* species) forests and wetlands include pitch pine (*Pinus rigida*) lowland forests, red maple (*Acer rubrum*) and Atlantic white cedar (*Chamaecyparis thyoides*) swamps, herbaceous and shrub wetlands, and open water bodies, such as ponds and stream impoundments.

Data Collection

Snake Capture. In 2019, we began capturing kingsnakes for this study opportunistically and radio tracked the snakes to their hibernacula. In the winter of 2019/2020, we used 1.2-m tall (0.64-cm mesh) hardware cloth to build large diameter corrals around 11 kingsnake hibernacula to capture the radio tracked kingsnakes as well as any other snakes that emerged in the spring of 2020 (Figure 3). Along with the 11 radio tracked kingsnakes, a total of six northern black racers (*Coluber constrictor constrictor*), one corn snake (*Pantherophis guttatus*), and one eastern ribbon snake (*Thamnophis sauritus*) emerged from the 11 corralled hibernacula. Although we routinely use hibernacula corrals to monitor populations of other species of snakes, we abandoned the use of corrals and reverted to opportunistic captures after the winter of 2019/2020 due to low rates of kingsnake communality at hibernacula and because the snakes chose different hibernacula the following winter.

Once captured, kingsnakes were kept in separate ventilated containers and transported to Herpetological Associates, Inc., or the Pinelands Commission headquarters. Snakes were weighed and measured initially, each time they were recaptured or brought back for a new radio transmitter, and upon release at the end of the study. We weighed and measured the snout-vent length (SVL) and total length of each snake and inserted a unique passive integrated transponder (PIT) tag in the lower third ventral portion of the body for permanent identification. Snakes that were gravid when initially captured were held in the laboratory to lay eggs, and the eggs were incubated until hatching occurred. Hatchlings were weighed, measured, PIT tagged, sexed by hemipenal eversion, and, after shedding, released where the gravid snake was originally captured.

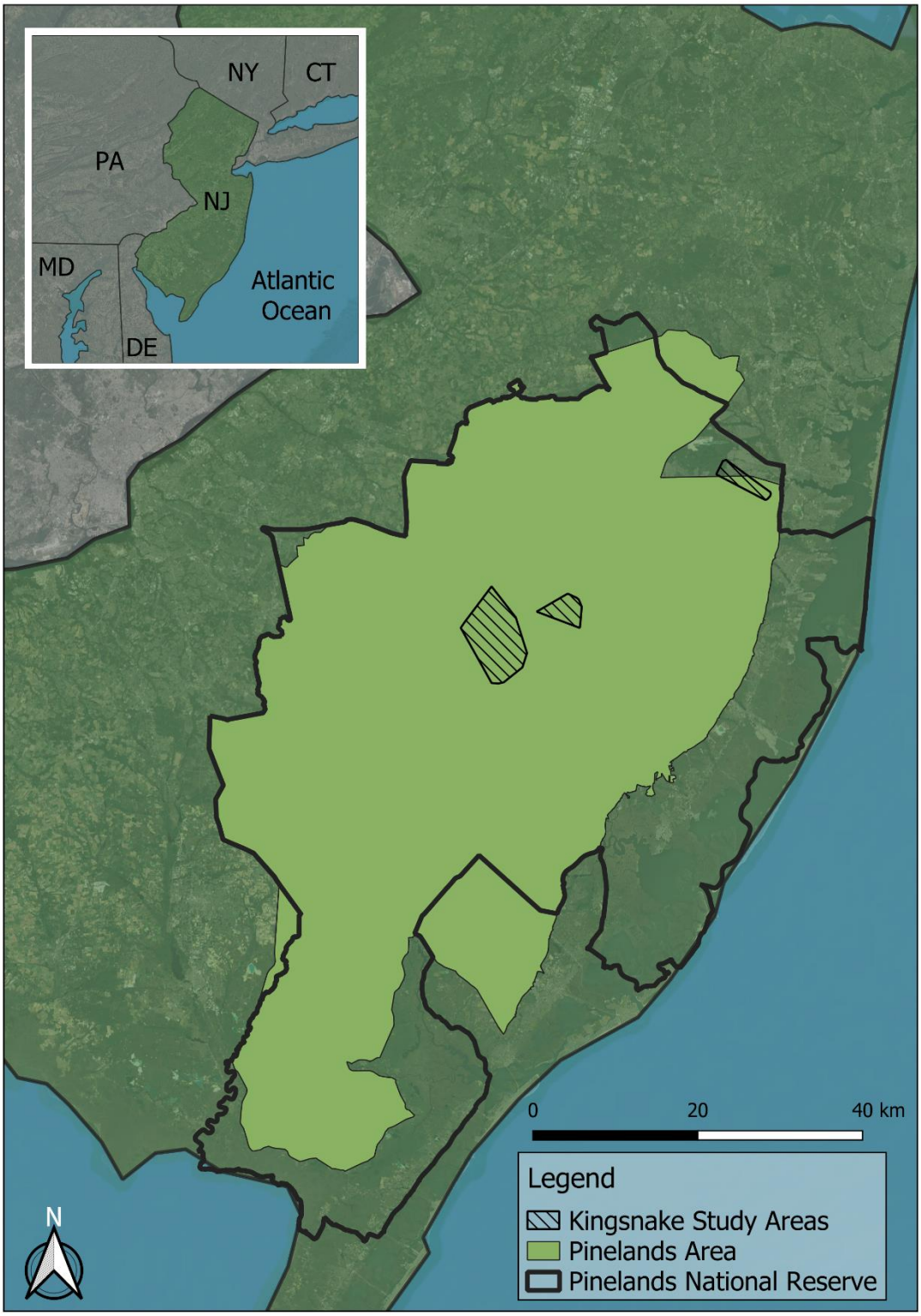

Figure 2. Location of New Jersey, Pinelands National Reserve, Pinelands Area, and eastern kingsnake study areas.

Radiotelemetry. Radio transmitters (Advanced Telemetry Systems, model R1680, Isanti, Minnesota, USA) were surgically implanted into each adult snake using methods in Reinert and Cundall (1982) and Bryant et al. (2010). See the Acknowledgements Section for people that performed snake surgeries. Upon request, ATS modified the model R1680 design by moving the battery from the end of the transmitter to the center to keep the transmitter more horizontal in the body cavity and reduce ventral rubbing from having the heavier battery on the end. We also had ATS use a longer, more flexible antenna wire for detection at greater distances. Transmitters had an expected battery life of just over one year and were therefore replaced annually during early spring.

After surgery, we released each snake at the point of capture and relocated the snakes every 48 – 72 hours during daylight hours from mid-March through late-November 2019 – 2022 using model TRX-1000WR receivers (Wildlife Materials, Murphysboro, IL, USA) and 3-element folding Yagi antennas. During the winter, snakes were checked periodically at their hibernacula. Upon each relocation, we recorded the geographic coordinates of the snake's location in decimal degrees using either a Garmin Oregon 700 or an Android Galaxy A53 5G smartphone. All work

Figure 3. Hardware cloth corral built around a hibernaculum to capture snakes that emerge from overwintering.

was conducted under New Jersey Department of Environmental Protection, Division of Fish and Wildlife, Endangered and Nongame Species Program scientific collecting permits.

Mortality. When mortality of a radio-tracked snake occurred, we attempted to identify the cause of death. In cases when the cause of death appeared to be predation, we attempted to identify the most likely predator based on the remains or damage to the transmitter.

Radiotelemetry Data. At each snake relocation, we collected a set of 25 habitat covariates (Table 1). These included 5 covariates reflecting thermal and humidity conditions at the snake's position, 8 covariates reflecting the physical microhabitat structure measured within a 1-m^2 plot centered on the snake's location, and 12 covariates measured outside the plot reflecting the surrounding habitat composition and structure. We only measured litter depth in uplands and mineral soil wetlands, which had a discrete litter/organic layer over sand. Starting in 2020, we repeated the measurements above at paired control locations that could potentially have been accessed and used by the snake. We used a random number generator to select a random direction between 0 and 359 degrees and a random distance between 1 m and 30 m to locate the available location. We used 30 m as the upper bound because approximately 95% of successive telemetry relocations in 2019 were within 30 m of the previous tracked location.

In addition to the habitat data described above, we also recorded six variables related to the snake's state (Table 2), including snake body temperature, its behavior when possible, visibility, and ecdysis (shed) status. If the snake was not visible, we estimated its temperature by placing a thermometer in the leaf litter, hole, log, etc., near the snake.

Data Analysis

Biometrics. Most tracked snakes were weighed and measured multiple times during the study. For snakes that were gravid when initially captured, we used the paired t-test to compare the body weight when gravid vs when not gravid. For each tracked snake, we averaged their body weight and SVL and used the Mann Whitney U test to compare mean body weight and mean SVL between all male and female kingsnakes. To evaluate the relationship between snake length and weight, we used linear regression to relate mean body weight and mean SVL for all snakes and for males and females separately.

Clutch size. Female kingsnakes that were visibly gravid when initially captured were held in the lab to lay eggs. To determine if larger females laid more eggs, we used linear regression to relate clutch size to mean body weight and mean SVL.

Seasonal and daily activity. We used observations during radiotelemetry to investigate temporal patterns in kingsnake concealment, ecdysis, and mating behavior (Table 2). To examine seasonal shifts in concealment, for each Julian day we calculated a 10-day sliding average and 95% confidence interval for the proportion of relocations in which an individual was at least partially visible (i.e., fully or partially exposed) using nonparametric bootstrap

Table 1. Habitat data collected at each eastern kingsnake relocation. Symbols: * = variable was used in a microhabitat model, c = collinear with another variable used in a microhabitat model, x = not considered in microhabitat models, and *c = collinear with distance to tall shrub so it was not used in the global microhabitat model, but it was used in Expert surveyor model #1 where tall shrub was not considered for that model.

Category	Covariate	Description
At or 1 m above snake location	Air temperature 1 m above snake [C]	Kestrel pocket weather meter
	Relative humidity 1 m above snake [C]	Kestrel pocket weather meter
	Air temperature at snake *	Kestrel pocket weather meter
	Relative humidity at snake *	Kestrel pocket weather meter
	Soil temperature at snake *	Taylor 12.5-cm thermometer
Within 1-m^2 plot centered on snake location	Percent vegetation *	Visual estimate
	Percent litter [C]	Visual estimate
	Percent woody debris *	Visual estimate
	Percent soil *	Visual estimate
	Percent water *	Visual estimate
	Percent human materials [X]	Visual estimate
	Dominant ground cover vegetation [X]	Species with greatest % cover
	Litter/organic layer depth *	Centimeter ruler
Outside 1-m^2 plot plot	Percentage canopy cover *	Convex Model A spherical densiometer
	Distance to nearest overstory tree *[C]	Forestry tape measure
	Diameter of nearest overstory tree *	Diameter tape measure
	Species of nearest overstory tree [X]	
	Distance of nearest understory tree [C]	Forestry tape measure
	Diameter of nearest understory tree *	Diameter tape measure
	Species of nearest understory tree [X]	
	Distance to nearest tall shrub (> 1.5 m) *	Forestry tape measure
	Species of nearest tall shrub (> 1.5 m) [X]	
	Distance to nearest log *	Forestry tape measure
	Diameter of nearest log *	Diameter tape measure
	Forest/Habitat Type [X]	Open canopy pine upland forest, pine upland forest, pine-oak upland forest, upland field/grass, railroad bed, dike of cranberry bog, pine lowland forest, pine-maple swamp, maple swamp, cedar swamp, cedar-maple swamp, scrub-shrub wetland, herbaceous wetland, leatherleaf spung, abandoned cranberry bog, pond

resampling with replacement for 1,000 iterations. We followed the same bootstrap procedure to investigate daily patterns, calculating a 30-minute sliding average proportion every 5 minutes across a 24-h day. To determine seasonal patterns in ecdysis, we removed observations in which snakes were not visible and thus their condition could not be determined. We then used the remaining observations to calculate a 10-day sliding average proportion of snakes in ecdysis (i.e., snakes had visibly cloudy or opaque skin or eyes). In both analyses, we excluded calculations from date or time windows with < 20 observations, which coincided with very early

Table 2. Data collected for each eastern kingsnake when relocated during radio telemetry.

Snake variable	Method/choices for each snake variable
Snake body temperature	Raytek MT4 laser non-contact thermometer or analog thermometer inside metal tube
Snake condition (i.e., ecdysis)	Opaque Not opaque Undetermined
Snake behavior	Crawling, arrested crawl, basking, mating/courtship, feeding, nesting, ecdysis, bromating, or undetermined
Snake location relative to ground surface	On ground Below surface Inside log Above surface in tree/shrub
Snake visibility	Totally concealed Partially concealed (<50% visible) Exposed (>50% visible)
Shelter snake is using	Leaf litter Soil / underground Vegetation Root ball / tip up mound Stump hole Hummock Woody debris / log Metal Board / lumber Human trash None

spring and late fall or very early morning and late evening, when few observations occurred. To examine mating phenology, we plotted the number of observations in which individuals were collocated with the opposite sex, which we presumed represented reproductive behavior, across the active season.

We summarized the frequencies with which kingsnakes used different types of shelter, exhibited different putative behaviors, and positioned themselves on, below, or above the ground surface (Table 2). Using observations when snakes were above the ground surface in shrubs, trees, standing snags, or suspended woody debris, we calculated their average height above the ground and report the mean (± SD) and range.

To test if the active season was longer for males or females, we used snakes that were tracked from hibernaculum egress to ingress and performed a two-sample t-test to compare the number of days a snake was active between sexes. We used the Kruskal-Wallis ANOVA to compare the number of days snakes were active during 2020, 2021, and 2022 to determine if activity season length varied by year.

Relationship to wetlands. We used our telemetry dataset along with the New Jersey Wetlands 2020 spatial dataset (NJDEP 2024b) to determine the extent to which wetlands, the 300-ft Pinelands-wide wetland buffer, and the 600-ft Toms River Corridor wetland buffer contained kingsnake activity. To accomplish this, we iteratively increased the size of the wetland buffer from 0 to 600 ft (0 to 182.9 m) and calculated the proportion of telemetry observations contained within the buffer upon each iteration. We plotted the results to visualize the effect of hypothetical buffer sizes on the inclusion of kingsnake activity. Spatial analysis and plotting were performed using R (R Core Team 2026).

To calculate the percentage of kingsnake home ranges composed of wetlands (see Home range estimates section below), we combined herbaceous wetland, cedar swamp, coniferous wetland, and deciduous wetland land cover classes and calculated the mean percentage across snakes. To test whether this differed by sex, we performed a linear mixed effects model with sex as a binary predictor of percentage wetland and included individual ID as a random effect to account for individuals tracked for multiple years.

Defining complete snake seasons. To ensure maximal comparability among snakes and account for potential seasonal changes in behavior, only complete snake-seasons were used in our movement and habitat selection analyses. Individuals that were tracked from spring hibernaculum egress to fall ingress were considered "complete" automatically. From those individuals we calculated the mean number of days between dispersal from hibernacula in spring to arrival at hibernacula in fall. We treated other snake seasons as "complete" only if the tracking duration exceeded this mean hibernaculum-to-hibernaculum interval.

Home range estimates. Using these complete snake-seasons, we modeled annual home ranges using three common home range estimators: minimum convex polygon (MCP), kernel density estimation (KDE), and Brownian bridge movement models (BBMM). See Box 1 for details on these three home range methods. We report all three because MCP and KDE remain widely reported in reptile spatial ecology literature. All home range estimates were obtained using the adehabitatHR package in R (Calenge 2011).

For KDE, which is sensitive to smoothing parameter choice, we used the reference bandwidth (Worton 1989). For BBMM, we chose a location error variance of 10 m to represent GPS error and calculated the motion variance for each animal. For KDE and BBMM home ranges, we considered the areas of the home range and core home range to fall within the 95% and 50% volume contours, respectively (Powell 2000, Crane et al. 2021). These two contours correspond to differing intensities with which portions of the home range are used, with the core home range identifying the regions with relatively frequent or prolonged use. We based all subsequent analyses involving home ranges (e.g., examining the effects of body size or landscape composition on home range area) on BBMMs, which may reflect actual space use better than traditional MCP and KDE estimators (Silva et al. 2020). Additionally, BBMMs better

Box 1. Three methods to estimate home ranges for animals.

Minimum Convex Polygon (MCP)

MCP constructs the smallest possible convex polygon that contains all recorded animal locations (Mohr 1947). MCPs are relatively simple to generate and remain one of the most reported estimators in reptile home range literature (Crane et al. 2021). However, MCP estimates are highly sensitive to sample size and outlier locations, and often include large areas not actually used by the animal.

Kernel Density Estimate (KDE)

In contrast, KDE and BBMM are probabilistic approaches that generate a utilization distribution (UD) for each animal that estimates the relative probability of space use (Worton 1989, Crane et al. 2021). Traditional KDE estimates the UD by smoothing over observed locations with a kernel function (typically Gaussian) and a user-defined bandwidth parameter. Although KDE provides a more biologically realistic estimate of space use than MCP, standard KDE assumes locations are independent and does not explicitly account for temporal autocorrelation or irregular sampling intervals, both of which are common in radiotelemetry datasets (Row and Blouin-Demers 2006). We used the reference bandwidth (Worton 1989) when calculating KDE home ranges.

Brownian Bridge Movement Model (BBMM)

BBMM incorporates the sequential and temporal structure of movement data (Horne et al. 2007). Specifically, BBMM estimates the probability of an animal's path between successive observed locations based on movement models. BBMM better accounts for differences in sampling effort among individuals as well as challenges inherent in reptile movement data (e.g., highly zero-inflated movement distances caused by long periods when the animal is stationary; Silva et al. 2020). For BBMM, we chose a location error variance of 10m to represent GPS error and calculated the motion variance for each animal. For both KDE and BBMM, we used the 95% and 50% probability volume contours to represent home ranges and core areas, respectively (Powell 2000, Crane et al. 2021). These two contours correspond to differing intensities with which portions of the home range are used, with the core home range identifying the regions with relatively frequent or prolonged use.

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We compared BBMM home range area between males and females using a generalized linear mixed model (GLMM) with sex as a fixed effect and individual as a random effect, specifying a Gaussian distribution with a log link function to accommodate the right-skewed home range values. Similarly, we used GLMMs and log link functions to test for relationships between home range area and body size, using z-score standardized SVL as a linear predictor and home range area as a continuous response.

Movement metrics. In addition to home range area, we calculated five movement metrics for each snake-season: (1) the total distance moved (the sum of all linear distances between locations), (2) home range length and (3) width (the side lengths of a minimum bounding rectangle of the 95% Brownian bridge home range), (4) mean distance moved per day (the total distance moved divided by the total number of days monitored), and (5) the maximum distance (the maximum distance moved from the spring hibernaculum). All variables appeared reasonably normally distributed, and we used separate linear mixed effects models to test for differences between males and females, specifying a random effect of individual to account for individual variation and the multiple tracking seasons of some snakes.

Identifying transitional and active states. To determine whether habitat selection shifted according to season, we assigned each snake observation to one of two putative behavioral states – transitional behavior and active behavior. To classify observations into these states, we plotted both the cumulative and net distance of each snake's relocations from its spring overwintering or capture location to identify shifts in movement behavior. We considered the snake's behavior to be "transitional" if it was stationary at or near its den or actively traveling to or from its summer habitat. Once snakes completed their spring dispersal, their net distance became more erratic, and we would designate their behavior as "active" until they initiated their return migrations toward hibernacula in fall. We used these designations to investigate seasonal shifts in both macrohabitat and microhabitat selection analyses.

GIS data preparation for macrohabitat selection analyses. The second and third order GIS-based macrohabitat selection analyses described below were based on the New Jersey Land Use-Land Cover (LULC) dataset (NJDEP 2024a). For modeling tractability, we collapsed the 50 LULC classes occurring within our study area into eight macrohabitat types that we felt represented important structural and functional habitat groupings for the snakes: Atlantic cedar swamps, coniferous forested wetlands, deciduous forested wetlands, upland field, upland forest, herbaceous wetlands, urban (development ranging in intensity), and water (Table 3). We converted the resulting GIS layer to 3-m rasters for analysis. We excluded urban and water from modeling because their scarcity within snake home ranges caused model instability. GIS and raster manipulations were conducted in ArcMap 10.8.2 (ESRI 2021) and in R (R Core Team 2026) using the packages terra (Hijmans et al. 2023) and raster (Hijmans et al. 2015).

Table 3. List of the 50 original Land Use-Land Cover classes found within the eastern kingsnake radio telemetry study area and the 8 macrohabitat types into which they were reclassified. Land Use-Land Cover classes are from New Jersey Land Use Land Cover 2020 Update (NJDEP 2024a).

Original Land Use-Land Cover classes	Macrohabitat type used for modeling
Atlantic White Cedar Wetlands	Atlantic cedar swamp
Coniferous Scrub/Shrub Wetlands	Coniferous forested wetland
Coniferous Wooded Wetlands	Coniferous forested wetland
Mixed Scrub/Shrub Wetlands (Coniferous Dom.)	Coniferous forested wetland
Mixed Wooded Wetlands (Coniferous Dom.)	Coniferous forested wetland
Deciduous Scrub/Shrub Wetlands	Deciduous forested wetland
Deciduous Wooded Wetlands	Deciduous forested wetland
Mixed Scrub/Shrub Wetlands (Deciduous Dom.)	Deciduous forested wetland
Mixed Wooded Wetlands (Deciduous Dom.)	Deciduous forested wetland
Agricultural Wetlands (Modified)	Herbaceous wetland
Former Agricultural Wetland (Becoming Shrubby, Not Built-Up)	Herbaceous wetland
Herbaceous Wetlands	Herbaceous wetland
Cropland and Pastureland	Upland field
Orchards/Vineyards/Nurseries/Horticultural Areas	Upland field
Other Agriculture	Upland field
Old Field (<25% Brush Covered)	Upland field
Coniferous Brush/Shrubland	Upland forest
Coniferous Forest (>50% Crown Closure)	Upland forest
Coniferous Forest (10-50% Crown Closure)	Upland forest
Deciduous Brush/Shrubland	Upland forest
Deciduous Forest (>50% Crown Closure)	Upland forest
Deciduous Forest (10-50% Crown Closure)	Upland forest
Mixed Deciduous/Coniferous Brush/Shrubland	Upland forest
Mixed Forest (>50% Coniferous with >50% Crown Closure)	Upland forest
Mixed Forest (>50% Coniferous with 10-50% Crown Closure)	Upland forest
Mixed Forest (>50% Deciduous with >50% Crown Closure)	Upland forest
Mixed Forest (>50% Deciduous with 10-50% Crown Closure)	Upland forest
Altered Lands	Urban
Extractive Mining	Urban
Transitional Areas	Urban
Undifferentiated Barren Lands	Urban
Athletic Fields (Schools)	Urban
Commercial/Services	Urban
Industrial	Urban
Mixed Urban or Built-Up Land	Urban
Other Urban or Built-Up Land	Urban
Recreational Land	Urban
Residential, High Density or Multiple Dwelling	Urban
Residential, Rural, Single Unit	Urban
Residential, Single Unit, Low Density	Urban
Residential, Single Unit, Medium Density	Urban
Stormwater Basin	Urban
Transportation/Communication/Utilities	Urban
Upland Rights-of-Way Undeveloped	Urban
Disturbed Wetlands (Modified)	Urban
Managed Wetland in Maintained Lawn Greenspace	Urban
Wetland Rights-of-Way	Urban
Artificial Lakes	Water
Natural Lakes	Water
Streams and Canals	Water

Home range and core area selection from the landscape. We investigated second order home range and core area selection by comparing macrohabitats within each activity area with surrounding available alternatives (Figure 4). For each snake-season, we obtained the macrohabitat proportions within the used BBMM-based home range and core area (see Home range estimates section). To generate a biologically realistic availability domain, we simulated home ranges and core areas that preserved their original size and shape while allowing shifting to account for imperfect fidelity to overwintering locations. First, we fit an exponential distribution to observed low value-inflated distances between spring and fall overwintering locations ($\lambda = 0.0029$). To simulate an available area, we shifted the contours of the used area by a random distance drawn from this distribution and in a random direction and applied random rotation (0–359°) and random horizontal reflection ($p = 0.5$). Macrohabitat proportions were calculated for each simulated area, with 10 simulations for each used area.

We compared used and available home ranges using GLMMs with macrohabitat proportions as predictors and home range type (used = 1, available = 0) as a binary response. All covariates had reasonably low pairwise collinearity ($r < 0.7$; Dormann et al. 2013), but the covariates herbaceous wetland and forested upland resulted in high multicollinearity (VIF > 5). We therefore fit all possible combinations of predictors, excluded candidate models with VIF > 5, and performed weighted model averaging on the remaining models using conditional estimates. The same procedure was applied to core areas. We did not use individual as a random effect due to the low number of seasons per individual, and we excluded macrohabitat interactions with sex due to model convergence failures. Models were fit using the R package lme4 (Bates et al. 2015), assessed with the package DHARMa (Hartig and Hartig 2017), and model-averaging was performed using MuMIn (Barton and Barton 2015).

Macrohabitat selection within home range. To assess third order macrohabitat selection within home ranges, we relied on the BBMM home range to define the available habitat for each snake. For each snake location point, we generated ten random (available) points within the 95% contour of the BBMM home range to represent locations that were plausibly available to the snake for selection. To examine patterns of habitat use and availability within kingsnake home ranges, we calculated and plotted the proportions of different macrohabitat types among the used and randomly generated available points for each snake. For snakes tracked multiple years, proportional habitat use and availability were calculated for each year separately and then averaged. We evaluated whether the composition of macrohabitat types differed significantly among used and available points for each snake using a Chi-Square test in the adehabitatHS package (Calenge 2011) in R.

To investigate macrohabitat selection, we first calculated the Euclidian distances between each point and each macrohabitat type (Steen et al. 2010). We assigned a distance of 0 to the macrohabitat type that contained a given point. Next, we compared used points to available points with generalized linear mixed models (GLMMs), specifying interactions between sex and the distances to each macrohabitat type predictor with location type (1 = used vs. 0 = available) as a binary response. We included individual as a random effect to account for differences in sampling effort among years as well as behavioral variation among individuals. We fit a general

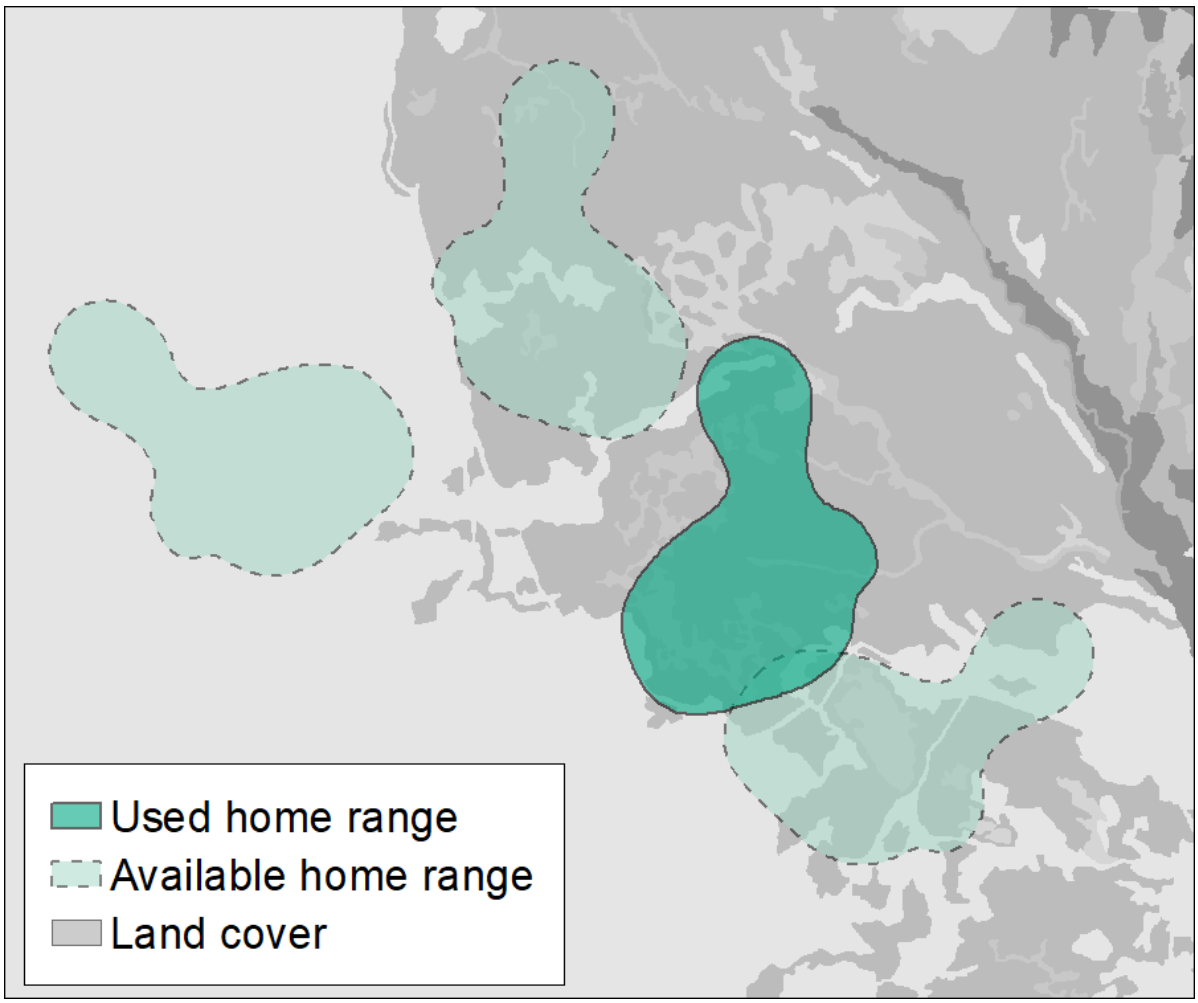

Figure 4. Example of used and simulated home ranges that were the basis of our second order home range and core area selection analysis. Simulated home ranges preserved the size and shape of the used home range, but were randomly flipped, rotated, and shifted to account for observed patterns in hibernaculum switching. The figure shows the the used home range (95% BBMM volume contour) of kingsnake KS2020.05 (solid contour with dark shading) and three simulated available home ranges (dotted contours). In our analysis, we generated 10 simulated home ranges per used home range, but for simplicity only three are shown.

selection model that included no sex or behavioral period information, as well as fitting models separately for the transitional and active behavioral periods that included habitat interactions with sex. All covariates were z-score standardized prior to model fitting. All covariates were reasonably non-collinear ($r < 0.7$; Dormann et al. 2013) and independent (VIF = 5.0). Models were fit using the package lme4 (Bates et al. 2015) and their stability assessed with the package DHARMa (Hartig and Hartig 2017).

Influence of macrohabitats on home range size. Using the coefficients from our home range selection model, we identified the macrohabitats that had significantly positive and significantly negative effects on home range selection (i.e., “preferred” and “avoided” habitats, respectively). We then calculated the percent preferred macrohabitat type within each

individual's 95% home range and tested whether the amount of preferred or avoided macrohabitat influenced home range area. We accomplished this using linear mixed effects models where the percent of preferred or avoided macrohabitat was a continuous predictor and the 95% home range area was the response. We z-score standardized our predictors prior to model fitting. Because of collinearity between percent preferred and percent avoided macrohabitat, we fit the models separately. We included a random effect of individual to account for pseudoreplication.

Microhabitat selection. We used mixed effects conditional logistic regression models to test whether microhabitat and weather variables, measured at paired relocation and random control points, influenced snake presence. The individual snake ID was included as a random effect to account for repeated measures. We excluded one snake (KS2019.07) from the microhabitat selection analysis because it was associated with only a small number of paired random available locations (n = 10). Modeling was performed in R using the coxme package (Therneau 2024).

Numerical covariates were considered for model inclusion if they were recorded for both relocations and controls (Table 1). Missing values composed < 5% of the dataset. We replaced missing data with imputed means, based on the variable measurements for the month for weather covariates or the habitat type for microhabitat covariates. Data was recorded for some covariates using open-ended upper intervals (e.g., the distance to the nearest fallen log was > 30 m). To facilitate model use where this was the case, we reclassified ambiguous values to discrete values by adding one unit to the specified boundary and dropping the greater-than sign (e.g., > 30 m = 31 m). Litter depth was recorded using discrete values in uplands and mineral soil wetlands where exact measurements were possible, but surveyors adopted an open-ended upper interval of > 50 cm where they were not possible, such as in some organic soil cedar swamps. For consistency and to eliminate potential outliers, values over 50 cm were redefined as 51 cm. All covariates were then scaled and centered.

Dot charts were generated for each covariate to check for outliers and collinearity was assessed with variance inflation factors using the car package (Fox et al. 2012) and pair plots. Where collinearity was found to occur, we ran univariate general linear models and compared the resulting Akaike information criterion (AIC) values. We typically prioritized use of the covariate with the lower AIC value in our model hypotheses, unless there was an ecological reason to utilize the variable with the higher AIC value instead. This resulted in a global model with 14 covariates (Table 4).

We divided the data by behavioral period (i.e., transitional vs active) and sex. We defined 8 hypothesis models, based on the parameters we expected snakes to select strongly for or against during thermoregulation, ecdysis, and for concealment, or based on observations made by our surveyors and in the literature (Wund et al. 2007, Table 4). After running the global model for each dataset, we screened covariates using their odds ratios and confidence intervals, as well as resulting *p*-values and our understanding of kingsnake biology. We tailored a final model, which we called the optimal model, to each dataset (i.e., transitional and active

for males and females) that retained the covariates expected to be most significant, based on these factors (Table 4). AIC values were used to compare model fit.

Table 4. Microhabitat selection model names and covariates used in model development.

Model Name	Number of Covariates	Covariates
Global Model	14	Surface humidity, surface temperature, soil temperature, % vegetation cover in a 1-m plot, % woody debris in a 1-m plot, % exposed soil in a 1-m plot, % surface water in a 1-m plot, % south facing canopy cover, diameter at breast height (DBH) of nearest overstory tree, DBH of nearest understory tree, diameter of nearest fallen log, distance to the nearest tall shrub, litter depth, and distance to the nearest fallen log.
Ecdysis Model	6	Surface humidity, surface temperature, % woody debris in a 1-m plot, % south facing canopy cover, % surface water in a 1-m plot, and distance to the nearest fallen log.
Thermoregulation Model	6	Surface humidity, surface temperature, % vegetation cover in a 1-m plot, soil temperature, litter depth, and % south facing canopy cover.
Expert Surveyor Model #1	4	Distance to the nearest overstory tree, litter depth, % south facing canopy cover, and distance to the nearest fallen log
Expert Surveyor Model #2	3	Distance to the nearest tall shrub, surface temperature, and % south facing canopy cover.
Wund et al. (2007) Model	5	Litter depth, % vegetation cover in a 1-m plot, % woody debris in a 1-m plot, diameter of nearest fallen log, and distance to the nearest fallen log.
1-m Plot Model	4	% vegetation cover in a 1-m plot, % woody debris in a 1-m plot, % exposed soil in a 1-m plot, and % surface water in a 1-m plot.
Microhabitat StructureModel	6	DBH of nearest overstory tree, DBH of nearest understory tree, diameter of nearest fallen log, distance to the nearest tall shrub, litter depth, and distance to the nearest fallen log.
Cover Model	7	Distance to the nearest tall shrub, litter depth, and distance to the nearest fallen log, % vegetation cover in a 1-m plot, % woody debris in a 1-m plot, % exposed soil in a 1-m plot, and % surface water in a 1-m plot.
Optimal Active Period Female Model	10	Surface temperature, soil temperature, % vegetation cover in a 1-m plot, % woody debris in a 1-m plot, % south facing canopy cover, DBH of nearest overstory tree, distance to the nearest tall shrub, litter depth, distance to the nearest fallen log, and diameter of nearest fallen log.
Optimal Active Period Male Model	10	Surface temperature, soil temperature, % vegetation cover in a 1-m plot, % woody debris in a 1-m plot, % exposed soil in a 1-m plot, % surface water in a 1-m plot, % south facing canopy cover, DBH of nearest overstory tree, distance to the nearest tall shrub, and litter depth.
Optimal Transitional Period Female Model	7	Surface temperature, soil temperature, % woody debris in a 1-m plot, % south facing canopy cover, litter depth, distance to the nearest fallen log, and diameter of nearest fallen log.
Optimal Transitional Period Male Model	5	Surface temperature, % woody debris in a 1-m plot, % surface water in a 1-m plot, distance to the nearest tall shrub, and litter depth.

Overwintering. We attempted to locate each hibernacula revealed during radio telemetry. For each snake, we determined the number of hibernacula used during the study and number of winters spent in a hibernaculum. We also identified the on-ground habitat type and the feature used by the snakes to access the hibernacula. These data were summarized graphically by sex.

For each snake that was tracked throughout its overwintering period (i.e., fall ingress to spring egress), we calculated the number of days spent in a hibernaculum. The individual snakes and years included in this analysis differed somewhat from the active season analysis described above. To determine if the time spent overwintering differed between males and females, we used a two-sample t-test to compare the number of days spent in a hibernaculum between sexes. We used the Kruskall-Wallis ANOVA with Dunn's tests and Holm adjustments to compare the number of days spent in hibernacula for all snakes between the four winters (1999-2000, 2000-2001, 2001-2002, and 2002-2003) to determine if overwintering duration differed among years. We used the same test to compare air temperature values from October – March among the four winters. Air temperature was obtained from the Indian Mills, NJ (39.79952, -74.78042) weather station National Oceanic and Atmospheric Administration (2025).

To characterize the geology of each hibernaculum, we relied on the Soil Survey Geographic (SSURGO) Database for Burlington County and Ocean County, New Jersey (SSURGO 2024). Using ArcMap 10.8.2 (ESRI 2021), the SSURGO data, and hibernacula locations, we determined the soil type for each hibernaculum and whether the soils were upland, transitional, or hydric. We calculated the percentage of hibernacula and soil type of each hibernaculum for each of the on-ground habitat types and graphed the data along a wet-to-dry hydrologic gradient.

RESULTS AND DISCUSSION

Snake capture and radiotelemetry

From 2019 – 2022, we tracked 46 individual kingsnakes (24 males and 22 females) 4,083 times over 96 snake-seasons. After excluding incomplete snake seasons, our final dataset for habitat selection and home range analyses included 34 individuals (14 females and 20 males) tracked 3,587 times over 63 snake seasons. Each complete snake season consisted of an average of 53.4 ± 14.8 (range 24–82) relocations. Sixteen snakes were tracked for one complete season, nine were tracked for two complete seasons, seven were tracked for three seasons, and two were tracked for four complete seasons. Most snakes were captured while courting/mating with other tracked kingsnakes or were found opaque or gravid inside hollow logs or under artificial cover at shed sites/nest areas (Table 5). One kingsnake (KS2022.08) was captured because it ate a corn snake that was being radio tracked as part of another study.

Mortality

At the end of the study, 24 of the 46 radio-tagged kingsnakes (52%) were recaptured, their transmitters were removed, and the snakes were released (Table 6). Twenty-one snakes (46%)

Table 5. Location or method of eastern kingsnake capture for the radio telemetry study.

King snake capture location or method	Number of female snakes	Number of male snakes	Total number of snakes
Predated radio tracked corn snake	-	1	1
On paved road	1	-	1
Under random artificial cover	1	1	2
On impoundment shoreline	-	2	2
At abandoned railroad tracks	1	2	3
On sand road/dike/trail	1	3	4
At hibernacula	3	3	6
Mating/courting with tracked king snake	7	5	12
At shed site/nest area	8	7	15
Total number of snakes radio tracked	22	24	46

Table 6. Status of 46 radio tracked eastern kingsnakes at the end of the radio telemetry study.

Snake status	Number of snakes
Never recovered from anesthesia after surgery	1
Found dead while gravid (possibly egg bound)	1
Froze basking at winter hibernacula (transmitter wire protruding)	1
Missing (likely a transmitter battery failure)	1
Found dead from unknown causes	2
Likely killed by a raptor	4
Likely killed by a mammal	12
Transmitter successfully removed and snake released alive	24
Total number of snakes	46

died during the study. Based on tooth marks in the wax coating on the transmitters, the snake body being partly intact, or the transmitter being found in canid scat, 12 snakes were presumed to be killed by coyote, fox, weasel, or mink. We assumed 4 snakes were killed by raptors because the antenna wire was curly, possibly from a beak, and the snake skeleton was picked clean. Two snakes died from unknown causes: one was found stretched out completely intact on the ground in the summer, and one was a skeleton found on the ground inside its hibernacula corral in late winter. One snake was found frozen in January at its hibernaculum with the transmitter antenna protruding from its body, one snake died in mid-July while gravid (possibly egg bound), and one snake never recovered from its transmitter removal surgery. The signal was lost for one of the 46 snakes and the snake was never found, which may have been due to the transmitter battery failing prematurely, the snake being carried far away by a predator, a predator crushing the transmitter, or poaching.

While the predation rates we observed were high enough to suggest the possibility of substantial population-level effects, predation has not previously been proposed as a causal factor in kingsnake population declines elsewhere. Instead, authors have suggested other factors such as

illegal collection, drought, road mortality, parasites, and habitat loss may be primarily responsible for observed declines (Winne et al. 2007, Stapleton et al. 2008, Godley et al. 2017).

Biometrics

For the 46 tracked kingsnakes, we found a significant difference in mean body weight for males and females ($W = 113$, $p < 0.001$). Males were heavier than females (Table 7). Mean SVL also differed between males and females ($W = 93.5$, $p < 0.001$) with males being longer than females (Table 7). Such sexual size dimorphism is typical among snake species in which males must physically compete for access to females and mating opportunities. Male body length also exceeded that of females in Georgia (Linehan et al. 2010), Florida (Godley et al. 2017), and in the previous New Jersey study (Wund et al. 2007). However, contrary to our findings, Godley et al. (2017) found no significant difference in body mass by sex. We found a significant positive relationship between mean SVL and mean body weight for all kingsnakes ($R^2 = 0.87$, $p < 0.001$) and for male and female snakes separately (Figure 5).

Although nine females were gravid when initially captured, three were not radio-tracked long enough to be included in weight analyses. Two females (KS2022.14 and KS2022.15) were not radio tracked at all because they were captured during the last year of the study and one (KS2020.14) was only tracked for a short time before being killed. The other six gravid females (KS2019.06, KS2019.11, KS2020.15, KS2020.17, KS2021.13, and KS2022.09) were included in the telemetry study long enough to be weighed when gravid and weighed again at least once afterwards when not gravid. For these six snakes, we found no significant difference in body weight when gravid and not gravid ($t = 1.063$, $p = 0.337$). Therefore, we included all available body weight values when calculating a mean body weight for each radio tracked snake (Table 7).

The absence of detectable weight differences between gravid and nongravid females may indicate that, like many snakes, reproductive investment is largely supported through reallocation of existing energy reserves rather than food intake during gravidity. This interpretation is consistent with Godley et al. (2017), who reported substantially reduced feeding by gravid females during the breeding season.

Clutch size

Nine females were gravid when initially captured and were held in the lab to lay eggs (Tables 7 and 8, Figure 6). One of these snakes (KS2021.13) laid eggs a second time under concrete rubble while being radio tracked the following year. Her eggs were excavated and brought back for incubation and hatching. For all ten clutches of eggs, clutch size ranged from 6 – 17 eggs ($\bar{x} = 12.5 \pm 3.3$) with KS2021.13 laying the two largest clutches. Not all eggs from every clutch hatched, and none of the eggs from KS2019.06 hatched. Hatchling sex ratios were mostly female dominated (male:female ratio = 1.55), but the difference was not statistically significant ($t = -1.6$, $p = 0.14$). For the nine females that laid eggs, we found a significant positive relationship between mean SVL and clutch size ($y = 0.26x - 11.08$, $R^2 = 0.89$, $p < 0.001$) and mean body weight and clutch size ($y = 0.02x - 3.97$, $R^2 = 0.85$, $p < 0.001$).

Table 7. Mean snout-vent length (SVL), total length (TL), tail length, and body weight for 46 eastern kingsnakes. N = # of times a snake was weighed and measured, g = female was gravid when captured, and s = tail was shortened from damage, predation, etc.

Snake ID	Sex	Mean SVL (cm)	Mean TL (cm)	Mean tail length (cm)	Mean weight (g)	N
KS2019.01	M	116	133	17	621	5
KS2019.03	M	82	94	12	236	5
KS2019.04	M	96	111	15	409	4
KS2019.05	M	105	122	17	501	5
KS2019.07	M	108	123	15	463	3
KS2019.08	M	106	123	17	584	6
KS2019.10	M	96	111	15	494	1
KS2019.14	M	104	119	15	447	4
KS2019.15	M	83	96	12	269	4
KS2019.17	M	95	110	14	317	4
KS2020.04	M	109	126	18	605	5
KS2020.07	M	137	147	10(s)	964	1
KS2020.08	M	114	131	18	597	1
KS2020.19	M	91	106	15	287	5
KS2021.02	M	110	124	15	757	3
KS2021.03	M	124	142	17	808	1
KS2021.05	M	116	132	16	683	4
KS2021.09	M	104	119	15	452	4
KS2021.10	M	122	140	18	587	4
KS2022.01	M	117	131	14	720	3
KS2022.05	M	108	124	16	682	3
KS2022.06	M	107	122	15	541	3
KS2022.08	M	93	108	15	414	3
KS2022.13	M	108	124	16	616	3
KS2019.06	F(g)	85	95	11	298	6
KS2019.11	F(g)	85	96	12	313	5
KS2019.16	F	76	86	10	223	3
KS2020.01	F	101	113	12	438	5
KS2020.02	F	98	100	2(s)	487	1
KS2020.05	F	99	112	13	444	5
KS2020.06	F	102	115	13	446	5
KS2020.09	F	90	102	12	307	3
KS2020.11	F	79	89	10	195	3
KS2020.14	F(g)	94	108	14	427	1
KS2020.15	F(g)	102	115	13	487	5
KS2020.17	F(g)	87	97	11	278	5
KS2020.18	F	88	100	12	218	3
KS2020.21	F	78	89	11	237	4
KS2020.23	F	95	107	12	504	4
KS2021.04	F	86	96	10	296	3
KS2021.07	F	98	110	12	510	4
KS2021.11	F	92	103	11	441	1
KS2021.12	F	97	110	13	403	1
KS2021.13	F(g)	102	115	14	533	4
KS2021.20	F	98	111	13	407	4
KS2022.09	F(g)	100	114	13	486	3
Grand Mean ±1 SD Males		106 ± 13	122 ± 13	15 ± 2	544 ± 179	
Grand Mean ±1 SD Females		92 ± 8	104 ± 9	11 ± 2	381 ± 109	

Table 8. Clutch data for nine female eastern kingsnakes. Except for KS2022.14 and KS2022.15, all snakes were part of a radio telemetry study. Except for KS2021.13[b], all eggs were laid and incubated in the lab. KS2021.13[b] laid her second clutch of eggs in the field, and the eggs were excavated and taken to the lab for incubation and hatching. None of the eggs from KS2019.06 hatched.

Snake ID	Clutch size	Number of eggs that did not hatch	Number of eggs that hatched	Number of male hatchlings	Number of female hatchlings	Mean SVL (cm) for hatchlings	Mean weight (g) for hatchlings
KS2019.06	10	10	0	0	0	-	-
KS2019.11	11	0	11	4	7	23.8	8.2
KS2020.14	14	5	9	3	6	21.5	8.6
KS2020.15	15	1	14	7	7	23.0	8.9
KS2020.17	10	0	10	3	7	24.0	9.0
KS2021.13	16	0	16	7	9	24.9	8.6
KS2021.13[b]	17	0	17	4	13	24.7	9.9
KS2022.09	14	3	11	4	7	23.6	8.2
KS2022.14	6	4	2	2	0	20.2	6.0
KS2022.15	12	1	11	7	4	26.4	9.9
Total Number	125	24	101	41	60	-	-
Mean ± SD	12.5 ± 3.3	2.4 ± 3.2	10.1 ± 5.5	4.6 ± 1.9	7.5 ± 2.6	23.6 ± 1.9	8.6 ± 1.2

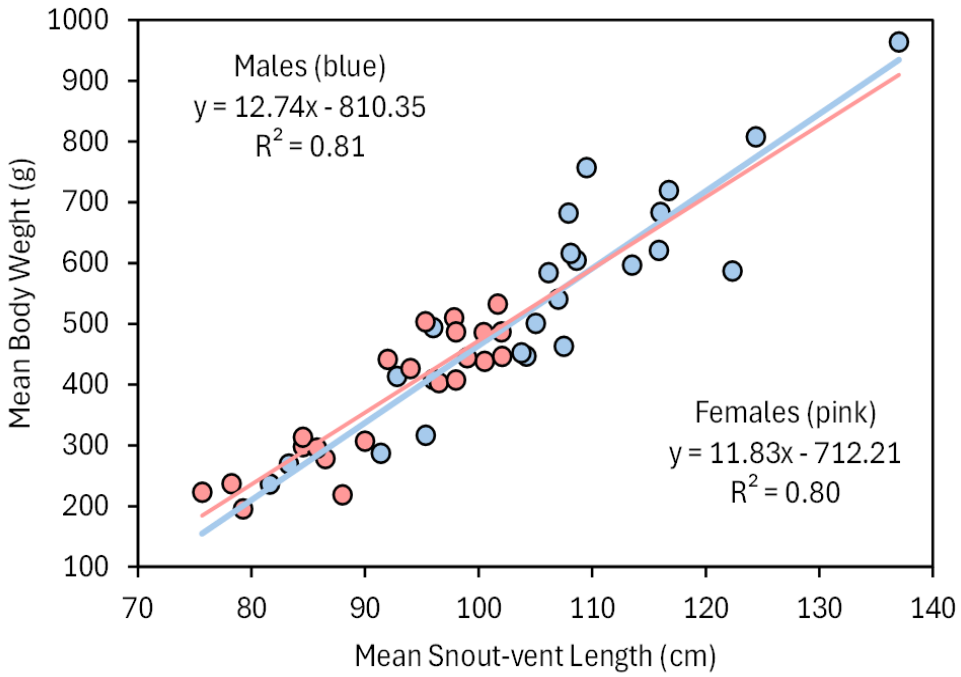

Figure 5. Relationship between mean snout-vent length and mean body weight for 46 eastern kingsnakes (24 males and 22 females). Linear regression indicated that the relationship for all snakes ($y = 12.26x - 755.38$, $R^2 = 0.87$, $p < 0.001$) as well as separate male and female relationships shown here were significant ($p < 0.001$).

Figure 6. Eastern kingsnakes hatching from eggs incubated in the lab.

Seasonal and daily activity

During the active season, kingsnakes were fully exposed 19% of the time, partially concealed 15% of the time, and totally concealed 66% of the time. The observed highly secretive behavior was consistent with the previous New Jersey report in which kingsnakes were concealed during 79% of observations (Wund et al. 2017). We observed no difference in exposure between males and females. Kingsnakes were most visible between April and June, after which their visibility declined sharply (Figure 7a). Average daily concealment patterns revealed that kingsnakes were seen least often in the morning (e.g., 0730 – 0900) and evening (e.g., 1600 – 1800) compared to during the day (Figure 7b), supporting previous reports of primarily diurnal activity (Howze and Smith 2012, Godley et al. 2017). We observed ecdysis in all active-season months, but there appeared to be four peaks in shedding activity in mid-spring (mid-May), early summer (mid-June), mid-summer (late July-early August), and early autumn (late September), consistent with field observations suggesting kingsnakes typically shed 3-4 times per year (Figure 7c). All mating activity occurred between 27 April and 7 June, with a peak in mid-May (Figure 7d).

Kingsnakes were below the surface in refugia during 65.9% of telemetry observations (Table 9). Underground refugia often consisted of mammal burrows and stump holes, similar to reports by Godley et al. (2017) and Steen et al. (2010). Kingsnakes were above the ground surface in approximately 3.0% of observations, during which their average height above the ground was 0.67 ± 1.0 m (range = 0.02 – 6.0 m). Common refugia when on or above the soil surface included vegetation (30.0% of observations), leaf litter (27.8% of observations), and raised hummocks (11.1% of observations), with other categories each comprising < 10% of refugia use. Although kingsnakes used hollow logs and standing live hollow trees only about 5% of the time (Table 9), these features were important for hiding during ecdysis (Figure 8). Because kingsnakes were frequently concealed, their behavior was only assessed during 35.9% of observations. During these, kingsnakes were most often observed basking (17.8% of observations), denning (8.7% of observations), or in an arrested crawl (6.5% of observations), and were presumably traveling and became motionless upon approach, but may also have been stretched out basking.

Kingsnakes emerged from hibernacula from mid-March to mid-May and entered hibernacula to overwinter from late September to late December (Figure 9). About 63% of the snakes left hibernacula in April and about 53% of the snakes entered hibernacula in November. For the 35 seasons in which both hibernaculum egress and ingress were observed, the number of active days in a season ranged from 156 d to 265 d. The mean number of active days in a season was 199 ± 24 for males and 200 ± 28 for females (Table 10). We found no significant difference in the number of active days between sexes ($t = 0.509$, $p = 0.614$). We also found no difference in the number of active days between the three years (2020 – 2022) in which we tracked snakes with complete active seasons ($H = 0.777$, $p = 0.678$). To our knowledge, reliable information on ingress and emergence timing has not been previously reported for kingsnakes, despite this information being important for regulating potentially disruptive human activities near snake hibernacula (Jesper et al. 2023).

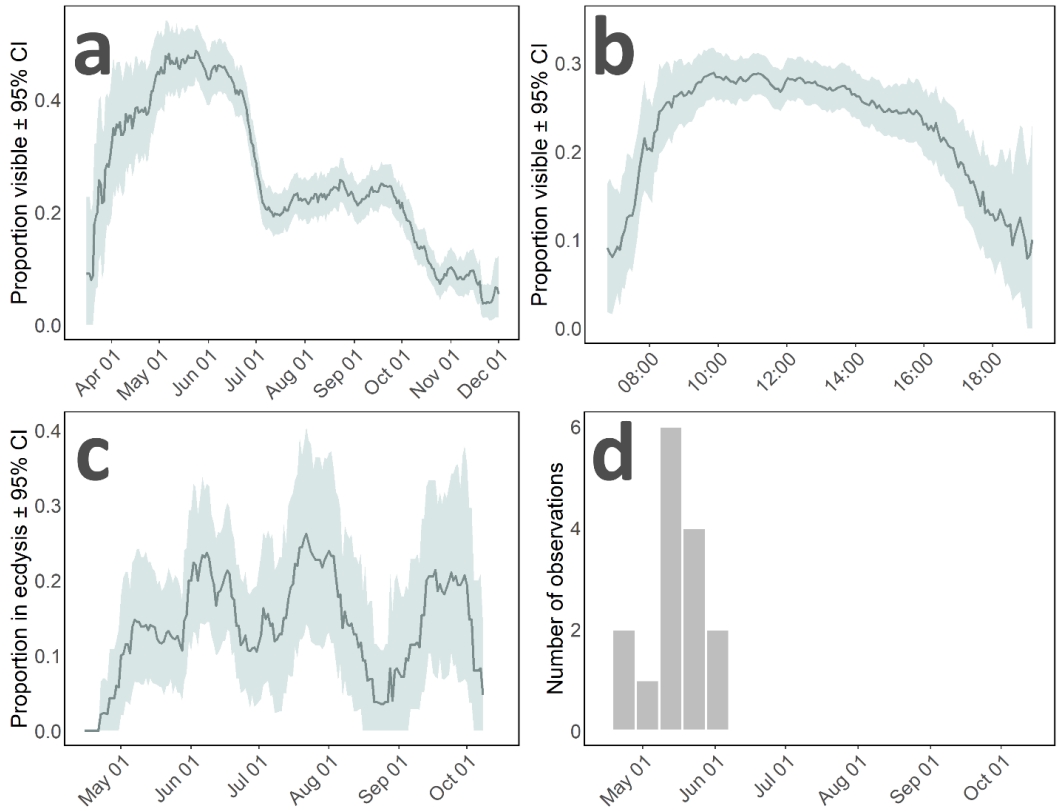

Figure 7. Seasonal and daily timing of concealment, ecdysis (shedding), and mating behaviors for eastern kingsnakes. Seasonal visibility (a) was highest in April – June. Daily visibility (b) was highest between 0900 and 1600, suggesting diurnal activity. Seasonal timing of ecdysis (c) suggests shedding periods in mid-spring, early summer, mid-summer, and autumn. Mating behaviors (d) took place from late April to early June.

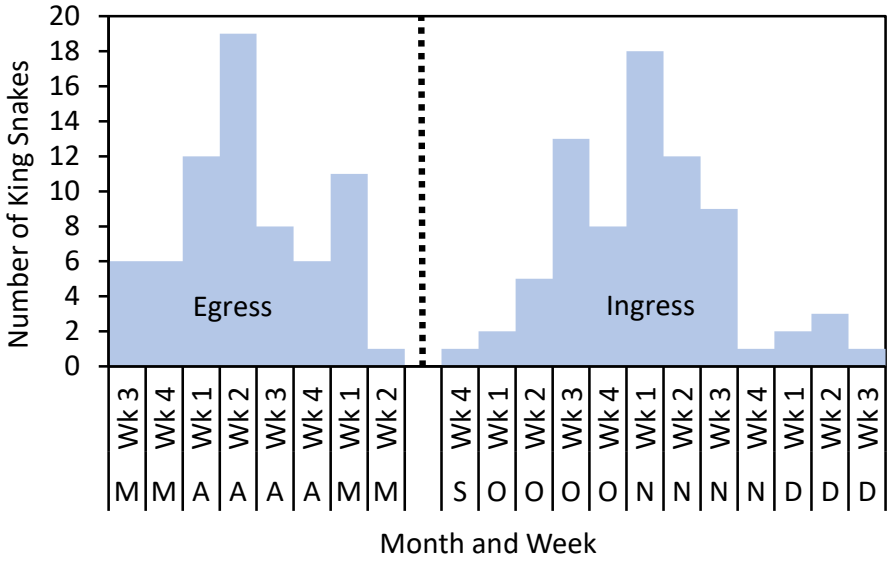

Figure 9. Egress and ingress timing for eastern kingsnakes during a four-year telemetry study. Egress data are from 36 male and 36 female egress dates and ingress data are from 36 female and 39 male ingress dates. Months were divided into four roughly equal parts (= weeks).

Figure 8. Eastern kingsnakes using standing live hollow trees for ecdysis, hollow logs for ecdysis, water bodies for foraging, and open canopy uplands to digest predated snakes.

Table 9. Frequencies of eastern kingsnake positions, shelters, and behaviors observed during radiotelemetry observations.

Variable	Category	% Observations
Snake position	Below surface	65.9
	On surface	31.2
	Above surface	3.0
Shelter	Vegetation	30.0
	Leaf litter	27.8
	Hummock	11.1
	Soil	9.5
	Woody debris	5.3
	Log	4.7
	None	3.7
	Root ball / tip up mound	3.7
	Stump hole	1.3
	Artificial cover (other)	0.9
	Artificial cover (metal)	0.8
	In tree	0.5
	Artificial cover (wood)	0.5
	Beaver dam / lodge	0.1
	Concrete	0.1
Snake behavior	Undetermined	64.1
	Basking	17.8
	Denning	8.7
	Arrested crawl	6.5
	Foraging / feeding	1.5
	Ecdysis	0.7
	Mating / courtship	0.3
	Crawling	0.2
	Nesting	0.1
	Swimming	0.02
	Drinking	0.02

Relationship to wetlands

Most of the 3,587 kingsnake telemetry relocations (83.5%) occurred within wetlands (Figure 10). Increasing the size of a hypothetical upland buffer to wetlands from 0 – 600 ft (0 – 182.9 m) gradually increased the proportion of kingsnake observations contained, with the 300-ft (91.4-m) maximum buffer for wetland protection under the CMP containing 93.0% of all telemetry relocations and the 600-ft (182.9 m) extended buffer in the Toms River Corridor portion of the Pinelands containing 96.0% of all observed kingsnake locations. The relatively minor increase in relocations contained within successive buffers beyond 400 ft (121.9 m) was due to a few snakes that spent most of their time far from wetlands or traveled far beyond wetlands for a period of their active season. Even though kingsnakes were within wetlands during 83.5% of telemetry observations, their home ranges – which included areas of lower predicted use-intensity between and surrounding observed locations – contained relatively lower amounts of wetlands (62.9%, on average). Male and female home ranges contained similar amounts of wetland ($\beta = -2.57 \pm 9.48$, $p = 0.79$).

Table 10. Number of days that tracked eastern kingsnakes were above ground. These snakes were tracked over one to three complete seasons (i.e., hibernacula egress to hibernacula ingress) for a total of 35 complete seasons. There was no significant difference in the number of aboveground days in a season between sexes (t = 0.509, p = 0.614).

Sex	Snake ID	Study year	Date emerged from hibernaculum	Date entered hibernaculum	# of days active
Males (n = 17)	KS2019.01	2020	3/18/2020	11/18/2020	245
	KS2019.01	2021	4/9/2021	12/30/2021	265
	KS2019.04	2020	5/4/2020	10/23/2020	172
	KS2019.05	2020	4/21/2020	12/13/2020	236
	KS2019.05	2021	4/28/2021	10/28/2021	183
	KS2019.08	2020	5/2/2020	10/22/2020	173
	KS2019.08	2021	4/10/2021	11/2/2021	206
	KS2019.08	2022	4/14/2022	11/9/2022	209
	KS2019.15	2020	5/2/2020	10/19/2020	170
	KS2019.17	2020	5/8/2020	11/14/2020	190
	KS2020.04	2021	3/27/2021	11/3/2021	221
	KS2020.04	2022	3/22/2022	10/18/2022	210
	KS2020.19	2021	5/3/2021	11/1/2021	182
	KS2020.19	2022	5/5/2022	10/18/2022	166
	KS2021.05	2022	3/18/2022	11/15/2022	242
	KS2021.09	2022	4/29/2022	11/4/2022	189
	KS2021.10	2022	4/22/2022	10/27/2022	188
Females (n = 18)	KS2019.06	2020	5/1/2020	11/4/2020	187
	KS2019.06	2021	4/21/2021	10/25/2021	187
	KS2019.06	2022	4/26/2022	11/9/2022	197
	KS2019.11	2020	4/21/2020	12/13/2020	236
	KS2019.11	2021	4/23/2021	11/17/2021	208
	KS2020.01	2021	4/7/2021	10/14/2021	190
	KS2020.01	2022	3/22/2022	9/26/2022	188
	KS2020.05	2021	3/30/2021	10/27/2021	211
	KS2020.05	2022	4/8/2022	11/17/2022	223
	KS2020.06	2021	4/10/2021	11/9/2021	213
	KS2020.06	2022	4/14/2022	10/17/2022	186
	KS2020.15	2021	4/7/2021	10/29/2021	205
	KS2020.15	2022	4/25/2022	11/3/2022	192
	KS2020.17	2021	4/30/2021	10/22/2021	175
	KS2020.17	2022	5/5/2022	10/18/2022	166
	KS2020.21	2021	3/13/2021	11/1/2021	233
	KS2021.07	2022	4/1/2022	11/3/2022	216
	KS2021.13	2022	5/4/2022	10/7/2022	156
Mean ± SD number of days active for males					199 ± 24
Mean ± SD number of days active for males					200 ± 28

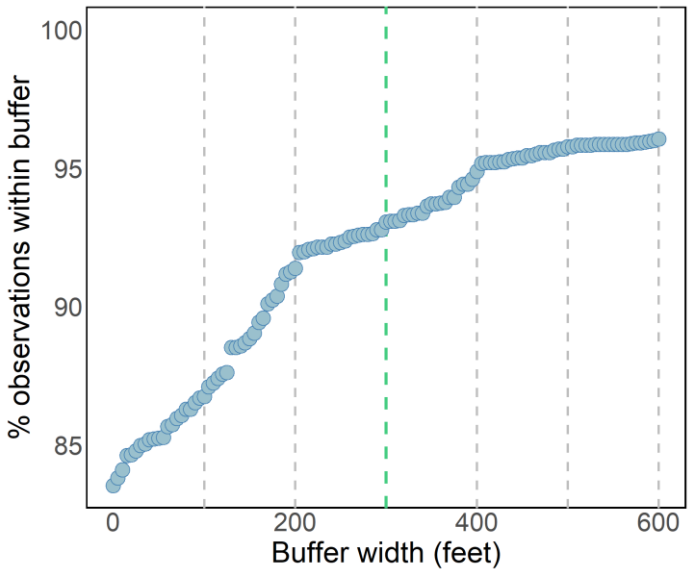

Figure 10. Proportion of eastern kingsnake relocations contained within a wetland buffer experimentally increased from 0 to 600 ft (0 – 182.9 m). Existing 300-ft wetland buffer under Pinelands regulations contained 93.0% of observed kingsnake locations and 600-ft wetland buffer as required in the Toms River Corridor contained 96.0% of observed kingsnake locations.

Home range estimates

Kingsnake home range area estimates depended on the model used, with kernel density producing the largest home range estimates and minimum convex polygons the smallest (Tables 11, 12 and 13, Figure 11). Male home ranges were generally larger than those of females, but these differences were not significant (β_{MCP} = 0.55 ± 0.29, p = 0.06; β_{BBMM} = 0.61 ± 0.32, p = 0.053; and β_{KDE} = 0.59 ± 0.33, p = 0.075). For example, BBMM home ranges were 178.7 ± 176.9 ac (72.3 ± 71.6 ha) and 96.6 ± 64.0 ac (39.1 ± 25.9 ha) for males and females, respectively. Within both sexes home range areas varied by over an order of magnitude, resulting in large standard deviations. MCP, the only home range estimator used in both previous kingsnake studies, yielded home range estimates that were 94.2% larger than those previously reported for kingsnakes in New Jersey by Wund et al. (2007) and 38.8% smaller than those reported by Linehan et al. (2010) in Georgia. BBMM home range estimates, which are expected to better reflect long-term space use (Box 1), averaged 54.4 ha and were 79.5% larger than MCP estimates.

Table 11. Overall, male, and female eastern kingsnake home ranges using three different methods: minimum convex polygon (MCP), 95% Brownian bridge movement models (BBMM), and 95% kernel density estimation (KDE). Values are mean ± SD (minimum, maximum). Model estimates (β) reflect differences in home range area by sex*. Male home ranges averaged larger, but this difference only approached statistical significance ($p > 0.05$).

	MCP (ha)	BBMM (ha)	KDE (ha)
Overall	31.6 ± 23.4 (2.5, 115.6)	57.0 ± 57.5 (4.3, 308.3)	86.9 ± 65.5 (6.0, 288.8)
Female	25.2 ± 18.0 (2.5, 63.3)	39.1 ± 25.9 (4.3, 92.9)	73.4 ± 53.8 (6.0, 195.3)
Male	37.0 ± 26.2 (7.1, 115.6)	72.3 ± 71.6 (8.6, 308.3)	98.5 ± 72.9 (19.7, 288.8)
β (slope)	0.55 ± 0.29 (p = 0.06)	0.61 ± 0.32 (p = 0.053)	0.59 ± 0.33 (p = 0.075)

*glmer(home range ~ sex + (1 | ID), family=gaussian(link="log"))

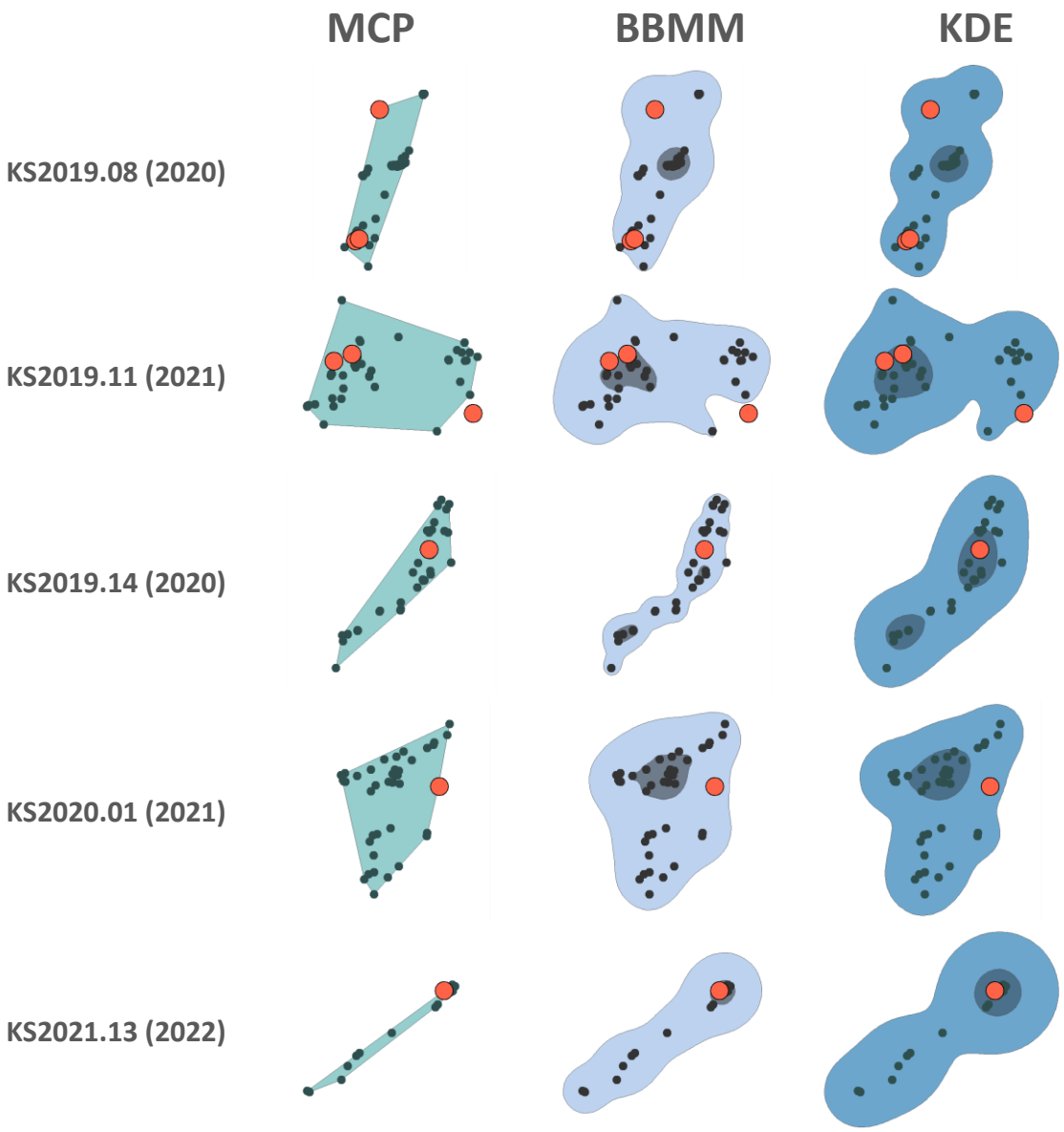

Figure 11. Outputs of minimum convex polygon (MCP), Brownian bridge movement model (BBMM), and kernel density estimate (KDE) home ranges of five selected eastern kingsnakes during a particular year. Small points represent tracking relocations from which models were derived. Large orange points depict all hibernaculum locations of a given individual. The dark-shaded regions of the BBMM and KDE home ranges reflect the core home range (50% volume contours).

Table 12. Movement metrics for female eastern kingsnakes. Core area, home range length, and home range width are based on the Brownian bridge (BBMM) home range.

Snake #	Year	Sex	Relocations (n)	New locations (n)	MCP area (ha)	KDE area (ha)	BBMM area (ha)	Core area (ha)	Home range length (m)	Home range width (m)	Cumulative distance (m)	Mean daily distance (m)	Mean distance between obs. (m)	Max. distance from den (m)
KS2019.06	2019	F	40	27	37.4	102.4	52.5	7.7	1356.5	711.8	6219.7	54.5	155.5	660.9
KS2019.06	2020	F	67	56	49.1	115.4	45.5	8.4	1486.8	729.0	8532.9	50.2	127.4	686.6
KS2019.06	2021	F	54	40	33.8	102.9	43.1	7.4	1400.2	683.7	5646.9	30.2	104.6	854.6
KS2019.06	2022	F	42	30	51.8	157.6	79.6	10.8	1516.9	756.7	7658.3	42.3	182.3	886.4
KS2019.11	2020	F	77	53	59.4	108.5	71.2	13.7	1387.1	740.5	10164.2	54.3	132.0	1207.9
KS2019.11	2021	F	61	46	63.3	104.1	85.1	16.0	1294.0	967.6	10538.7	54.0	172.8	835.7
KS2020.01	2020	F	57	27	7.8	15.9	9.1	1.3	423.9	364.7	2527.1	19.0	44.3	260.9
KS2020.01	2021	F	57	43	8.2	18.0	17.3	3.6	520.5	456.2	4786.5	25.2	84.0	375.8
KS2020.01	2022	F	42	34	10.6	19.6	18.6	3.9	490.5	480.9	4013.0	21.3	95.5	374.6
KS2020.05	2020	F	60	45	12.3	24.1	19.7	4.5	564.3	485.6	5348.8	34.0	89.1	385.4
KS2020.05	2021	F	64	39	16.4	29.0	23.2	4.1	749.5	496.1	5094.5	27.0	79.6	429.5
KS2020.05	2022	F	45	34	29.5	73.7	52.9	10.8	1172.5	698.5	6340.5	28.4	140.9	566.5
KS2020.06	2020	F	54	39	18.2	60.7	31.4	6.8	1040.8	447.3	6042.3	44.7	111.9	865.0
KS2020.06	2021	F	80	48	28.4	49.0	36.2	7.0	1020.9	573.7	8357.2	39.3	104.5	796.2
KS2020.06	2022	F	46	31	21.2	65.7	36.5	9.6	1056.5	492.3	5626.3	30.3	122.3	849.8
KS2020.09	2020	F	60	45	4.9	9.8	8.1	2.3	371.2	299.0	4199.3	25.4	70.0	279.6
KS2020.15	2020	F	45	29	27.9	107.8	25.8	3.2	1603.9	460.6	3134.8	25.4	69.7	502.4
KS2020.15	2021	F	53	43	38.0	195.3	61.7	9.4	2057.3	582.0	7559.6	36.9	142.6	976.9
KS2020.15	2022	F	32	24	23.2	141.5	57.4	4.0	1837.5	517.9	4716.2	24.6	147.4	1314.8
KS2020.17	2021	F	58	39	41.3	88.7	50.4	10.3	1104.5	814.8	7224.0	41.3	124.6	624.2
KS2020.17	2022	F	33	23	18.5	104.4	61.7	13.8	1424.0	629.9	5148.5	31.0	156.0	870.1
KS2020.21	2021	F	64	48	19.7	46.4	26.7	5.2	830.8	476.8	5285.6	22.7	82.6	487.3
KS2021.04	2021	F	75	57	4.3	7.1	5.9	1.5	358.9	228.2	3555.7	20.3	47.4	225.6
KS2021.07	2021	F	77	54	2.5	6.5	4.3	0.9	374.4	161.5	2884.9	15.5	37.5	233.1
KS2021.07	2022	F	72	48	3.5	7.6	6.1	1.0	399.4	198.3	3590.3	16.6	49.9	315.9
KS2021.13	2021	F	41	20	51.6	94.1	37.7	2.3	1965.9	806.8	4024.9	35.0	98.2	1457.8
KS2021.13	2022	F	41	30	11.7	165.1	92.9	9.5	1989.9	663.9	6525.1	41.9	159.1	1158.3
KS2021.20	2022	F	51	34	34.7	100.7	69.0	13.8	1485.1	679.2	7371.5	35.8	144.5	831.7
KS2022.09	2022	F	49	38	2.9	6.0	5.6	1.2	293.1	279.2	2403.8	17.4	49.1	195.4

Table 13. Movement metrics for male eastern kingsnakes. Core area, home range length, and home range width are based on the Brownian bridge (BBMM) home range.

Snake #	Year	Sex	Relocations (n)	New locations (n)	MCP area (ha)	KDE area (ha)	BBMM area (ha)	Core area (ha)	Home range length (m)	Home range width (m)	Cumulative distance (m)	Mean daily distance (m)	Mean distance between obs. (m)	Max. distance from den (m)
KS2019.01	2019	M	50	33	22.1	54.1	29.9	5.9	890.7	557.1	4819.7	27.1	96.4	418.1
KS2019.01	2020	M	73	38	21.5	37.0	27.1	3.7	814.2	552.5	4450.8	20.7	61.0	453.1
KS2019.01	2021	M	65	43	46.7	87.3	60.6	11.4	1251.0	797.3	9051.8	44.0	139.3	652.0
KS2019.03	2022	M	37	30	75.1	158.3	106.1	25.5	1446.7	1199.3	7397.4	47.1	199.9	1457.7
KS2019.04	2019	M	46	26	45.1	128.4	112.8	19.0	1690.0	894.9	7841.9	55.3	170.5	1233.2
KS2019.04	2020	M	62	43	23.2	73.5	41.1	8.0	1168.3	493.5	8652.4	50.3	139.6	739.7
KS2019.05	2019	M	55	34	66.7	94.2	44.4	4.5	1826.8	796.7	5865.5	36.0	106.6	854.4
KS2019.05	2020	M	70	35	7.1	28.6	9.7	1.8	757.1	214.1	3160.5	15.0	45.2	456.7
KS2019.05	2021	M	44	37	17.7	47.5	23.7	3.4	872.1	421.7	3538.5	19.3	80.4	490.9
KS2019.07	2019	M	53	44	20.7	50.0	26.2	5.2	847.2	629.0	4786.3	30.7	90.3	434.6
KS2019.08	2019	M	34	31	45.7	173.1	96.0	22.7	1794.2	786.8	6241.7	47.3	183.6	991.4
KS2019.08	2020	M	64	49	43.3	116.0	107.3	17.6	1753.3	849.7	11193.6	70.0	174.9	848.4
KS2019.08	2021	M	80	57	58.7	179.1	65.2	9.7	1841.6	578.6	10502.5	54.2	131.3	743.9
KS2019.08	2022	M	50	31	33.0	124.3	79.9	16.3	1592.2	690.4	7389.2	35.4	147.8	1183.0
KS2019.14	2020	M	82	47	57.3	200.6	69.8	14.6	2131.7	601.8	9748.9	47.1	118.9	873.6
KS2019.15	2020	M	62	43	9.7	25.4	8.6	1.6	724.1	302.0	3066.6	20.7	49.5	413.7
KS2019.17	2020	M	70	55	70.3	134.9	89.2	18.8	1491.1	963.5	10417.3	57.8	148.8	1083.2
KS2020.04	2020	M	57	38	17.6	65.1	25.9	3.7	1149.0	372.6	3528.7	23.2	61.9	571.5
KS2020.04	2021	M	67	60	18.9	59.4	39.9	6.0	1312.1	487.2	8227.4	42.0	122.8	554.2
KS2020.04	2022	M	36	28	15.8	31.3	59.9	7.2	986.8	758.9	4546.7	21.6	126.3	584.4
KS2020.19	2021	M	55	29	24.7	63.0	39.3	7.5	899.9	675.7	5007.6	27.5	91.0	597.5
KS2020.19	2022	M	40	30	41.4	108.8	67.2	14.7	1104.2	838.6	6806.5	41.0	170.2	610.5
KS2021.02	2021	M	72	57	12.8	31.9	23.0	3.7	1043.6	327.4	7678.1	42.4	106.6	536.8
KS2021.05	2021	M	36	30	69.6	184.5	282.9	39.5	1961.5	1779.4	7259.8	41.5	201.7	939.1
KS2021.05	2022	M	24	14	77.0	276.1	308.3	42.2	2393.1	1567.9	6230.7	25.7	259.6	1317.5
KS2021.09	2021	M	28	26	115.6	288.8	209.0	48.3	2280.7	1287.9	10765.7	72.3	384.5	1184.2
KS2021.09	2022	M	24	18	67.5	204.5	158.4	26.1	1934.3	1130.0	6477.4	34.3	269.9	1315.7
KS2021.10	2021	M	41	29	31.0	74.6	40.2	4.3	1095.2	561.8	4323.7	28.4	105.5	782.6
KS2021.10	2022	M	33	23	8.0	25.0	16.2	3.6	519.1	459.3	2924.5	15.6	88.6	316.9
KS2022.01	2022	M	60	45	7.9	19.7	11.4	2.7	642.9	292.5	3471.5	21.5	57.9	297.9
KS2022.05	2022	M	48	37	23.6	53.2	49.6	5.5	1231.1	541.3	5176.3	32.1	107.8	693.4
KS2022.06	2022	M	51	42	9.3	28.3	38.2	6.2	967.4	468.6	6584.0	37.4	129.1	519.8
KS2022.08	2022	M	39	30	42.2	98.8	76.4	16.3	1306.3	771.6	6919.7	43.0	177.4	809.8
KS2022.13	2022	M	50	37	9.5	23.2	15.2	3.2	749.4	365.2	4179.0	30.2	83.6	406.0

Movement metrics

On average, kingsnakes moved 114.8 ± 44.0 ft (35.0 ± 13.4 m) per day, and 3.8 ± 1.4 mi (6.1 ± 2.3 km) per season (Table 14). Home ranges tended to be elongated in one direction, averaging roughly twice as long as wide. Like Wund et al. (2007), we found no significant differences between males and females in total distance moved, mean daily distance moved, maximum distance moved, or home range length or width, although males averaged slightly larger than females across all movement metrics (Tables 12, 13, and 14).

Table 14. Movement metrics (mean ± SD) for male and female eastern kingsnakes. Cumulative distance was the sum of individual step lengths between telemetry relocations. Mean daily distance was the cumulative distance divided by the number of days monitored. Maximum distance was the greatest distance between a telemetry relocation and that snake's spring hibernaculum. Home range length and width were the side lengths of a minimum bounding rectangle surrounding the 95% Brownian bridge home range. Test statistics (*t*- and *p*-values) were based on linear mixed effects models*. Males and females did not differ significantly with respect to any of these five movement metrics.

	Total distance moved (m)	Daily distance moved (m)	Maximum distance (m)	Home range length (m)	Home range width (m)
Overall	6,075.4 ± 2,302.7	35.0 ± 13.4	712.3 ± 330.5	1,207.1 ± 532.7	633.3 ± 303.5
Female	5,673.1 ± 2,133.6	32.6 ± 11.7	672.7 ± 346.7	1,088.9 ± 551.5	547.7 ± 200.3
Male	6,418.6 ± 2,415.9	37.0 ± 14.6	746.0 ± 317.4	1,307.9 ± 502.3	706.3 ± 356.5
β (slope)	822.6 ± 710.3, $p = 0.26$	5.4 ± 4.1, $p = 0.19$	100.6 ± 112.8, $p = 0.38$	254.4 ± 180.2, $p = 0.17$	170.2 ± 104.4, $p = 0.11$

*lmer(metric ~ sex + (1 | ID))

Home range and core area selection from the landscape

In our second order analysis, kingsnakes selected home ranges with significantly more coniferous wetland ($\beta = 1.68 \pm 0.79$, $p = 0.03$) and herbaceous wetland ($\beta = 2.21 \pm 0.63$, $p < 0.001$) and significantly less upland forest ($\beta = -1.66 \pm 0.53$, $p = 0.001$) than available home ranges (Table 15, Figure 12). Core area selection was similar with respect to avoidance of upland forest ($\beta = -1.73 \pm 0.48$, $p < 0.001$) and selection for herbaceous wetlands ($\beta = 1.92 \pm 0.50$, $p < 0.001$), but unlike home ranges, observed core areas contained significantly more deciduous wetland ($\beta = 2.51 \pm 1.16$, $p = 0.03$) than available core areas.

A comparable analysis by Steen et al. (2010) found no evidence of selection for wetland habitat types in Georgia. Although Wund et al. (2007) did not formally examine home range selection, they observed that kingsnake home ranges in New Jersey contained both wetland and upland habitats and suggested that kingsnakes were macrohabitat generalists. In contrast, we found that kingsnakes configure their home ranges to include more wetlands (specifically herbaceous and coniferous wetlands, which primarily corresponded to abandoned cranberry bogs and pine lowland forest, respectively) and less upland forest (primarily pine uplands) relative to their availability on the landscape.

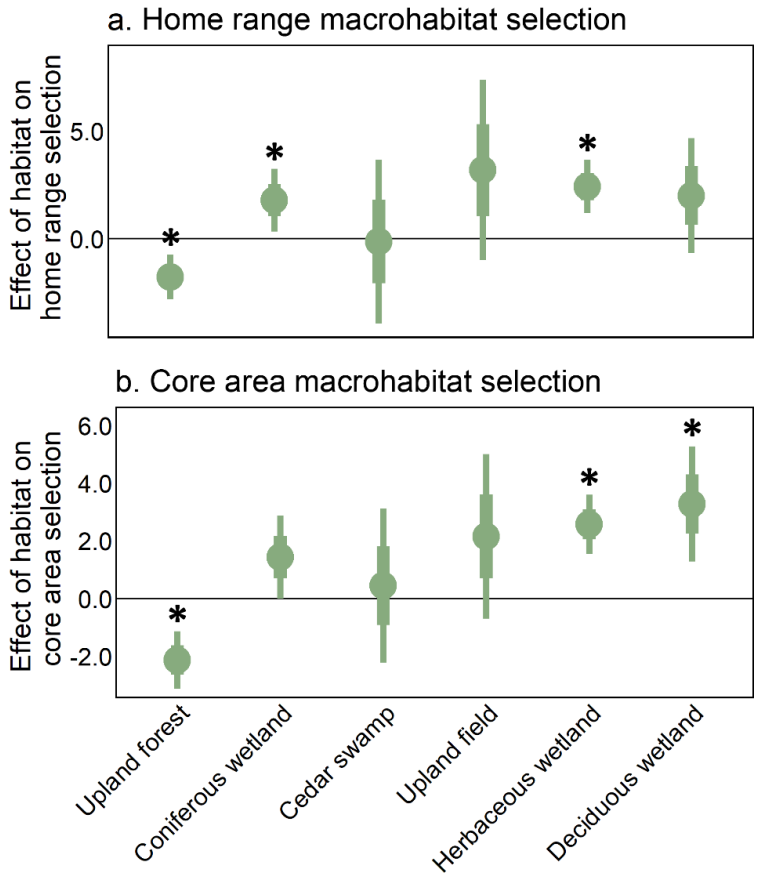

Figure 12. Home range and core area (second order) macrohabitat selection by eastern kingsnakes. Kingsnake home ranges (a) contained more coniferous wetland and herbaceous wetland and less upland forest than simulated available home ranges. Core ranges (50% volume contour; b) contained more deciduous wetland and herbaceous wetland and less upland forest than available home ranges. * = significant results.

Table 15. Second order (home range and core range) macrohabitat selection by eastern kingsnakes. Values depict model-estimated effect sizes ± SE (log-odds). Statistically significant effects are shown in bold.

Term	Home range	Core range
Cedar swamp	-0.83 ± 1.92, p = 0.67	-0.18 ± 1.38, p = 0.90
Coniferous wetland	**1.68 ± 0.79, p = 0.03**	1.09 ± 0.86, p = 0.20
Deciduous wetland	1.48 ± 1.37, p = 0.28	**2.51 ± 1.16, p = 0.03**
Upland field	2.90 ± 2.23, p = 0.19	2.40 ± 1.58, p = 0.13
Upland forest	**-1.66 ± 0.53, p = 0.001**	**-1.73 ± 0.48, p < 0.001**
Herbaceous wetland	**2.21 ± 0.63, p < 0.001**	**1.92 ± 0.50, p < 0.001**

Macrohabitat selection within home range

For our third order analysis, macrohabitat availability within the home range differed vastly for individual snakes, with 5 snakes having all six habitat types available within their home range, 8 snakes had 5 habitats, 7 snakes had 4 habitats, 10 snakes had 3 habitats, 3 snakes had 2 habitats, and 1 snake's entire home range consisted of upland forest. Macrohabitat selection differed significantly in 19 out of 34 snakes, 6 out of 14 females and 13 out of 20 males (Figure 13). Upland forest was available within the home ranges of 31 out of 34 snakes tracked (91%), followed by coniferous wetland (82%), herbaceous wetland (74%), deciduous wetland and cedar swamp (59%), and upland field (32%). Differences in macrohabitat availability among individuals likely weakened model inferences about habitat types that were only available for selection to some snakes.

Macrohabitat selection differed by sex and by behavioral period (Table 16, Figure 14). During transitional periods (Figure 14b), females selected deciduous wetlands and herbaceous wetlands while avoiding coniferous wetland. Males also selected deciduous wetland, but unlike females, they avoided herbaceous wetland and upland forest and used coniferous wetlands roughly in proportion to their availability.

During their active periods (Figure 14c), females again selected deciduous wetlands while avoiding coniferous wetlands, but showed no significant responses to any other land cover categories. Active males, on the other hand, selected upland field and herbaceous wetland while avoiding cedar swamps. Despite significance among several covariate-level differences between males and females, the main effect of sex on transitional, active, and overall habitat selection was not significant ($p > 0.05$). The mechanisms underlying these sex-specific patterns remain unclear, but may reflect differences in foraging ecology (e.g., prey preferences related to body size dimorphism), thermoregulation, sex-specific responses to habitat-mediated predation risk, differing reproductive demands, or other ecological factors.

Table 16. Within home range (third order) macrohabitat selection by kingsnakes, separated by sex and behavioral period. Statistically significant differences between male and female selection coefficients were identified using Wald's W. Statistically significant effects are shown in bold.

	Macrohabitat Type	Females	Males	Comparison
Transitional	Cedar swamp	0.01 ± 0.08, p = 0.945	0.08 ± 0.09, p = 0.355	0.65, *p* = 0.516
	Coniferous wetland	**-0.19 ± 0.06, p = 0.004**	-0.07 ± 0.06, p = 0.246	1.22, *p* = 0.221
	Deciduous wetland	**0.32 ± 0.08, p < 0.001**	**0.23 ± 0.09, p = 0.010**	-0.77, *p* = 0.441
	Upland field	-0.17 ± 0.11, p = 0.109	-0.21 ± 0.11, p = 0.057	-0.25, *p* = 0.800
	Upland forest	-0.09 ± 0.07, p = 0.190	**-0.12 ± 0.06, p = 0.040**	-0.35, *p* = 0.730
	Herbaceous wetland	**0.16 ± 0.07, p = 0.025**	**-0.26 ± 0.07, p < 0.001**	**-4.30, *p* < 0.001**
Active	Cedar swamp	-0.02 ± 0.07, p = 0.780	**-0.14 ± 0.07, p = 0.029**	-1.31, *p* = 0.191
	Coniferous wetland	**-0.18 ± 0.05, p < 0.001**	0.06 ± 0.05, p = 0.193	**3.61, *p* < 0.001**
	Deciduous wetland	**0.14 ± 0.06, p = 0.017**	-0.05 ± 0.06, p = 0.383	**-2.33, *p* = 0.020**
	Upland field	-0.08 ± 0.09, p = 0.367	**0.17 ± 0.07, p = 0.024**	**2.16, *p* = 0.031**
	Upland forest	-0.03 ± 0.05, p = 0.601	-0.06 ± 0.04, p = 0.107	-0.57, *p* = 0.566
	Herbaceous wetland	0.10 ± 0.05, p = 0.056	**0.11 ± 0.05, p = 0.029**	0.14, *p* = 0.886

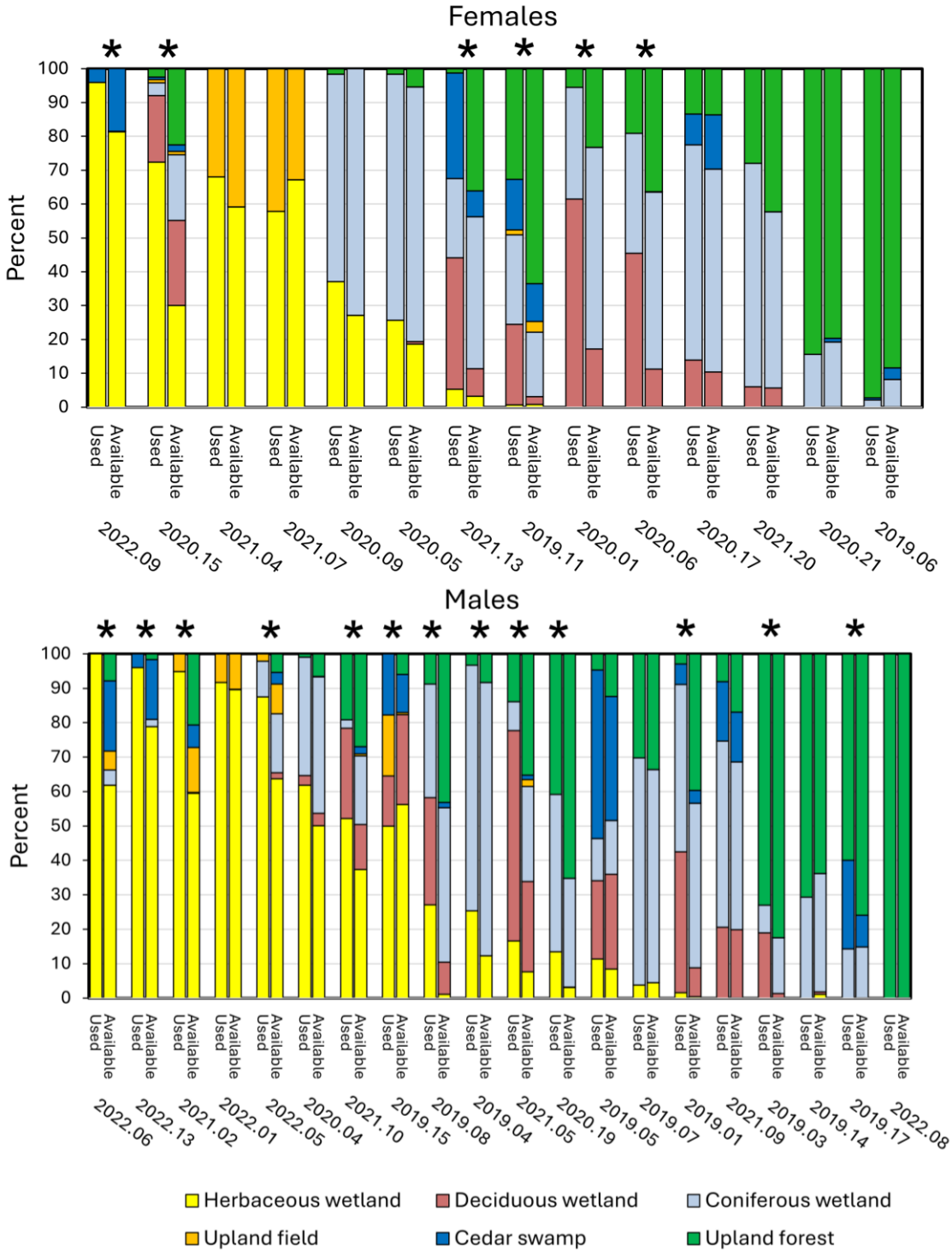

Figure 13. Macrohabitat profiles for female (top panel) and male (bottom panel) eastern kingsnake activity seasons. Used = percent of snake relocations in macrohabitat type. Available = percent of random points within macrohabitat type. * indicates significant difference (p < 0.05) between used and available macrohabitats.

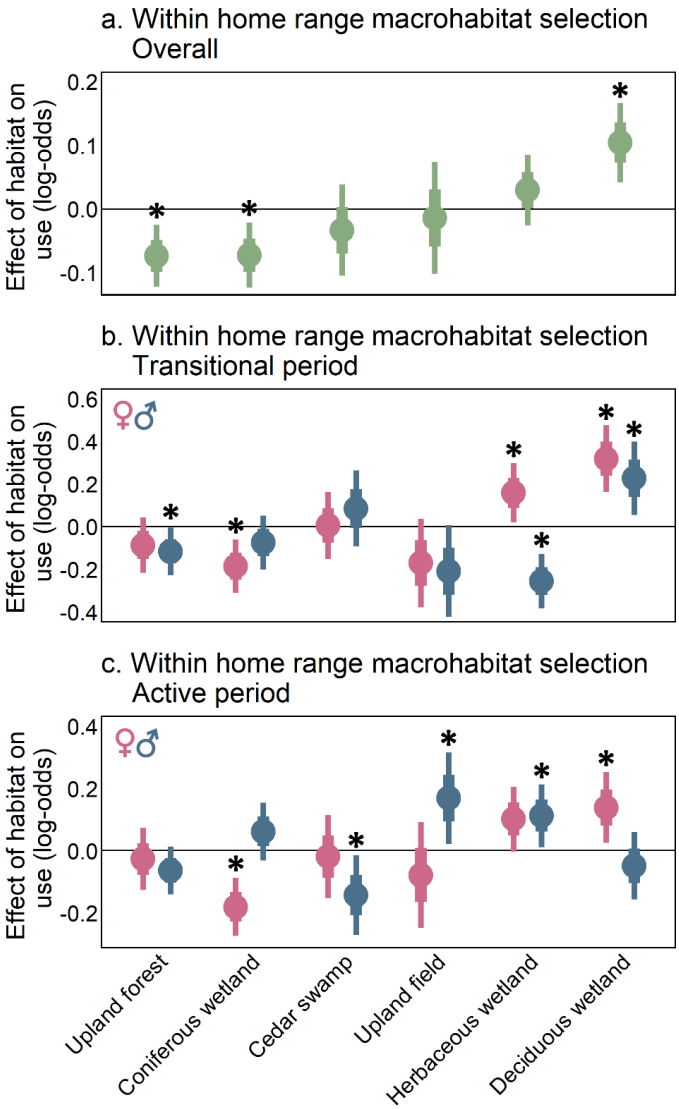

Figure 14. Within home range (third order) macrohabitat selection in kingsnakes overall (a), during spring and fall transitional periods (b), and during the active period (c). * = significant results.

Influence of habitat on home range size

We found that both home range and core area selection were significantly affected by their composition (Figure 15). Home ranges composed of greater amounts of preferred cover (coniferous wetland and herbaceous wetland) were significantly smaller (β = -29.4 ± 7.1, p = 0.0001); Figure 15a). Likewise, home ranges containing more avoided cover (upland forest) were larger (β = 30.4 ± 6.9, p < 0.0001; Figure 15b). Preferred and avoided cover were highly collinear (r = 0.82). These results indicated that kingsnakes traveled further to access preferred habitat types. Habitat composition has been shown to influence home range size in other snake species (Kapfer et al. 2010), and our results suggest that the amount of preferred and avoided habitat may be a stronger determinant of kingsnake home range size than either body size or sex.

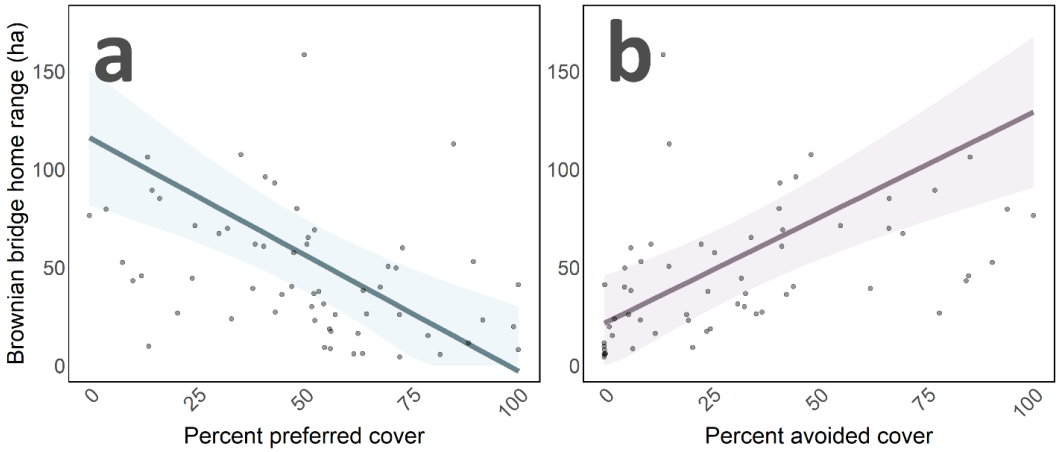

Figure 15. Influence of amount of preferred (a) and avoided (b) macrohabitats on home range area. Lines depict predicted mean values and ribbons depict 95% confidence intervals. Home ranges composed of more preferred macrohabitat types (herbaceous and coniferous wetlands) were smaller, while home ranges composed of more avoided macrohabitat types (upland forest) were larger.

Microhabitat selection

The dataset used for microhabitat selection analysis consisted of 2,797 snake relocations and an equal number of paired available locations from 33 individual kingsnakes. Each snake had an average of 84.8 (range 35 – 185) used and available paired locations. The optimal model resulted in the lowest AIC value for each dataset (transitional and active for males and females), followed by the global model for all groups except males during the transitional behavioral period, which was better explained by the cover hypothesis model. The model inspired by Wund et al. (2007) performed reasonably well, ranking above the other hypothesis models for all datasets except males during the transitional behavioral period.

Our results show that kingsnake relocations occurred in association with deeper leaf litter and a higher availability of woody debris than paired controls, regardless of behavioral period or sex (Figure 16). Males and females during the active behavioral period and females during the transitional behavioral period were in areas with higher soil temperatures, lower surface temperatures, and a more open canopy than measured at random points. In the active behavioral period, both males and females appeared to select for higher vegetation densities, and females were linked to additional structural variables, such as large diameter logs, tall shrubs, and large diameter overstory trees. Log diameter was also significant to females during the transitional behavioral period. Males during both behavioral periods typically occurred in locations with less visible water. Males associated more closely with tall shrubs during the transitional behavioral period than at random.

These results highlight the importance of protective refugia within kingsnake habitats, which is consistent with their highly secretive behavior. Our findings largely align with those of Wund et al. (2007), who reported that kingsnakes disproportionately selected microhabitats with deeper leaf litter and greater amounts of woody vegetation and large-diameter woody debris. Kingsnakes in Georgia also seemingly prioritized concealment by selecting microhabitats with less bare ground, more woody debris, and more woody vegetation cover (Steen et al. 2010). Predation risk is apparently high in the New Jersey population, and the availability of microhabitats with ample concealment opportunities (e.g., deep needle pack at the base of large diameter pine trees and along large logs, deep litter layer, and dense shrubs) may help offset this risk.

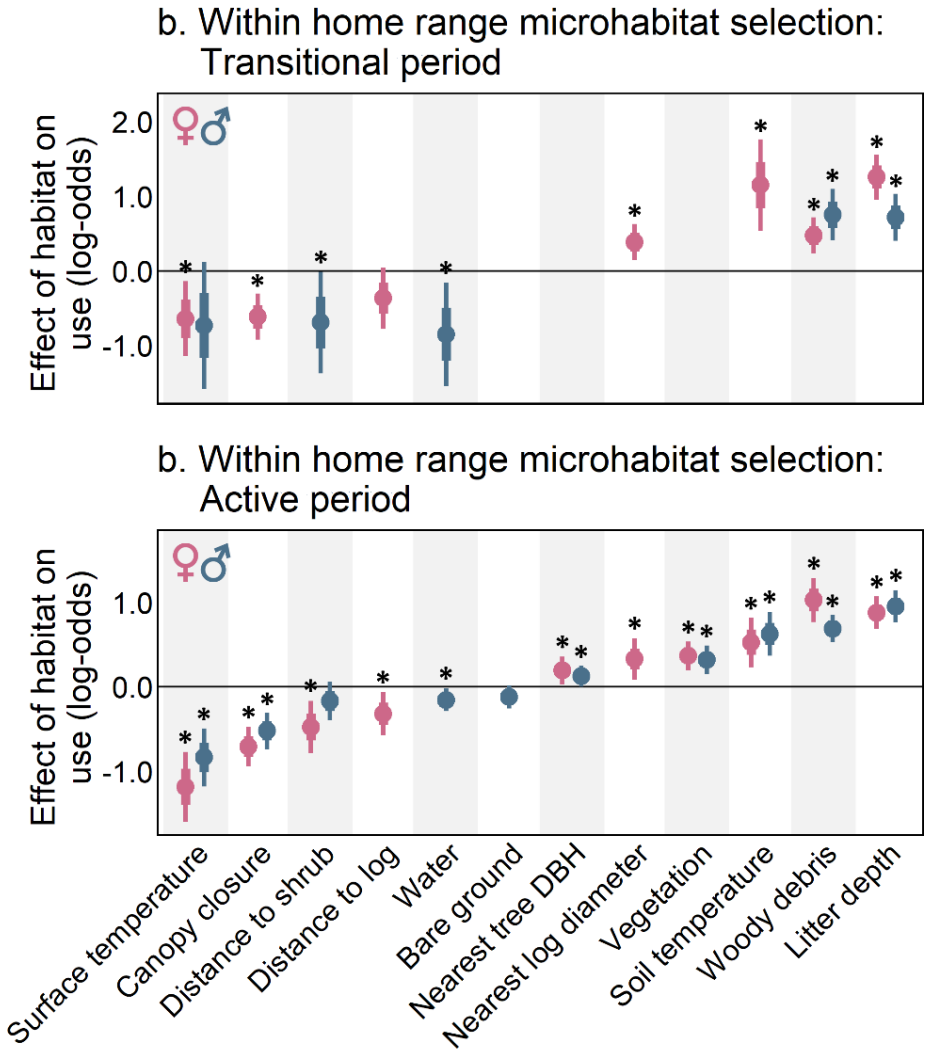

Figure 16. Influence of microhabitat covariates on kingsnake habitat selection during spring and fall transitional periods (a) and during the active period (b). If a male or female symbol is missing, that variable was not included in the optimal model. See Table 4 for variables included in models. * = significant results.

Overwintering

During the four-year study, 37 kingsnakes (19 males and 18 females) were tracked to their overwintering locations, revealing 51 different hibernacula (Table 17). Most kingsnakes brumated singly, but we observed instances of communal denning. Of the 51 hibernacula, 47 hibernacula contained a single tracked kingsnake and four hibernacula contained more than one tracked snake. Of the four hibernacula with more than one tracked snake, one hibernaculum contained two tracked snakes but during different winters, two hibernacula contained two tracked snakes during the same winter, and one hibernaculum contained two tracked snakes in the same winter and three tracked snakes in a different winter. Male and female snakes overwintered together in each instance where more than one tracked snake was in the same hibernacula.

Fidelity to hibernacula was variable, but relatively low (Figure 17). Fifteen snakes were tracked to a hibernaculum for one winter, ten snakes were tracked for two winters, ten snakes were tracked for three winters, and two snakes were tracked for four winters. Twenty-two snakes used a single hibernaculum, 11 snakes used two different hibernacula, and four snakes used three different hibernacula. The number of snakes tracked to hibernacula multiplied by the number of winters each snake spent in hibernacula resulted in a total of 73 different overwintering events.

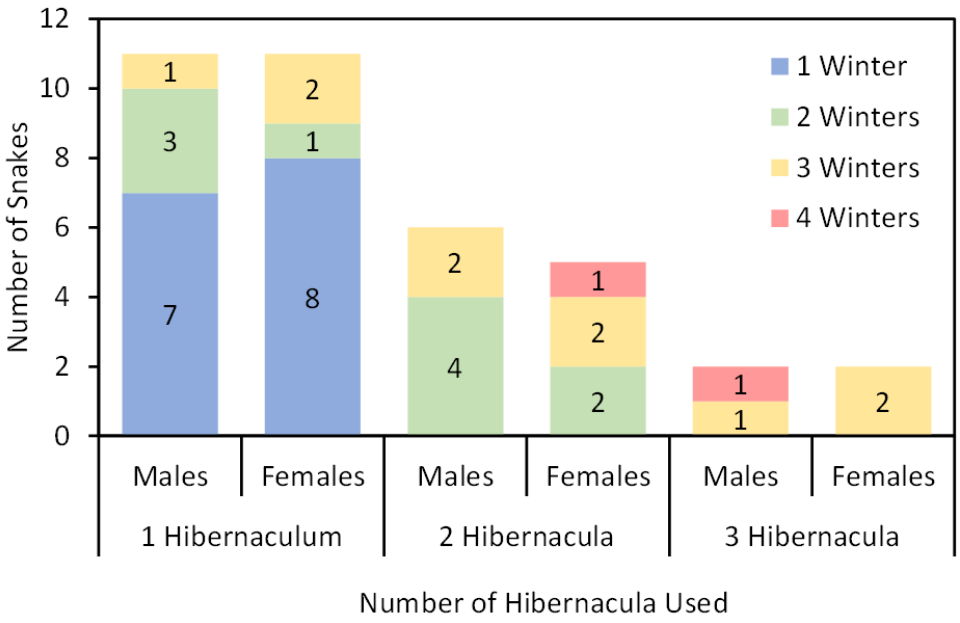

Figure 17. Number of hibernacula used and number of winters radio tracked for 37 eastern kingsnakes (19 males and 18 females). Winters are 2019/2020, 2020/2021, 2021/2022, and 2022/2023. The number of snakes x the number of winters in a hibernaculum = 73 total overwintering events.

Table 17. Data for 51 hibernacula used by 37 radio tracked eastern kingsnakes that overwintered. M = male and F = female. Years are 2019, 2020, 2021, and 2022. Superscript numbers indicate that other snakes were present in a hibernaculum, where Yes[1] = KS2021.05 (2022-2023, M), Yes[2] = KS2021.07 (2021-2022, F), KS2022.01 (2021-2023, M), Yes[3] = KS2021.07 (2022-2023, F), and Yes[4] = KS2022.09 (2022-2023, F).

Snake ID	Sex	Number of years used	Overwintering years used	Other tracked kingsnakes present	Habitat type	Hibernacula feature
KS2019.01	M	1	21-22	No	Pine lowland	Base of live shrub
KS2019.01	M	1	19-20	No	Pine lowland	Base of live tree
KS2019.01	M	1	20-21	No	Pine lowland	Base of live tree
KS2019.03	M	1	19-20	No	Pine upland	Old tree/shrub stump
KS2019.03	M	1	22-23	No	Pine upland	Old tree/shrub stump
KS2019.04	M	2	19-20, 20-21	No	Pine lowland	Base of live tree
KS2019.05	M	2	20-21, 21-22	No	Cedar swamp	Base of live tree
KS2019.05	M	1	19-20	No	Cedar swamp	Overturned root ball
KS2019.06	F	3	19-20, 20-21,21-22	No	Pine lowland	Old tree/shrub stump
KS2019.06	F	1	22-23	No	Pine upland	Base of live tree
KS2019.07	M	1	19-20	No	Pine lowland	Base of live shrub
KS2019.08	M	2	19-20, 20-21	No	Maple swamp	Old tree/shrub stump
KS2019.08	M	1	22-23	No	Pine/Maple swamp	Base of live shrub
KS2019.08	M	1	21-22	No	Pine/Maple swamp	Base of live tree
KS2019.11	F	1	19-20	No	Pine lowland	Base of live shrub
KS2019.11	F	1	21-22	No	Pine lowland	Overturned root ball
KS2019.11	F	1	20-21	No	Pine/Maple swamp	Base of live shrub
KS2019.14	M	1	20-21	No	Pine upland	Base of live shrub
KS2019.15	M	2	19-20, 20-21	No	Pine/Maple swamp	Overturned root ball
KS2019.16	F	1	19-20	No	Pine/Maple swamp	Base of live tree
KS2019.17	M	1	19-20	No	Pine lowland	Old tree/shrub stump
KS2019.17	M	1	20-21	No	Pine/Maple swamp	Old tree/shrub stump
KS2020.01	F	3	20-21, 21-22, 22-23	No	Cedar swamp	Old tree/shrub stump
KS2020.04	M	1	22-23	No	Pine/Maple swamp	Base of live shrub
KS2020.04	M	2	20-21, 21-22	No	Pine/Maple swamp	Base of live tree
KS2020.05	F	2	21-22, 22-23	No	Herbaceous wetland	Base of live shrub
KS2020.05	F	1	20-21	No	Pine lowland	Base of live tree
KS2020.06	F	1	20-21	No	Pine lowland	Base of live tree
KS2020.06	F	1	21-22	No	Pine/Maple swamp	Base of live shrub
KS2020.06	F	1	22-23	No	Pine/Maple swamp	Base of live shrub
KS2020.09	F	1	20-21	No	Pine lowland	Base of live shrub
KS2020.11	F	1	20-21	No	Pine lowland	Base of live shrub
KS2020.15	F	2	20-21, 22-23	Yes[1]	Maple swamp	Base of live tree
KS2020.15	F	1	21-22	No	Pine/Maple swamp	Base of live tree
KS2020.17	F	3	20-21, 21-22, 22-23	No	Pine/Maple swamp	Forest floor
KS2020.18	F	1	20-21	No	Pine/Maple swamp	Base of live shrub
KS2020.19	M	3	20-21, 21-22, 22-23	No	Pine/Maple swamp	Base of live shrub
KS2020.21	F	1	20-21	No	Pine upland	Base of live tree
KS2020.21	F	1	21-22	No	Pine/Maple swamp	Base of live tree
KS2020.23	F	1	21-22	No	Pine upland	Old tree/shrub stump
KS2021.02	M	1	21-22	Yes[2]	Field	Rubble
KS2021.04	F	1	21-22	Yes[3]	Field	Rubble
KS2021.05	M	1	21-22	No	Maple swamp	Base of live tree
KS2021.09	M	2	21-22, 22-23	No	Pine/Maple swamp	Base of live tree
KS2021.10	M	1	21-22	No	Herbaceous wetland	Base of live tree
KS2021.10	M	1	22-23	No	Herbaceous wetland	Overturned root ball
KS2021.13	F	2	21-22, 22-23	No	Pine lowland	Base of live shrub
KS2021.20	F	1	22-23	No	Pine upland	Old tree/shrub stump
KS2022.05	M	1	22-23	No	Pine lowland	Base of live shrub
KS2022.08	M	1	22-23	No	Pine upland	Old tree/shrub stump
KS2022.13	M	1	22-23	Yes[4]	Cedar swamp	Old tree/shrub stump

Two snakes (KS2019.04 and KS2019.15) died during their second winter at a hibernaculum. For the remaining 71 overwintering events, we found that females spent slightly more time in hibernacula than males (Table 17), but this difference was not statistically significant (t = 0.963, p = 0.339). However, we found a significant difference in the number of days spent in hibernacula among the four different winters of the study (H = 8.625, p = 0.035). Snakes spent more time in hibernacula over the 2019-2020 winter compared to 2020-2021 winter (p = 0.039, Figure 18). We found no differences for any other year-to-year comparisons.

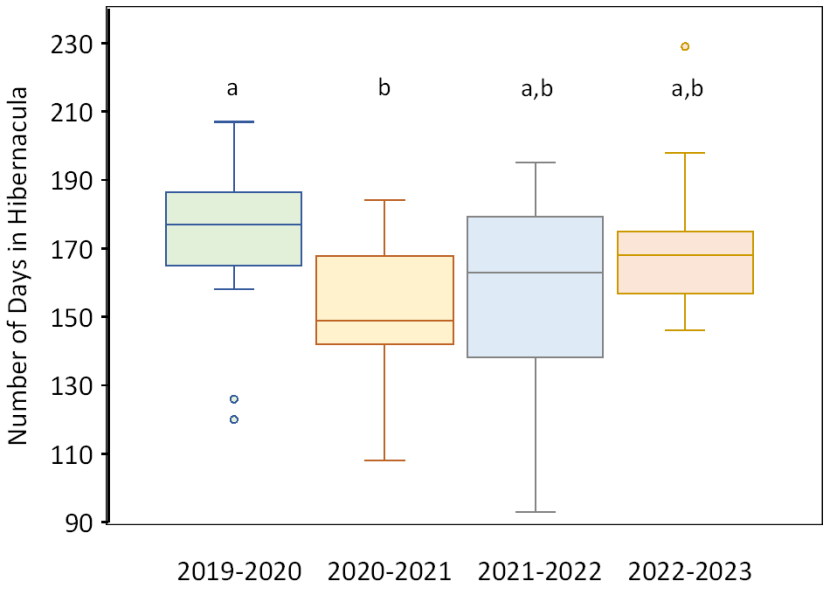

Figure 18. Box plots of the number of days that 37 eastern kingsnakes spent in hibernacula during four winters. Data represent 71 different snake-hibernacula combinations, where 2019-2020 (N = 11), 2020-2021 (N = 18), 2021-2022 (N = 20), and 2022-2023 (N = 22). Significant Kruskal-Wallis ANOVA results (p = 0.035) are indicated by letters above box plots.

The 51 hibernacula were in seven different habitat types (Figure 19). Although snakes used six types of features to access hibernacula for brumation, most snakes used the base of live or dead trees or shrubs for access. We observed no major differences in habitat types or hibernacula access features between male and female snakes. Although found in a range of upland and wetland habitat types, 77% of the hibernacula were pine/maple swamps, pine lowlands, and pine uplands (Figure 20). Hibernacula in pine/maple swamps and pine lowlands were primarily underlain by Atsion sand, which is a hydric mineral soil, whereas hibernacula in pine uplands were mostly associated with drier sands classified as upland or transitional soils. Fewer hibernacula were in maple swamps, which were all underlain by the hydric mineral soil Berryland, and cedar swamps, which primarily grow in organic soils with a deep layer of peat. Three hibernacula were in herbaceous wetlands, which are usually found embedded in pine lowland forests and often associated with Atsion sands. Two hibernacula were in upland fields and snakes used rubble from old foundations from an abandoned cranberry farm.

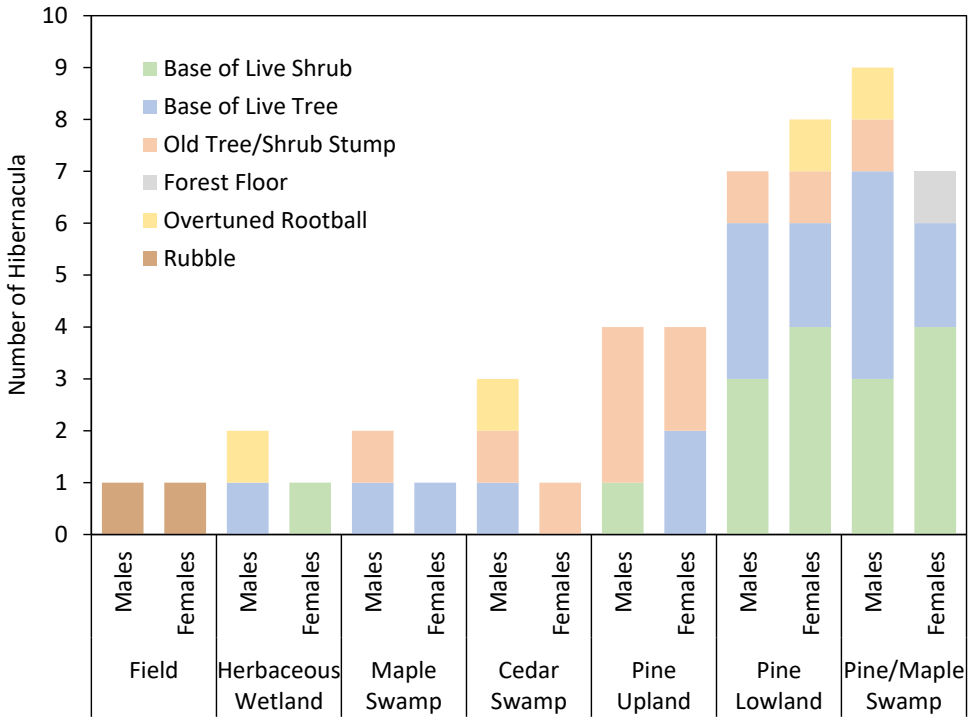

Figure 19. On-ground habitat types and features that snakes used to access hibernacula for 51 different hibernacula used by eastern kingsnakes during a radio telemetry study.

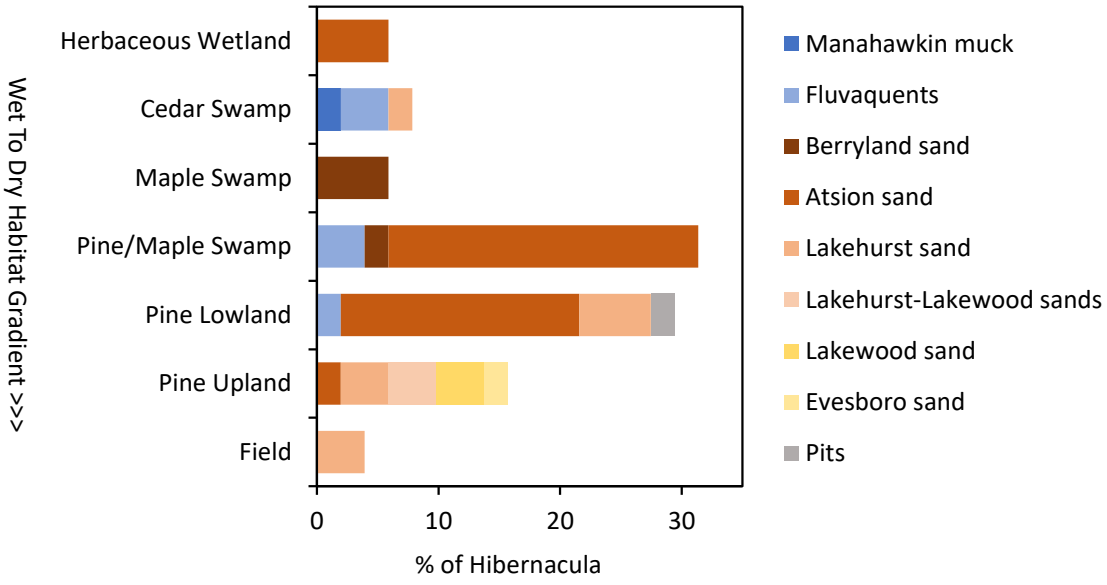

Figure 20. Percentage of 51 eastern kingsnake hibernacula associated with habitat types and soils. Habitat types and soils are ordered top to bottom along a wet to dry habitat gradient. Manahawkin and Fluvaquents are organic soils, Berryland and Atsion are hydric mineral soils, Lakehurst and Lakehurst-Lakewood are transitional mineral soils, Lakewood and Evesboro are upland soils, and pits are variable.

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