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Activity Ranges and Habitat Use of *Lampropeltis getula getula* (Eastern Kingsnakes)

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Abstract - The habitat use and activity range of *Lampropeltis getula getula* (Eastern Kingsnake) in the New Jersey Pine Barrens were studied from 1996–1998. Five male and four non-gravid female Eastern Kingsnakes were routinely radiotracked during daylight hours during one or two active seasons. Habitat and climatic conditions at snake locations were characterized using 9 climatic and 14 structural habitat features. Multivariate statistical comparisons with randomly selected locations indicated that Eastern Kingsnakes use available habitat in a non-random fashion with respect to microhabitat features (Wilks' lambda = 0.511; df = 28, 1066; $P < 0.01$). Eastern Kingsnakes preferred sites with thick leaf litter and dense shrub-layer foliage. They used a broad range of macrohabitats that spanned both wetland and pine-dominated upland areas. Moist areas were used for hibernation. Snakes exhibited a largely fossorial lifestyle, spending a great proportion of their time concealed under the cover of soil and/or leaf litter (79% of observations). Climatic conditions at selected sites did not differ between males and females. Analysis of movements revealed an affinity for specific locations within their established activity ranges. Males and females did not differ with respect to their activity ranges or measured movement patterns (e.g., mean distance traveled/day, total distance moved, range length).

Introduction

Given the generally secretive nature of snakes, it is not surprising that basic information regarding snake ecology is relatively limited compared to knowledge of other vertebrates. However, in the past two decades, the use of radiotelemetry has vastly improved our ability to study these animals in their natural habitats (e.g., Plummer and Congdon 1994, Reinert and Zappalorti 1988, Weatherhead and Hoysak 1989). Radiotelemetric field studies of snakes can yield important information regarding spatial movement patterns and habitat use (Blouin-Demers et al. 2005; Reinert and Zappalorti 1988; Reinert et al., in press; Weatherhead and Hoysak 1989), basic information that is integral to further investigating the role of a given species of snake in relation to its environment and community (Reinert 1993).

Lampropeltis getula getula Linnaeus (Eastern Kingsnake) is one of the most widespread snake species in North America, ranging from the Atlantic to the Pacific coast (Krysko and Judd 2006). Eight subspecies are currently

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recognized (Collins and Taggart 2002). With the exception of a few early observations (Fitch 1949, Stickel and Cope 1947), little quantitative information exists on the movement patterns of this widespread species. Likewise, most information regarding the habitat use and natural history of this species has been obtained opportunistically and is largely anecdotal in nature (e.g., Kauffeld 1957, Kennedy 1978, Lazell and Musick 1973). However, Krysko (2002) recently described the seasonal activity patterns of *Lampropeltis getula floridana* Blanchard (Florida Kingsnake), using systematic field surveys of visually located individuals. Our purpose was to acquire quantitative information on the movements and habitat use of Eastern Kingsnakes at the northeastern terminus of their geographic distribution.

Methods

Study area

Two areas in the Atlantic Coastal Plains Pine Barrens of southern New Jersey were used in this study. The first consisted of approximately 12 km^2 in Greenwood Wildlife Management Area, Ocean County. The other included approximately 5 km^2 in Wharton State Forest, Burlington County. In general, there are ten major macrohabitat types in the New Jersey Pine Barrens, which can be grouped into two main categories: a lowland complex and an upland complex (McCormick 1979). The upland forest habitats on the study sites (0.7–21 m above the water table) were dominated by *Pinus rigida* Mill. (pitch pine), *Quercus marilandica* Muench (blackjack oak), and *Q. velutina* Lam. (black oak), with dense shrubs that included *Vaccinium vacillans* Kalm. (lowbush blueberry) and *Gaylussacia baccata* Wangenh (black huckleberry). The lowland habitats that are near to or partially submerged within the water table are characterized by *Chamaecyparis thyoides* Linnaeus (Atlantic white cedar) and/or *Acer rubrum* Linnaeus (red maple) swamps as well as bogs. Both permanent and intermittent streams irrigate the lowland areas. Sand roads are a prominent feature within the upland habitats and on the edges of some lowland areas. In addition, abandoned railroad tracks traversed the study area in Wharton State Forest. A more detailed description of the New Jersey Pine Barrens can be found in McCormick (1979).

Radiotelemetry

Snakes used in the study were initially located by searching all habitats in the study areas; thus, the habitat preferences we observed should not be biased due to our broad initial sampling of snakes. Kingsnakes were located while radiotracking snakes from other studies, or by a direct effort to locate the snakes by M.A. Wund and M.E. Torocco. All Eastern Kingsnakes were monitored with radio transmitters (model SM1, AVM Instrument Company, Colfax, CA), each equipped with a mercuric oxide battery (Duracell 675), a 30-cm whip antenna, and potted in a 1 part beeswax:1 part paraffin mixture. The complete transmitter packages had a mass of 4–5 g, which typically represented less than 2% of snake body mass. Transmitters were surgically implanted into the body cavities of snakes following the procedure of Reinert and Cundall (1982) and Reinert (1992). Snakes were held in the lab for several days following surgery. Once they exhibited signs of full recovery, they were released at their captnre site. Transmission distances of transmitters averaged approximately 500 meters.

Movements and behavior

Transmitter-equipped snakes were tracked routinely during 1996–1998 and were located on average once every three days during their active season (April–October). Snakes were only located during daylight hours. Anecdotal records indicate that Eastern Kingsnakes are mainly diurnal in the northern parts of their range (Hulse et al. 2001, Mitchell 1994), and possibly crepuscular during the hottest portion of the active season in the southern parts of their range (Krysko 2002). At each location, an attempt was made to assess the actual position and behavior of the snake (in many cases, the snakes were concealed; see Results). Locations were recorded using a portable GPS unit. Activity ranges were calculated using harmonic mean analysis (Dixon and Chapman 1980), making it possible to define the activity ranges of each snake. The area contained within a 95% isopleth constituted a given snake's total activity range, whereas the area within a 50% isopleth was considered to define its core-activity area (Reinert 1992). Minimum-convex polygon (Jennrich and Turner 1969, Mohr 1947) areas were also calculated to facilitate comparisons with published reports. These activity-range descriptors were calculated using Micro-computer Program for the Analysis of Animal Locations (MCPAAL; Stüwe and Blohowiak 1992). Range length of an individual snake was calculated as the distance between the snake's two most-distant locations. We calculated each snake's total distance moved and average distance moved per day in order to characterize the overall movements of individuals. The total distance moved was calculated as the sum of linear distances between successive locations. The mean distance moved per day was calculated as the total distance moved during the active period divided by the total number of days that the snake was monitored during this period. Student's t-tests for independent samples (Sokal and Rohlf 1995) were used to compare parameters between males and females. However, small sample sizes likely resulted in low statistical power for this analysis.

Structural features and climatic factors

Macrohabitats used by the snakes in this study included upland dry oak forest, cedar swamp, red maple swamp, bog, or streambanks. At each snake location, the macrohabitat type was qualitatively determined. In addition, 14 structural habitat and 9 climatic variables were measnred (Table 1). The sampling methods for 11 of the habitat variables are described in detail in Reinert (1984a). Three additional variables (foliage density from 0–1 meter, foliage density from 1–2 meters, and litter depth) have not been previously described. Foliage density above the snake was estimated by the number of contacts made between discrete leaves and stems with a meter stick held from from 0–1 m and 1–2 m above a snake's location. A solid ruler was pressed into the leaf litter to measure its depth. Using an electronic thermometer/hygrometer, substrate surface and ambient (shaded, 1 m above ground) temperature and relative humidity as well as soil temperature at 5-cm depth were measured. Surface temperatures were taken within 3 cm of (but not in contact with) the surface. The thermometer/hygrometer was inserted directly into the soil to measure soil conditions at 5-cm depth. Light intensity (lux) at the snake and maximum surface light intensity within 2 m of the snake were measured using a light-intensity meter. Unlike structural habitat features, climatic variables were not measured at random locations. While structural habitat features remain relatively stable at a given location throughout a season, climatic conditions vary considerably over the course of minutes, hours, days, and months. Establishing the range of climatic

Table 1. Mean values (SE and N in parentheses) of structural habitat parameters measured at snake-selected sites and randomly sampled sites within Eastern Kingsnake habitats in the New Jersey Pine Barrens. Mean values for climatic variables adjusted for ambient conditions for snake-selected sites.

Habitat variable	Males (SE, N)	Females (SE, N)	Random (SE, N)
% canopy closure	47 (2.1, 204)	48 (2.9, 174)	60 (2.18, 174)
Foliage density from 0–1 m	15 (0.67, 204)	13 (0.06, 174)	8 (0.49, 174)
Foliage density from 1–2 m	2 (0.19, 204)	4 (0.42, 174)	2 (0.21, 174)
Distance to nearest overstory tree (m)	3.66 (0.37, 204)	3.54 (0.28, 174)	3.31 (0.38, 174)
Distance to nearest understory tree (m)	3.15 (0.28, 204)	4.30 (0.30, 174)	3.25 (0.26, 174)
Diameter of nearest overstory tree (cm)	15.67 (0.47, 204)	15.95 (0.62, 174)	14.86 (0.51, 174)
Diameter of nearest understory tree (cm)	4.28 (0.10, 204)	3.80 (0.10, 174)	4.51 (0.11, 174)
Distance to nearest fallen log (m)	6.82 (0.61, 204)	1.72 (0.20, 174)	4.67 (0.41, 174)
Diameter of nearest fallen log (cm)	10.4 (0.50, 204)	7.7 (0.37, 174)	6.9 (0.29, 174)
Leaf-litter depth (cm)	1.6 (0.80, 204)	2.1 (0.14, 174)	1.0 (0.09, 174)
% vegetation ground cover within 1 m^2	71 (1.97, 204)	61 (2.34, 174)	63 (2.33, 174)
% leaf litter ground cover within 1 m^2	23 (1.60, 204)	27 (2.02, 174)	33 (2.17, 174)
% log ground cover within 1 m^2	4 (0.62, 204)	5 (0.87, 174)	1 (0.18, 174)
% soil ground cover within 1m^2	2 (0.46, 204)	4 (0.87, 174)	2 (0.67, 174)
Surface temp. adj. for ambient temp. (°C)	26.9 (0.23, 80)	26.7 (0.19, 116)	-
Soil temp. adj. for ambient temp. (°C)	20.7 (0.33, 80)	20.0 (0.28, 115)	-
Surface humidty adj. for ambient humidity (%)	69.7 (0.63, 80)	68.4 (0.52, 117)	-
Solar rad. at snake adj. for max. radiation (lux)	3936 (1367.1, 78)	2816 (1130.6, 114)	-
Mean score on the first discriminant axis	-0.17 (0.07, 202)	-0.75 (0.09, 172)	0.93 (0.06, 174)
Mean score on the second discriminant axis	0.74 (0.08, 202)	-0.57 (0.08, 172)	-0.29 (0.06, 174)

conditions present at each random location at multiple times of day throughout the active season would have been impractical given our time and manpower resources.

To determine if Eastern Kingsnakes used habitat randomly with respect to structural features, 174 sites within the study area were randomly sampled for the same structural habitat variables as snake locations. These sites were sampled along transects randomly placed within each snake's activity range. Measurements were made every 10 m in small home ranges, and every 20 m in large home ranges. One snake (KS98.04) was primarily located within or near an abandoned railroad grade; thus, sampling in the manner described above would either bias locations to be similar only to the railroad grade (if the transect ran along the grade) or would exclude this important feature of the snake's activity range (if the transect ran orthogonal to the tracks). For this activity range, a random distance and bearing were taken from a point every 20 meters along the tracks, and these locations were sampled.

Multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) were used to examine differences among group centroids based upon all of the structural habitat variables and to identify specific variables that contributed most strongly to group separation (Blouin-Demers et al. 2005; Morrison 1990; Reinert 1984a, 1992). Analysis of variance (ANOVA) of discriminant scores was followed by Tukey's *a posteriori* comparison of means (Sokal and Rohlf 1995) to determine whether differences in the first and second discriminant functions existed among males, non-gravid females, and random locations (Reinert 1984b, 1992).

In using these statistical analyses, we assumed that snake locations were sampled randomly. In nature, it is likely impossible to obtain a random sample of organisms, especially in the case where individual organisms were repeatedly sampled. Secretive snakes such as Eastern Kingsnakes are difficult to find, so obtaining a large enough number of individuals to treat each snake as a single observation would be impossible. Because no single snake in this analysis accounted for a large proportion of the variation in data, each snake location was treated as an independent observation. This is a common practice in similar studies (e.g., Blouin-Demers et al. 2005; Reinert 1984a, 1992; Weatherhead and Charland 1985).

Analysis of covariance (ANCOVA) was performed to detect differences in climatic variables between male and female snake locations while adjusted for ambient conditions. The behavior (traveling, basking, or concealed) of the snake was recorded at each location event. These were then analyzed to determine general trends in Eastern Kingsnake behaviors and lifestyle. All statistical analyses were performed using SYSTAT (version 5.2 for Macintosh, SYSTAT, Inc, Evanston, IL).

Results

Nine Eastern Kingsnakes (5 males and 4 females) were monitored from 1996–1998, and each snake was tracked for at least 94 days per active season

(April–November). Three snakes were monitored over the course of two active seasons, whereas the other six snakes were monitored for one active season. This resulted in a total of 393 field observations (Table 2). For the three snakes that were tracked over two years, ANOVA comparisons showed that the values for movement parameters did not differ significantly from one year to the next. Consequently, the mean values derived from both years were used to avoid pseudoreplication.

The most obvious characteristic of Eastern Kingsnakes was their highly secretive nature. In 1996–1998, the snakes were found to spend 79% (308 out of 392 observations) of their time concealed under the surface cover (soil, leaf litter, sand, and logs). For the remaining 21% (84 out of 392 observations) of the observations, Eastern Kingsnakes were found to be actively traveling, basking, or otherwise exposed on the surface. The frequency of observation in each of these behavioral categories did not differ between males and females ($\chi^2_{s(2)} = 0.053$, P = 0.98).

Pearson product-moment correlations (Sokal and Rohlf 1995) showed no significant relationships between snout–vent length (SVL) of individuals and any measured movement parameter. Size of a snake did not strongly influence the extent of its movements (Table 2). For example, KS 98.06, the largest snake in the study (SVL = 122.3cm), had the smallest activity range (5.64 ha), whereas one of the other large snakes, KS98.05 (SVL = 93 cm), had a relatively large range (17.6 ha). KS98.04, a comparatively small snake (SVL = 65 cm), had a very large activity range (21.5 ha).

Student's t-tests showed no differences between males and non-gravid females in any movement parameter (Table 2), although sample sizes possibly limited our ability to detect small, but potentially meaningful, effects. Radiotelemetry clearly indicated that there was a strong tendency for the snakes to spend much of their time in relatively small proportions of their overall established home range. Harmonic meau analysis showed that, on average, 80% of the snakes' total activity was restricted to two to three core activity areas, which represented only 42% (on average) of each individual's total range area. On average, 50% of each snake's total activity was restricted to only 6.7% of the area of their total activity range. After establishing an activity range, Eastern Kingsnakes spent the entire season moving back and forth between a few core areas of activity, often revisiting an exact location multiple times. Activity ranges almost invariably included both the dry, upland macrohabitat complex, and the moist, lowland complex (Figs. 1a, b).

On average, snakes took 48 days to reach their maximum range length (S.E. = 10.54, n = 5; Fig. 2) during the 1998 active season. For any given snake, it typically required between 35 and 65 days of radiotracking to determine the maximum range length for the entire active season. Even for KS98.06, whose final range length (354.2 m) was established after 103 days, a range length of 340 m was attained after only 25 days (Fig. 2). Snakes with larger ranges took longer to establish them (Pearson r = 0.90, df = 4, P = 0.39; Fig. 2). The time it took to determine a snake's maximum range length was not related to the date

Table 2. Movement data for Eastern Kingsnakes radiotracked in the Pine Barrens of New Jersey in 1996–1998.

Snake number	Sex	Locations/ individual	Period monitored	Snout–vent length (mm)	Total distance (m)	Distance/ day (m)	Range length (m)	Convex polygon (ha)	Harmonic mean 95% isopleth (ha)	Harmonic mean 50% isopleth (ha)
KS98.02	F	44	6/8/98–11/5/98	882	4339	33.6	503	8.0	9.2	1.5
KS98.04	M	45	6/20/98–11/5/98	650	4521	32.5	784	18.0	21.5	2.0
KS98.05	F	41	7/4/98–11/5/98	930	5910	47.3	691	15.0	17.6	3.0
KS98.06	M	36	7/4/98–11/5/98	1223	2681	21.5	354	4.0	5.6	1.0
KS98.07	F	32	7/15/98–11/2/98	725	2564	23.1	546	4.0	5.3	0.0
KS97.03	M	25	5/1/97–11/18/97	1134	5952	37.0	1653	27.4	49.5	2.2
KS96.01	F	62	6/14/96–10/9/96; 4/14/97–9/15/97	915	5983	51.5	1335	28.2	35.7	5.7
KS96.02	M	59	6/18/96–10/25/96; 4/4/97–10/14/97	1010	6055	43.5	970	16.5	30.7	2.2
KS96.03	M	49	7/2/96–10/25/96; 3/14/97–10/18/97	930	3745	34.6	1068	26.2	33.0	1.1
Male Mean	-	-	-	989	4591	34	965	18.4	41.6	1.83
(SE)				(98.6)	(646.4)	(3.6)	(210.8)	(4.18)	(15.58)	(0.36)
Female Mean	-	-	-	863	4699	39	762	12.2	16.9	2.54
(SE)				(47.1)	(806.4)	(6.3)	(186.4)	(3.93)	(6.80)	(1.22)
Total Mean	-	-	-	933	4639	36	875	15.6	30.6	2.14
(SE)				(59.7)	(875.0)	(3.3)	(139.4)	(2.93)	(9.70)	(0.55)
$t_{s(7)}$	-	-	-	1.060	0.106	0.696	-0.704	-1.052	-1.325	0.618
(p)				(0.193)	(0.92)	(0.52)	(0.50)	(0.34)	(0.23)	(0.56)

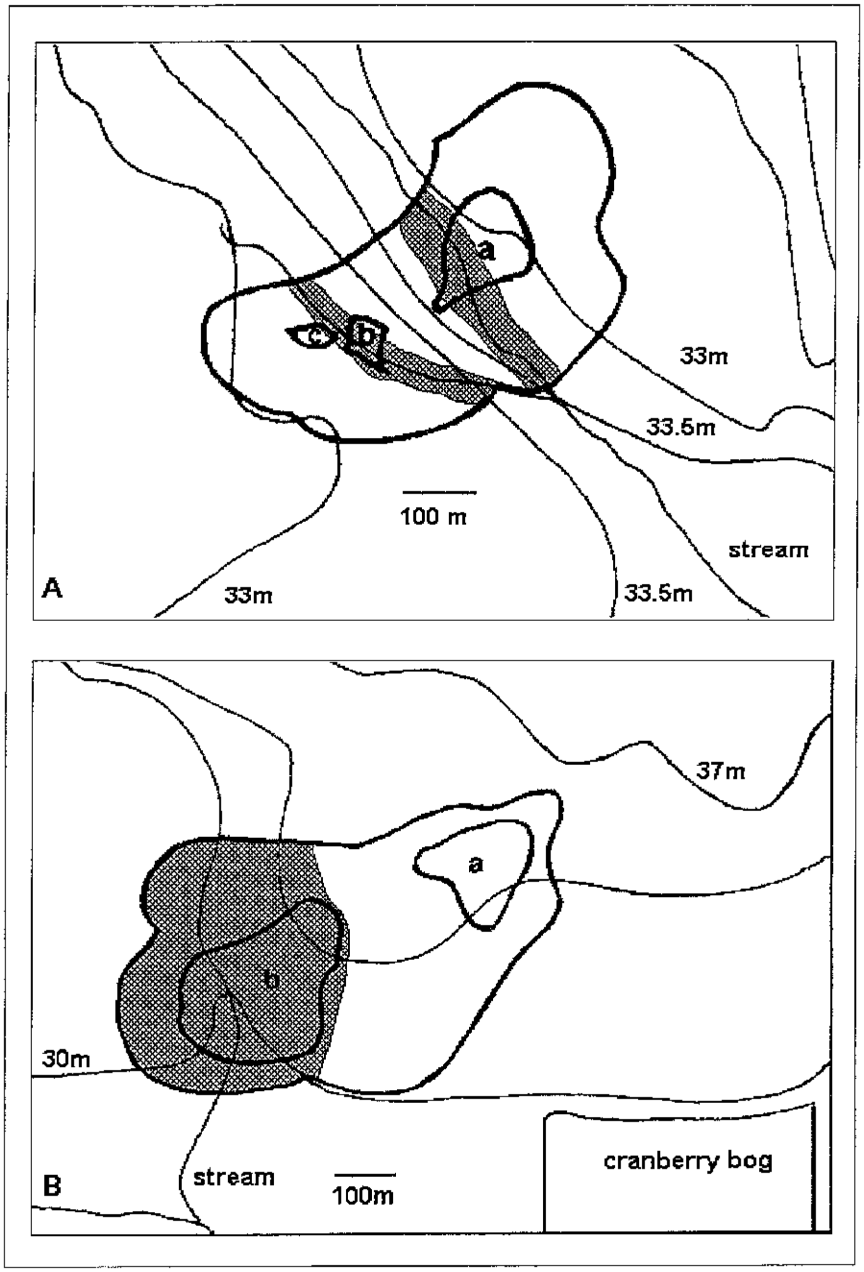

Figure 1. Representative activity ranges of *Lampropeltis g. getula* (Eastern Kingsnake) in the New Jersey Pinelands. Note that snakes commonly frequented both dry upland and moist lowland habitats. A. Activity range of KS98.02 (female). The large enclosed area represents the 95% isopleth area, while the smaller enclosed areas represent 80% isopleths. Stippled areas represent wetland regions within the snake's home range. a: 6/8–6/11 (followed by a recapture due to a failed transmitter); 7/20; 7/29; 8/2;

of initial observation. For example, KS98.07 was released on July 4 (Table 2), and established its maximum range length by August 25, forty days later (Fig. 2). Contrast these data with that of KS98.04, who was released on June 20 (Table 2) and did not establish its maximum range length until September 1, seventy days later (Fig. 2). KS98.02 established its maximum range length by the end of June, before KS98.06 entered the study (July 4); nevertheless, both of these snakes had similar range lengths. These results indicate that once an Eastern Kingsnake established its range, it repeatedly traversed that range for the rest of the season.

Eastern Kingsnakes frequented diverse macrohabitat types in both upland and wetland areas (Figs. 1 and 3). In the wetlands, they were often located in dense shrub aggregations within bogs, partially washed-out root systems in cedar and maple swamps, and areas under logs and sphagnum moss. In the uplands, the snakes were often concealed within the leaf litter

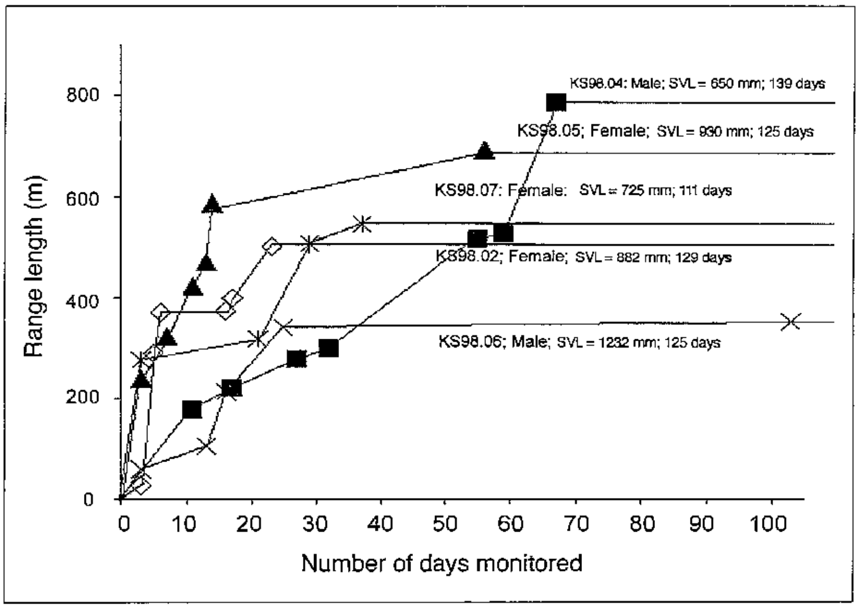

Figure 2. Number of days required to establish maximum range lengths of 5 Eastern Kingsnakes in 1998. Open diamonds: KS98.02 (female); Solid Squares: KS98.04 (male); Solid triangles: KS98.05 (female); X: KS98.06 (male); Asterisk: KS98.07 (female). Snout–vent lengths and total days monitored are listed after each snake ID.

Figure 1, continued: 8/7–8/20; 8/24–8/26; 9/7–9/24; 10/18–hibernation. b: 7/4–7/6; 7/18; 7/24–7/27; 8/22; 10/8. c: 7/8–7/15. B. Activity range of KS 98.05 (female). The large enclosed area represents the 95% isopleth area, while the smaller enclosed areas represent 80% isopleth areas. Stippled areas represent wetland regions within the snake's home range. A sand road separates the wetland area from the dry, upland area within the snake's home range. a: 7/4–7/6; 7/17–7/24; 8/10–8/16; 9/2–9/10; 10/12–10/15. b: 7/9–7/15; 7/27; 7/31–8/2; 8/18–8/24; 8/30; 9/14–10/5.

of scrub oaks, within the root systems of shrubs, and under logs. MANOVA indicated that group centroids of 14 structural habitat variables for males, non-gravid females, and randomly sampled habitat locations (Table 1, Fig. 4) were different (Wilks' lambda = 0.511; df = 28, 1066; $P < 0.01$). DFA showed these differences were primarily related to microhabitat structure. The first discriminant axis was most strongly associated with leaf-litter depth ($r = -0.449$) and foliage density from 0–1 m ($r = -0.444$), and described a structural environmental gradient that ranged from habitats with deep litter depth and high foliage density to sites with shallow litter and sparse foliage (Fig. 4). The second discriminant axis was most highly correlated with the distance to the nearest log ($r = 0.518$) as well as the diameter of the nearest log ($r = 0.433$), and separated sites that were close to narrow logs to sites that were far from thick logs. There was also a negative correlation between foliage density from 0–1 m ($r = -0.338$) and foliage density from 1–2 m ($r = -0.304$) on this axis (Fig. 4). Independent samples t-tests showed that all of the variables that were strongly associated with either the first or second discriminant function differed between males and females (all $P < 0.05$).

Because microhabitat features seemed to be the most important determinants of Eastern Kingsnake habitat selection, we also performed multivariate analyses while considering only microhabitat variables (foliage densities, litter depth, and ground cover by vegetation, leaf litter, and logs). MANOVA indicated that group centroids of these 6 microhabitat variables for males,

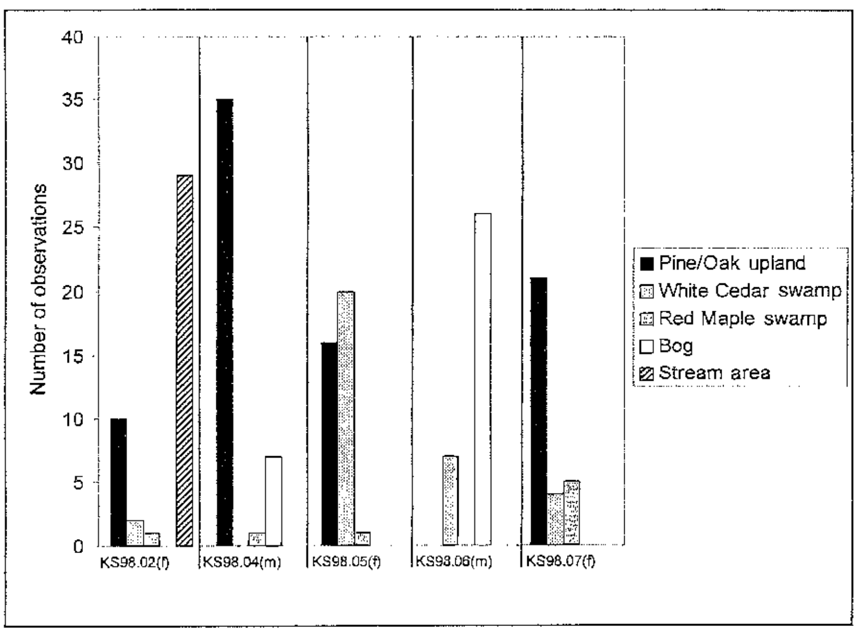

Figure 3. Number of observations of Eastern Kingsnakes tracked in 1998 in each macrohabitat type available in the New Jersey Pine Barrens (see McCormick 1979).

females, and random locations differed significantly (Wilks' lambda = 0.675; df = 12, 1090; $P < 0.01$), and correlations between variables and discriminant axes followed the same pattern as with the more complete analysis. ANOVA of these discriminant scores followed by Tukey's a posteriori comparison of means showed that for the first discriminant axis, there were significant differences among male locations, non-gravid female locations, and random locations ($F_{s(2, 550)} = 98.3$, $P < 0.01$). Both males and females selected sites with deeper leaf litter and greater shrub density than found at random sites. For the second discriminant axis, male locations differed from both female and random locations; however, there was no difference between female and random locations ($F_{s(2, 550)} = 25.3$, $P < 0.01$). Females were more likely than males to be located closer to narrow logs, deep litter, and high foliage density.

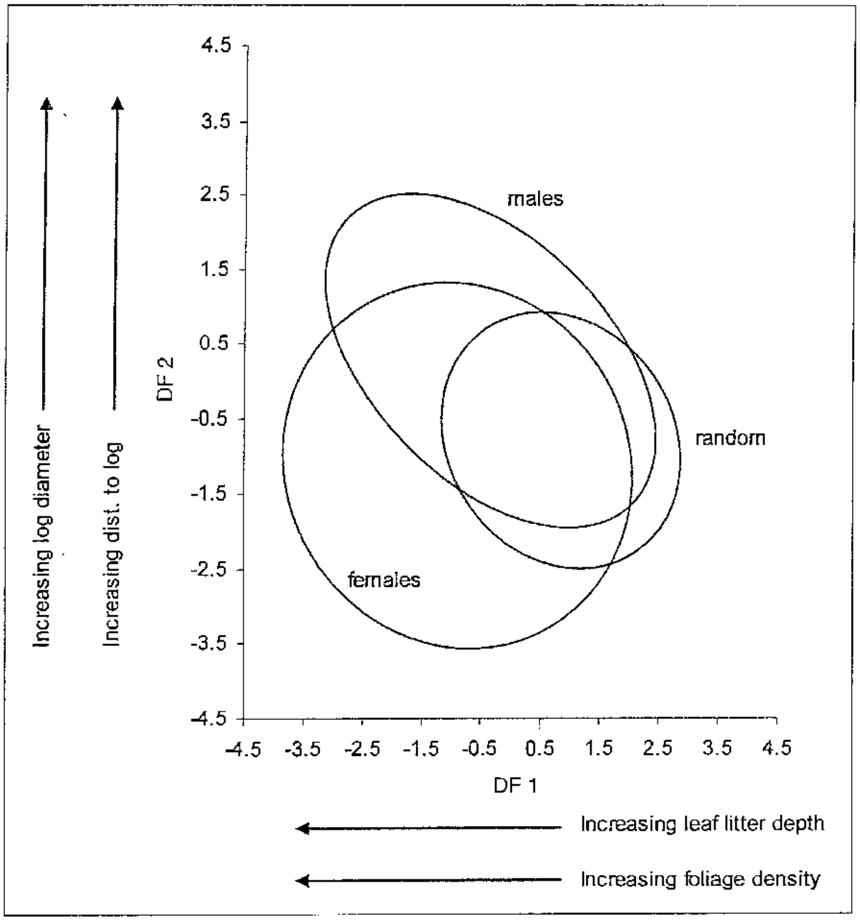

Figure 4. Discriminant-function plot of male, non-gravid female, and random group centroids. Highly correlated structural habitat variables are depicted adjacent to each discrminant axis. Ninety-five percent confidence ellipses of items shown for all three groups.

Males, on the other hand, were more generally at sites with relatively shallower litter and lower foliage density than female sites (Table 1).

Analysis of covariance revealed that climate variables did not differ between male and female snake locations. As required for ANCOVA, all covariates demonstrated a significant linear relationship with test variables (Sokal and Rohlf 1995).

These analyses suggest that Eastern Kingsnakes actively selected sites largely on the basis of structural microhabitat features. Within the wide variety of habitats occupied by this species, the specimens in this study preferred sites that were characterized by deeper leaf litter and denser shrub-layer foliage than generally available in the surrounding environment.

Except in the cases of transmitter failure (1 snake) or mortality (1 snake), Eastern Kingsnakes were tracked until they entered hibernation. All snakes hibernated within or beneath root systems of trees or shrubs in either wetland areas (e.g., red maple swamps) or in areas directly adjacent to a wetland swale. One snake was excavated from its hibernaculum, and was found to be in water beneath the root system of a shrub. Many snakes hibernated in areas that had experienced fire within the past several years. Several snakes hibernated in areas that were not contained within their summer activity range. Several Eastern Kingsnakes were caught or observed in the vicinity of hibernacula of study snakes, suggesting the possibility of communal denning.

Discussion

Considering the secretive, highly fossorial behavior displayed by Eastern Kingsnakes, it is not surprising that so little is known about the natural history of this widespread reptile. Our results suggest that Eastern Kingsnakes select their habitat non-randomly based predominantly upon microhabitat structure that afforded them opportunity for concealment. Of the variables measured, the most important in characterizing snake locations were parameters such as leaf-litter depth and shrub-layer foliage density. On average, snake locations had a litter depth of nearly 2 cm, whereas randomly selected locations within their home ranges had only 1 cm of litter. Foliage density in the proximity of snakes was about twice that of random locations as well. These associations with deep litter and dense foliage are not likely to be explained simply by a general preference for forest macrohabitats because canopy cover and distance to the nearest over- and understory trees were not associated with Eastern Kingsnake habitat selection. Instead, snakes were often located in relatively open areas; however, within those open areas, they selected microhabitats under bushes and/or within leaf litter. Females tended to prefer sites with even deeper litter, denser foliage, and closer proximity to small logs than males. Given that we tracked non-gravid females, we had no a priori expectation that males and females would differ in any parameter we measured.

Along the two primary discriminant functions, there was more variation among snake locations than among randomly sampled locations. Thus, the snakes did not select the "typical" habitat available, but instead actively sought out sites that were rare enough that they were much less likely to be sampled as a random location. Perhaps there was more variability among these rare microhabitats because the snakes were using some threshold criteria for habitat selection. For example, a microhabitat with 2 cm of litter might be equally as acceptable as a microhabitat with 5 cm of litter, but the common microhabitat, with less than 1 cm of litter, was not preferred by the snakes.

It is possible that Eastern Kingsnakes are primarily secretive only during the day, and at night more commonly come out from under cover. Anecdotally, Eastern Kingsnakes are considered to be mainly diurnal and possibly crepuscular (Hulse et al. 2001, Krysko 2002, Mitchell 1994). We observed snakes active or basking in 18% of our observations, supporting the notion that the daytime is an important part of Kingsnakes' activity period. Furthermore, when we located snakes later in the afternoon, they were nearly always concealed. Out of 116 locations between 3:00 pm and 9:00 pm, snakes were concealed 101 (88%) times. Of 58 locations after 6:00 pm, snakes were concealed 53 (91%) times. Nevertheless, further study examining the role of nocturnal activity in these snakes may prove usefnl, particularly in the warmest months of the active period.

Our study also demonstrated that Eastern Kingsnakes are macrohabitat generalists, occupying suitable sites within a variety of both upland and lowland communities. Previous sources suggested that the prinicipal habitat preferred by Eastern Kingsnakes was characterized by the proximity of water. For example, Kauffeld (1957), who had extensive field experience with this species, stated that "[Eastern Kingsnakes] are never found far from water-moisture in some form: stream, swamp, bog, sinkholes, canals, or drainage and irrigation ditches. Despite statements to the contrary, they are never found in dry pinewoods." Conant and Collins (1998) consider the species to be "chiefly terrestrial," but indicated that it had "a distinct liking for streambanks and the borders of swamps." The current study showed that Eastern Kingsnakes might, in fact, spend a greater proportion of their time than previously assumed in dry, upland forests dominated by pine and oak. Conseqnently, ample opportnnity for concealment or the presence of subterranean foraging opportunities might be more important than macrohabitat structure in determining suitable habitat. It is worth noting that this study area is at the northeastern limit of the Eastern Kingsnake's range, and geographic variation in habitat preference remains a possibility. On the other hand, being a macrohabitat generalist may contribute to the Eastern Kingsnake's wide geographic distribution. These hypotheses remain to be tested. While the snakes in this study were active in a variety of habitats, only wetlands or areas adjacent to wetlands provided sources of hibernacula. All individnals hibernated in moist areas, typically beneath trees, stumps, or dense shrubs.

The Eastern Kingsnakes established their annual activity range relatively quickly, as evidenced by the relatively short amount of time it took snakes to reach their maximum range length, relative to their total activity period. Once this range was established, individuals continually revisited core activity areas, and even exact locations, throughout the active season. The maximum range lengths we observed were unrelated to the time monitoring began. Consequently, the activity patterns we observed are probably consistent throughout the active period of these snakes, rather than exhibiting seasonal variation. Given that the Eastern Kingsnakes in this study repeatedly moved among a few core areas, the snakes that were monitored later in the active season probably had already established their maximum range length, and we observed them during their second or third pass through their home range.

The snakes in this study often showed high levels of site fidelity within their core activity areas. Many snakes were repeatedly located in the same hole or within the root system of the same plant. Snakes tracked for two consecutive seasons could sometimes be found at the precise location of the previous season within a few days of the date on which they were found there the previous year. This pattern is similar to movement patterns demonstrated by *Elaphe o. obsoleta* Say (Black Rat Snake) in Maryland, which showed an affinity for specific locations within core activity areas that were revisited repeatedly (Durner and Gates 1993). Similar results were obtained for *Hoplocephalus bungaroides* Schlegel (Broad-headed Snakes; Webb and Shine 1997) and *Crotalus durissus unicolor* Klauber (Aruba Island Rattlesnake; Reinert et al., in press). In an extreme case of site fidelity, *Coluber viridiflavus* Lacepede (Dark Green Snake) moved in a series of loops throughout their active season that radiated from a single den that also served as a hibernaculum (Ciofi and Chelazzi 1991). However, few snakes seem to demonstrate such fidelity to any particular site within their home range. Many rattlesnakes (e.g., *Crotalus viridis* Rafinesque [Western Rattlesnake], *Crotalus horridus* Linnaeus [Timber Rattlesnake], and *Crotalus cerastes* Hallowell [Desert Sidewinder]) spend most of their active season establishing their range and usually move in a large, looping pattern without revisiting previous locations (King and Duvall 1990, Reinert and Zappalorti 1988, Secor 1994). In direct contrast, Mills et al. (1995) reported that *Nerodia taxispilota* Holbrook (Brown Water Snakes) showed no apparent fidelity or directionality to their movements.

Interestingly, snakes tracked in 1996 and 1997 had larger ranges than those tracked in 1998. A notable observation is that most of the snakes tracked in the first two years hibernated some distance from their core areas (thus inflating the overall range size), whereas those tracked in 1998 hibernated in close proximity to their core areas. While total range sizes differed in these two groups of snakes, core-area size did not, and neither did the total distance moved. Snakes tracked in the first two years used the same amount of core area as snakes tracked in the third year, and snakes with relatively small ranges moved just as much within those ranges as snakes with larger ranges. These observations lend further support to the idea that Eastern Kingsnakes prefer very specific locations within their home range, and the total size of the home range may reflect the abundance of sites with preferred microhabitats.

When snakes were concealed, particularly in wetland areas, they were often concealed within root systems of trees and shrubs, or in tunnel networks, rather than being concealed within a layer of leaf litter. Selection of concealed microhabitat in Eastern Kingsnakes may play a role in both predator avoidance and prey capture. Often, a snake's core activity area was found to include tunnel networks that may have contained small mammals or other snakes, which Easteru Kingsnakes are known to eat (Conant and Collins 1998, Ernst and Ernst 2003). Specifically *Diadophis punctatus* Linnaeus (Ringneck Snake), *Crotalus horridus* Linnaeus (Timber Rattlesnake), *Opheodrys aestivus* Linnaeus (Rough Green Snake), *Thamnophis sauritus* Linnaeus (Eastern Ribbon Snake), *Lampropeltis triangulum* Lacepede (Milk Snake), *Elaphe guttata* Linnaeus (Corn Snake), *Pituophis melanoleucus* Daudin (Eastern Pine Snake), and *Nerodia sipedon* Liunaeus (Northern Water Snake) were observed by us in the types of habitats occupied by Eastern Kingsnakes. We also observed small mammals such as *Clethrionomys gapperi* Vigors (red-backed vole), *Synaptomys cooperi* Baird (southern bog lemming), and *Peromyscus leucopus* Rafinesque (white-footed mouse). Because the Eastern Kingsnake is also a potential prey item (one snake was killed and eaten by a skunk during the course of this study), being secretive may help them to avoid predation. Eastern Kingsnakes may also be regularly concealed as a by-product of selecting cooler, subterranean microclimates. A more direct examination of these hypotheses is necessary before any conclusions can be drawn regarding the factors responsible for the demonstrated microhabitat preference of Eastern Kingsnakes, and in particular, why females and males differed somewhat in their microhabitat preference. Radiotelemetry enabled us to locate the snakes and quantify their habitat conditions, but the study was limited largely to surface features. Consequently, subterranean aspects of Eastern Kingsnake habitat remain poorly understood, and such features may be paramount in creating a preferred site.

Considering their broad diet (Ernst and Ernst 2003) and wide range of macrohabitat types occupied, Eastern Kingsnakes may play an important role in the structure and energy flow within a broad range of ecological communities of the New Jersey Pine Barrens. Use of habitat and movement information will hopefully lead to a better understanding of the ecological role of these animals in their environments. Currently, this species is considered a species of special concern by the New Jersey Department of Environmental Protection (NJDEP 2005) due to their possibility of becoming threatened as a result of habitat loss or modification and because little is known about the status of their populations. Our research suggests that Eastern Kingsnake conservation intitiatives should take into account both wetland and upland habitats. Wetlands and their immediate surroundings are particularly important areas for overwinter survival of Eastern Kingsnakes.

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