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Ecology of the Eastern Kingsnake (Lampropeltis getula) at Rainey Slough, Florida: A Vanished Eden

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ABSTRACT: Eastern Kingsnakes (Lampropeltis getula) are an important component and predator in herpetofaunal communities, but many Eastern Kingsnake populations have declined precipitously in the last few decades, particularly in the southeastern United States. Here, we describe an intensive capture–mark–recapture study of L. getula conducted during 1974–1978 in a canal bank–Water Hyacinth (Eichhornia crassipes) community at Rainey Slough in southern Florida, where annual capture probabilities of adults ranged from 0.662–0.787. Population size and structure, seasonal activity, movements, microhabitat use, behavior, thermal ecology, and predator–prey relationships are described. At this site kingsnakes were susceptible to capture mostly in winter and spring, were diurnal, used rodent (Sigmodon hispidus) burrows on canal banks as nocturnal retreats, and emerged from burrows on 13–26% of the sampling days. Overlap of burrow use by both sexes was extensive with no evidence of territoriality. Kingsnakes readily entered the Water Hyacinths to bask, pursue mates, and forage. At Rainey Slough only snakes were detected in the diet of kingsnakes. Concurrent sampling of potential snake prey in the hyacinths and on canal banks revealed 10 species that varied in use of the two sampled habitats and in body size. A range-wide analysis confirmed that in descending order snakes, reptile eggs, and lizards dominate the diet of L. getula in Florida (94.8%) and remain important prey types elsewhere (80.2%). At Rainey Slough the density of six species of semiaquatic snakes in Water Hyacinths averaged 3534 individuals/ha with a mean annual biomass of 135.8 kg/ha, and kingsnake biomass was only 2.2–3.9% of prey snake biomass. We estimated that the kingsnake population consumed 36.82–63.58 kg/yr, or about 10.0–17.2% of the standing crop of snakes in the Water Hyacinth community. Adult male L. getula lost on average 39.3% of their body mass associated with the spring reproductive season, whereas females lost only 3.4% in the same period. Body condition indices for both sexes improved substantially thereafter. In follow-up surveys at Rainey Slough during 2006–2010 no kingsnakes were found. Semiaquatic snake densities in the Water Hyacinths were 77.2% lower (807.4/ha) than in the 1970s and consisted of only three species. Compared to the enigmatic declines and extirpation of L. getula populations elsewhere, at Rainey Slough the primary cause likely was unsustainable mortality from road reconstruction and paving in the winter–spring of 1979 and subsequent roadkill. Other potentially causative agents of extirpation of L. getula in this system are discussed.

Key words: Body condition index; Community ecology; Extirpation; Predator–prey relationships; Road mortality; Snakes; Water Hyacinth community

Kingsnakes of the genus Lampropeltis are an important component of the snake faunas of North, Middle and northern South America. The diversity of species, body sizes, colors and patterns including mimicry with New World coral snakes, activity patterns, diet and foraging behavior, and ecology of kingsnakes has long attracted the attention of an equally diverse array of herpetologists; indeed, the first captive snake of many budding North American herpetologists was a kingsnake. Although the taxonomy of this group has been relatively stable over the last 80 yr (Blanchard 1921; 11 recognized species), the recent application of molecular phylogenetics suggests at least 21 extant species of Lampropeltis (Ruane et al. 2014), with five species in the transcontinental L. getula complex (Pyron and Burbrink 2009a).

Recognition of the taxonomic and niche conservatism or divergence in a species complex such as Lampropeltis getula (Pyron and Burbrink 2009b) suggests that natural selection on populations in ecologically different habitats may affect many aspects of the life histories of these species. For example, although kingsnakes are anatomically adapted to eat elongate prey such as snakes (Jackson et al. 2004), they also consume a variety of other types of prey (Rodríguez-Robles and de Jesús-Escobar 1999) that likely vary ontogenetically, seasonally, and by habitat and species (Greene 1997). Within this species complex, the ecology of the Eastern Kingsnake (L. getula) has received the most attention in recent years, yet there is not a single estimate of the density or biomass of this species or their prey, and many other aspects of their biology remain poorly known. This dearth of information is particularly critical in Florida, USA, where many populations are in serious decline (see below) and the species is phenotypically (historically, five named subspecies) and genetically diverse (Krysko and Judd 2006), and as such, may warrant distinct population status (US Department of the Interior 1996) listing under the US Endangered Species Act.

This study summarizes 3 yr of intensive capture–mark–recapture (CMR) work on a population of Lampropeltis getula inhabiting a canal bank–Water Hyacinth (Eichhornia crassipes) community in southern Florida in the 1970s where we also had extensive data on the density and biomass of their primary prey, other snakes (Godley 1980, 1982). We provide a statistical analysis of the size and structure of this population of kingsnakes, their seasonal activity patterns, microhabitat use, movements, behavior and thermal ecology, and predator–prey relationships. Follow-up surveys conducted four decades later (2006–2010) confirmed that this L. getula population has been extirpated, as have many others in the southeastern United States (Krysko and Smith 2005; Winne et al. 2007; Stapleton et al. 2008; Steen et al. 2014). Publishing these data provides historical context to the biology of L. getula and serves as a benchmark to evaluate more recent studies of this species. Finally, we close by speculating why Eastern Kingsnakes may have been
extirpated from our study site and how it may differ in important ways from other such sites.

**Materials and Methods**

**Study Area**

We studied *Lampropeltis getula* and their prey during 1974–1978 with similar follow-up surveys during 2006–2010 in a canal bank–Water Hyacinth community at Rainey Slough, Glades County, Florida (26.9844°N, 81.4919°W; datum = WGS84). Rainey Slough is a 24-km ribbon of seasonally flooded (June–October in most years) wet prairies and marshes that drain southeast into Fisheating Creek, eventually emptying into the western side of Lake Okeechobee. During the initial time of this study, Live Oak (*Quercus virginiana*)–Cabbage Palm (*Sabal palmetto*) hammocks bordered the slough and pine flatwoods formed the predominant habitat in the uplands. The site consisted of two hyacinth-choked canals on either side of an elevated, unpaved roadbed (State Route [S.R.] 731) oriented in a north–south direction. The canals (1.1 km in total length, 2.7 ha in total area) were connected below a 43-m wooden bridge that crossed Rainey Slough near its center and was used to divide the study site into five areas: northeast, northwest, southeast, and southwest canals, and bridge. The road was 6.1 m in width and bordered by a level, approximately 4-m shoulder that was mowed several times each year. The sides of the canals averaged 2:1 (horizontal:vertical) in slope and varied 2–3 m in width, depending on location and water level. The side slopes were not mowed regularly and consisted primarily of herbaceous vegetation and occasional shrubs. The vegetated uplands on either side of the roadbed adjacent to the canals totaled 0.8 ha. Winter frosts first killed back aboveground vegetation in late December of 1976 and 1977, but not until mid-February of 1978. By June of each year, vegetation on the canal banks had regrown, making observations difficult until the next freeze and dieback. For our initial study period we used weather data from records maintained at the Archbold Biological Station (ABS), located 23.8 km NNE of Rainey Slough.

Immediately following the 1974–1978 fieldwork, S.R. 731 in Glades County was paved, and by May 1979 all wooden bridges on this roadway were replaced with concrete structures, including the one at Rainey Slough (J.S. Godley, personal observation). When examined in June 1981 the northeast and southeast canals had been re-excavated and the extracted material deposited along the southeast and southwest canal banks, smothering the existing vegetation and any burrows.

When we resurveyed Rainey Slough in 2006–2010, the hydrology and marshes seemed intact, although Carolina Willow (*Salix caroliniana*) had increased in density. Water Hyacinths were common but no longer formed a monoculture in the canals. The mat-forming exotic Cuban Bulrush (*Scirpus cubensis*) was dominant on the surface, presumably as a result of repeated herbicide treatments of Water Hyacinths that also occurred in the 1970s. Although the Live Oak–Cabbage Palm hammock fringing Rainey Slough remained largely intact, much of the surrounding flatwoods had been converted to pine plantations to the north and improved pasturelands to the south. Comparative aerial and ground photos of the study site in the two major sampling periods are provided in the Supplemental Material.

**Field Sampling**

The herpetofauna of the Rainey Slough Water Hyacinth community was quantitatively sampled during 21 events (1–3 d each) during November 1974–April 1977, primarily with a 0.56-m² hyacinth sieve described by Godley (1984). In addition, the canal banks at Rainey Slough were systematically searched for snakes on 38 d (14 of which were contemporaneous with hyacinth sampling) during November 1975–May 1978. Systematic searches involved 1–4 researchers slowly walking the length of each canal bank to detect snakes, their burrows, and shed skins with an attempt to search each canal bank equally. Sampling of Water Hyacinths and canal banks primarily occurred during daytime. Detailed descriptions of the study area and hyacinth sampling methods were provided elsewhere (Godley 1980, 1984).

In general, *Lampropeltis getula* and other reptiles captured during searches of the canal banks were sexed, measured (snout–vent length [SVL]; total body length [TBL]), weighed to the nearest gram, permanently marked by scale-clipping (Blanchard and Finster 1933), and released at the capture location on the same day or on the next visit to the site (58 of 62 kingsnakes released ≤1 d of capture). Most reptiles collected in hyacinth samples also were measured and weighed, but they were preserved for future study. Because only 2.9% of the total hyacinth habitat was sampled during 1974–1977, effects on the kingsnake prey base (mostly other snakes, see below) were judged to be minimal. To obtain estimates of fasting body mass and to identify prey, we forced all individual *L. getula* with detectable food in their stomachs to regurgitate in the field or allowed each to defecate in the laboratory prior to release (Fitch 1987). Cloacal body temperature (Tₜ), shaded substrate temperature (Tₛ), ambient temperature (Tₐ, measured 3 cm above substrate) and burrow temperature (Tₜ) were taken with a Schultheis quick-reading thermometer. Other frequently recorded data included date and time of capture (standardized to Eastern Standard Time), location on canal bank, distance from known burrow(s), activity (emerging from or entering into burrow, basking, moving, courtship behavior), percentage of body exposed from cover, and stage of shed cycle (shedding, clear). To track thermal regimes and hydrological conditions at Rainey Slough more closely, certain data were combined into seasons (winter = December, January, and February; spring = March, April, and May; summer = June, July, and August; fall = September, October, and November) and analyzed accordingly. Total search time, observations without capture, shed skins, and dead-on-road (DOR) specimens also were noted.

Kingsnakes and other snake species frequently used rodent burrows on the canal banks at Rainey Slough as refugia. We excavated a haphazard subset of located burrows with shovels and by hand in order to (1) collect snakes that were observed in or escaped down burrows, (2) map the topology of burrow systems, (3) identify the species that likely constructed the burrows, and (4) estimate the frequency of use of burrows by snakes.

We conducted follow-up surveys of Rainey Slough four decades later on seven total days in February and March
2006, September 2007, March 2008, and February 2010. These surveys employed identical systematic searches of the canal banks for snakes by 1–6 individuals on all sampling dates. We also quantitatively sampled the Water Hyacinth community on four dates in March of 2006 and 2008 with a bag seine that sampled 4.55 m$^2$ of hyacinths when it was stretched horizontally beneath the water.

Data Analysis

We used CMR methods to estimate annual abundance and survival of kingsnakes. We used Jolly–Seber open population mark–recapture models to estimate annual abundance, survival, recruitment, and population growth rates of *Lampropeltis getula* using Bayesian methods with data augmentation (Royle et al. 2007; Kéry and Schaub 2011). We defined annual study years to include only surveys conducted 10 October–15 May of 1975–1976, 1976–1977, and 1977–1978, when 59 of 61 *L. getula* captures occurred. All individual *L. getula* ($n = 34$) were captured one or more times in this period. Closed population models fitted to data from individual study years indicated that a model with constant capture probabilities within years received stronger support than models with time effects, behavioral response, individual heterogeneity, or effects of temperature, length, or sex on capture probability. Preliminary Cormack–Jolly–Seber models (Nichols 2005; Kéry and Schaub 2011) also did not indicate any effects of sex or size on apparent survival probability. We therefore used a robust-design Jolly–Seber model with daily capture probability constant within study years. We fitted models with all combinations of daily capture probability ($p$) constant across years or varying among years and apparent survival ($\phi$) constant across years or varying among years. The superpopulation parameterization of the model we used required that recruitment ($\gamma$) varied among years (Royle and Dorazio 2008; Halstead et al. 2011; Kéry and Schaub 2011). The four models we evaluated were $p \gamma \phi$, $p \gamma \phi \gamma$, $p \gamma \phi$, and $p \gamma \phi$.

For each model, we augmented the capture histories of observed individuals with 100 all-zero capture histories that represented a mixture of unobserved individuals and pseudoindividuals that were not present on the site. This approach is analogous to determining site occupancy (MacKenzie et al. 2002). We placed a uniform (0, 1) prior on $p$ and $\phi$ and a Dirichlet (1, 1, 1) prior on $\gamma$. We examined goodness-of-fit using the posterior predictive distribution and a Bayesian $P$-value (Gelman et al. 1996, 2004; Kéry 2010; Kéry and Schaub 2011) and determined the best-fit model using the deviance information criterion, which is interpreted in the same manner as Akaike’s information criterion (AIC; Spiegelhalter et al. 2002). We ran all models using Markov chain Monte Carlo (MCMC) methods as implemented in JAGS v3.4.0 (Plummer 2014) through R v3.2.1 (R Core Team 2015) using the package runjags (Denwood 2016). We ran all models using five chains of 400,000 iterations each, after a burn-in of 10,000 iterations. We thinned the output by a factor of 20, so posterior inference was based on a sample of 100,000 iterations from the stationary posterior distribution. The minimum effective sample size for any parameter was 28,286. We assessed convergence with history plots and the Gelman–Rubin statistic (Gelman and Rubin 1992), and observed no evidence for lack of convergence ($\hat{R} < 1.002$ for all monitored parameters).

We used an exact binomial test to determine if the sex ratio of *Lampropeltis getula* differed from 1:1, and an unequal variances $t$-test to examine sexual size dimorphism in SVL and in body mass. We examined assumptions of normality for the $t$-test with visual examination of boxplots and kernel density plots, and observed no obvious deviations from a normal distribution. We examined the spatial distribution of *L. getula* among the four canal banks with a log-likelihood test of independence, and the probability of *L. getula* occurrence on east vs. west banks and north vs. south banks using a binomial test. To determine if differences in $T_b$ were related to sex, time of day, or behavior, we used linear mixed models with individual as a random effect to account for multiple observations of the same individuals and $T_b$ as a covariate to control for differences in substrate temperature among observations. We used $T_a$, rather than $T_b$, as a covariate because individuals were usually in contact with the substrate and $T_b$ was more strongly correlated with $T_a$ than was $T_a$. $T_a$ and $T_b$ were also correlated ($r = 0.77, P < 0.001$), and it seemed unlikely that using $T_a$ rather than $T_b$ as a covariate would alter our results. We also used linear mixed models to examine variation in distance moved between subsequent observations and rate of movement between males and females, and by size (SVL). We examined changes in body mass through winter–spring of study years by calculating the percentage of mass change per day for each individual using the first and last mass measurements within the study year (10 October–15 April) and fitting linear models for an effect of sex and year on the percentage of mass change per day. To examine body condition, we calculated a body condition index (BCI) as $\text{BCI} = (\text{body mass}/\text{SVL}^3) \times 10^3$ (Winne et al. 2007) and examined the BCI of individuals using linear mixed models with individual as a random effect. We also examined the change in BCI of individuals during study years using linear models. We plotted Pearson residuals against fitted values to examine evidence for heteroscedasticity and nonlinearity in the residuals for all fitted linear models and linear mixed models and used AICc (AIC corrected for small sample bias; Burnham and Anderson 2002) to evaluate the strength of evidence for different linear models (hypotheses) within each model set.

Only other snake species were detected as prey of *Lampropeltis getula* at Rainey Slough. We calculated densities of potential snake prey at Rainey Slough by determining the probability of capturing an individual in a single dip of the hyacinth sieve with a binomial test of proportions. During the spring droughts of 1975 and 1977 when little surface water existed, we sampled potential prey by removing hyacinths from belt transects (see Godley 1980 for details). The 107 m$^2$ of transect data were converted to equivalent dips and combined with 687.3 m$^2$ of hyacinth sieve data to evaluate seasonal changes in prey densities.

Based on our experience with Eastern Kingsnakes, we hypothesized that the diet of *Lampropeltis getula* may vary geographically and be related to local variation in relative prey availability, but that snakes are the primary prey type throughout the range of the species. To test this, we used our data from Rainey Slough, summarized the published literature (excluding duplicate references and prey of captive
snakes), obtained reliable unpublished data, and dissected 29 wild-caught kingsnakes from Florida that had prey remains in their digestive tracts (identified to lowest possible taxon) based on X-rays of 376 specimens from the Florida Museum of Natural History (FLMNH) and the U.S. National Museum of Natural History (USNM). In cases where only snake scales were detected, we assumed they represented a single individual unless otherwise apparent (e.g., smooth and keeled scales in one kingsnake). To minimize bias in our analysis, we excluded published studies of bird nests that used remote videos or cameras to detect predation for the following reasons: (1) other prey types of kingsnakes rarely were monitored with remote devices compared to 918 bird nests, (2) the two bird nest studies within the range of L. getula (Staller et al. 2005; Ellis-Felege et al. 2012) did not report the number of snake predation events attributable to only kingsnakes, and (3) some individual kingsnakes likely depredated more than one monitored nest.

Because the diet of Lampropeltis getula may vary geographically and we had specific interest in kingsnakes from Florida, we examined differences in the number of individual snakes containing prey of different taxonomic and life-stage categories (turtle eggs, snakes, lizards, squamate eggs, mammals, bird eggs or nestlings, and other) in Florida vs. the remainder of their range using a Poisson analysis of variance (ANOVA) analyzed in a Bayesian framework (Kruschke 2015). We used a Bayesian analysis of this model because it allowed simple calculations of derived quantities with appropriate propagation of error (Link and Barker 2010). We used vague normal priors with a mean of zero for coefficients, and hierarchical gamma priors for the standard deviations of the normal distributions (Kruschke 2015). We also examined ontogenetic changes in prey category for kingsnakes using Bayesian random effects ANOVA (Kéry 2010), with individual L. getula mass or SVL as the response variable and prey category as the predictor variable. For this analysis we used vague priors: normal (mean = 391, SD = 411) prior for the grand mean mass, normal (99, 39) for the grand mean SVL, and uniform (0, 1000) priors for all standard deviations.

As Eastern Kingsnakes grow in body size, they may exhibit one of two patterns found in snakes with regard to the lower limit of prey size (Arnold 1993): (1) an ontogenetic shift where small prey are deleted from the diet or (2) an ontogenetic telescope where larger kingsnakes continue to consume small prey items. We examined evidence for ontogenetic shifts or ontogenetic telescopes in prey size of Lampropeltis getula using linear regression of ln-transformed individual prey mass on ln-transformed snake mass and of ln-transformed relative prey mass on ln-transformed individual snake mass (Arnold 1993; Hamilton et al. 2012). Measures of L. getula body mass (minus prey mass) were obtained directly or estimated from the regression equation of Kaufman and Gibbons (1975) for SVL and mass. Prey mass was measured directly or estimated from literature sources (e.g., regression equations of Kaufman and Gibbons [1975] for snake prey, Congdon and Gibbons [1985] for egg mass of turtle species). In cases where a snake prey was partially digested and only the tail length could be measured, we used species-specific ratios of tail length to TBL found in Ernst and Ernst (2003) to estimate SVL and then body mass (Kaufman and Gibbons 1975), accounting for sexual differences in tail length and assuming the mean of both sexes when the sex of the prey could not be determined. Because turtle and bird eggs are an important food resource for some populations of L. getula (Winne et al. 2007) and lower jaw length is strongly correlated with the maximum egg width that kingsnakes can consume (Gartner and Greene 2008), we evaluated the allometric relationship between these variables by the following methods: (1) mean egg width was measured from X-rays or by using species-specific mean values for turtles from Congdon and Gibbons (1985) and (2) lower jaw length was estimated from Krysko’s (2001: fig. 3.9) regression of SVL and lower jaw length for L. getula collected in Florida, who used the same method as Gartner and Greene (2008) to measure lower jaw length. As for other prey relationship analyses, we used Bayesian methods with vague normal (0, 100) priors on model intercepts and coefficients and uniform (0, 100) priors on standard deviations. Each model was analyzed using MCMC methods, with five independent chains of 200,000 iterations each, with a burn-in of 10,000 iterations and the output thinned by a factor of 10. All effective sample sizes were >10,000. We assessed convergence with history plots and the Gelman–Rubin statistic (Gelman and Rubin 1992) and observed no evidence for lack of convergence (R < 1.002 for all monitored parameters).

In addition to prey composition and predator–prey size relationships, we examined the rate at which adult kingsnakes (>50 cm SVL; Krysko 2002) of each sex foraged seasonally. We used range-wide counts of Lampropeltis getula containing prey for which sex and season (breeding, 1 February–31 May vs. nonbreeding, 1 June–31 January) could be determined and compared the number of L. getula in each sex–season category to sex- and season-specific capture rates of adult L. getula in Florida, based on Krysko’s (2001) database using the ln of sex- and season-specific captures as an offset in a Poisson regression model with a log link function. We used Bayesian methods with vague normal (0, 100) priors on model intercepts and coefficients. The model was analyzed using MCMC methods, with five independent chains of 20,000 iterations each after a burn-in of 10,000 iterations. All effective sample sizes were >10,000. We assessed convergence with history plots and the Gelman–Rubin statistic (Gelman and Rubin 1992), and observed no evidence for lack of convergence (R < 1.002 for all monitored parameters).

We used R v2.7.2 (R Core Team 2015) for all analyses except the CMR analysis and analyses of predator–prey relationships. Unless otherwise indicated, results are presented as a maximum likelihood estimate (95% confidence interval [CI]) for frequentist analyses and posterior mode (95% highest posterior density interval [HPDI]) for Bayesian analyses.

RESULTS

Population Structure and Size

Between November 1975 and May 1978, a total of 34 Lampropeltis getula were captured 62 times, 2 released individuals were observed repeatedly but not recaptured on the same day, and 9 others were seen but evaded capture (4 escaped and 5 never emerged from a burrow that day). The sex ratio of first-captured individuals was 1.13:1 (18 males, 16...
females; 95% CI = 0.54–2.36). Males were longer in SVL than females (male mean = 126.2 cm, female mean = 108.5 cm; 95% CI of difference = 3.8–31.6 cm), but did not have greater body mass (male mean = 853 g, female mean = 608 g; 95% CI of difference = −21 to 510 g). No individuals less than 80.0 cm SVL (immature; Krysko 2002) were observed. Model $p_1/c_1$ was selected as the best fit (Table 1). Eastern Kingsnake’s $p$ was 0.189 (95% HPDI = 0.129–0.259), and $\phi$, which likely was influenced by emigration, was 0.128 (0.020–0.345). Given the number of surveys conducted each year, annual capture probabilities for $L. \text{getula}$ at Rainey Slough were $0.662 \ (0.512–0.785)$ in 1976 (five independent surveys), $0.787 \ (0.643–0.892)$ in 1977 (seven independent surveys), and $0.734 \ (0.577–0.842)$ in 1978 (six independent surveys). Low apparent survival was offset by high recruitment of adult immigrants (Fig. 1), resulting in a 0.969 probability of increasing abundance ($n$) through the study period (Fig. 2). The estimated population growth rate also was positive during the study (Fig. 3). The total number of individual kingsnakes estimated to be alive at Rainey Slough during the 3 yr of the study was 45 (37–59).

Seasonal Activity

Seasonal activity of Lampropeltis getula at Rainey Slough was difficult to quantify because (1) sampling effort was not uniform among months or days sampled; (2) once captured, snakes typically were not released until the end of that day or the following sampling event (i.e., sampling without replacement on that day); and (3) as described below, $L. \text{getula}$ used burrows in the canal banks particularly during winter and spring months, limiting their aboveground exposure to detection to 13–26% of the sampling days. Nevertheless, some meaningful patterns were apparent.

Table 2 summarizes the total number of live Lampropeltis getula and shed skins observed each month at Rainey Slough, along with several measures of sampling effort and sampling success. The number of live kingsnakes and shed skins observed each month were marginally correlated (Spearman’s $p = 0.57, P = 0.052$), and the greatest number of both occurred January–May. At this site, shed skins lasted

![Figure 1](image1.png)  
**Fig. 1.**—Annual recruitment in Lampropeltis getula at Rainey Slough, Florida, in 1976 and 1977. Points represent posterior modes; error bars are 95% highest posterior density intervals.

![Figure 2](image2.png)  
**Fig. 2.**—Annual abundance of adults of Lampropeltis getula at Rainey Slough, Florida, from the winter of 1975–1976 through 1977–1978. Points represent posterior modes; error bars are 95% highest posterior density intervals.

![Figure 3](image3.png)  
**Fig. 3.**—Population growth rate of adults of Lampropeltis getula at Rainey Slough, Florida, in 1976 and 1977. Points represent posterior modes; error bars are 95% highest posterior density intervals. The horizontal dashed line indicates a population growth rate of 1, or no population change.
about a month in the field, and the relatively high number seen on 19 June 1976 (five) probably were shed mostly in May. When measured by the total number of individuals observed per sampling day, total searcher-days (sum of number of days multiplied by number of people searching each day) or total searcher-hours, sampling success was 8.3-, 7.9- and 6.7-fold higher, respectively, during January–May compared to June–December. The relatively lower success rates in February (2.17, 0.68, and 0.29) were related to the greater sampling effort and capture success for this month, which reduced the number of kingsnakes available for observation in subsequent sampling events. This result was consistent among study years.

Microhabitat Use

At Rainey Slough, the Eastern Kingsnake was closely associated with burrows in the canal banks, at least during winter and spring. Of the 64 observations of individual Lampropeltis getula not initially seen emerging from (n = 13) or entering (n = 2) a burrow, 49 (76.6%) were within 1.2 m of a known burrow, 5 were within 5 m of a L. getula burrow, 5 were excavated from burrows, and 5 individuals could not be associated with a burrow (Fig. 4). Three of these latter snakes were at locations where eight L. getula sheds were found in the same or next month, suggesting a nearby burrow. Previously unknown burrows were detected by (1) approaching individual L. getula that were aboveground and following them to a burrow down which they attempted to escape (n = 8), (2) releasing a snake at its capture site and repeating the above observation (n = 2), and (3) carefully searching for burrows near shed skins (17 of 28 sheds were within 2 m of a burrow confirmed to have been used by a kingsnake; as noted above, 8 other sheds were associated with likely burrow locations). By these methods, we detected 31 burrows used by adult kingsnakes during the study.

All burrows used by Lampropeltis getula appeared to be those constructed by small mammals. The Hispid Cotton Rat (Sigmodon hispidus) was the most commonly seen rodent at Rainey Slough, particularly along the unmowed side slopes of the canal banks, and frequently escaped into burrows. The openings of these burrows matched the widths (3.5–4.0 cm) of burrows used by kingsnakes, and their often extensive tunnel systems contained one or more nest chambers with adequate room for an adult snake(s). Most (63 of 65) excavated burrows did not have a second exit hole. In contrast to burrows actively used by S. hispidus, none of the burrows used by snakes had nest material in the chambers, suggesting abandonment by rodents. Burrows made by other species, including The Round-tailed Muskrat (Neofiber alleni), Eastern Mole (Scalopus aquaticus), mice, shrews,
and crayfish (*Procambarus* sp.) were excavated but not known to be used by adult *L. getula* at Rainey Slough.

Fourteen of 65 burrows excavated along the canal banks of Rainey Slough contained snakes, including 5 *Lampropeltis getula*, 13 *Nerodia fasciata*, 1 *N. floridana*, 5 *Farrancia abacura*, and 1 *Caluber constricior*. All of these snakes were adults and located in enlarged chambers within the burrow. Most (62 of 65) excavated burrows had a single chamber, typically at the end of a 0.4–1.2-m tunnel that was 20–30 cm below the surface. Four burrows contained a single kingsnake and one adult (SVL = 124.0 cm) occupied a burrow with a 156.0-cm SVL *F. abacura*. These two snakes were in separate chambers connected by a 1.5-m tunnel with the *F. abacura* in the last chamber. Seven of the nine other burrows with snakes contained multiple individuals (*n* = 2–7): three of these had mixed species assemblages including the species noted above, and one burrow had three distinct, connected chambers that contained three, three, and one snake each. The bottom of six chambers with snakes had either one (*n* = 5) or two smaller burrows that ended just below the water table and typically contained an ovigerous female crayfish (*Procambarus* sp.). Representative field notes and photos of occupied burrows are provided in the Supplemental Material.

Many of the burrows known to harbor *Lampropeltis getula* were used by multiple individuals and often over several years. Seven entry holes occurred within a distance of 4 m adjacent to the vertical abutment at the southwest corner of the wooden bridge. The horizontal wooden timbers extended above the ground and sheltered basking snakes from a north wind. At this specific site 16 marked *L. getula* were seen at least 19 additional times, 7 individuals of unknown status were observed, and 14 of 27 *L. getula* shed skins were found. Each of nine other burrows along the canal banks was occupied by at least two (*n* = 4 burrows), three (*n* = 4), or four (*n* = 1) different kingsnakes. When more than one kingsnake of known sex was observed at a burrow, subsequent observations the same or next day were of an individual of the opposite sex on all nine occasions. These burrows likely contained multiple nest chambers and housed more than one snake. Several *L. getula* were seen and shed skins were found at two other canal bank sites, but no burrows were located. Five of the seven entry holes at the bridge appeared to be used in all 3 yr of the study, and four other burrows along the canal banks were used in consecutive years by *L. getula*.

During this study three kingsnakes were observed in the Water Hyacinth community: one female was basking on top of a mat of hyacinth plants 1 m from the shore and a pair entered the water during courtship. In this latter case the female had exited a burrow at 1229 h and attempted to escape a pursuing male by moving 7 m along the bank and into the water. Upon release within 1 m of their original burrow, three other individuals of *Lampropeltis getula* also entered the Water Hyacinth community rather than the nearby burrow. As described below, kingsnakes at Rainey Slough fed principally on semiaquatic snakes and hyacinth rootlets were found in their stools. Both of these observations suggest that foraging occurred in the Water Hyacinth community.

Excluding multiple observations of the same individual on the same day, and those at the multiple-burrow site at the southwest corner of the bridge (*n* = 21), adult *Lampropeltis getula* were nonrandomly distributed among the four canal banks (G = 37, df = 3, *P* < 0.001). Individual kingsnakes were found equally on east- (northeast = 2, southeast = 27) and west-facing (northwest = 3, southwest = 14) canal banks (binomial probability of observation on east canal = 0.435, 95% CI = 0.316–0.560), but more were found south than north of the bridge (binomial probability of observation south of bridge = 0.928, 95% CI = 0.839–0.976). In addition, 10 of 18 recaptured *L. getula* were recorded from the southwest bridge site at least once, making this location a focal point of kingsnake activity at Rainey Slough and partially explaining the higher number of kingsnakes found south of the bridge. The distribution of observations of live adults and shed skins among canal banks were similar, whether the southwest bridge site was considered a separate location (G = 11, df = 9, *P* = 0.270) or not (G = 16, df = 16, *P* = 0.446). We could not estimate the total number of burrows on the canal banks during our initial study, and thus determine how burrow availability may have affected kingsnake distribution. However, our field notes describe mammal burrows as “numerous” north of the bridge and no difference in upland habitat quality was apparent.

The use of rodent burrows as retreats by kingsnakes also affected their vertical distribution on the canal banks. Twenty of 28 individuals of *Lampropeltis getula* recorded from the levee (road shoulder) portion of the canal banks were seen emerging from or found near a burrow at the southwest bridge site. Excluding observations at the bridge site, most other *L. getula* (78%, *n* = 28) were seen on the more densely vegetated side slopes of the canal banks, where most burrows were located, vegetation was thicker, and most *Signodon hispidus* were observed. To bask on shaded west-facing side slopes, adult *L. getula* often climbed onto tussocks of grass near their burrow. Kingsnakes observed on the levee or on east-facing slopes did not show this basking behavior.

Movements

During the study, 61% (11 of 18) of the marked male *Lampropeltis getula* were recaptured 19 times, whereas 44% (7 of 16) of the marked females were recaptured 9 times. Neither the distance moved between successive captures nor the days between successive captures was correlated for males (Spearman’s *ρ* = 0.12, *P* = 0.647), females (*ρ* = -0.41, *P* = 0.273) or both sexes combined (*ρ* = 0.018, *P* = 0.931), so we examined distance moved between successive burrows and the rate of movements separately. The best-fit model for distance between captures included an effect of SVL (Table 3), but this effect was not significant (maximum likelihood estimate of effect of SVL on distance between captures = 0.06, SE = ±0.05). The model-averaged mean distance between recaptures was 60 (36–85) m. Similarly, the best-fit model for rate of movement included an effect of SVL (Table 3), but this effect was not significant (0.01 ± 0.01). The model-averaged mean rate of movement was 3.7 (0.3 to 7.5) m/d. Three *L. getula* (two males and one female) moved >100 m in 1 wk or less.

No individuals of *Lampropeltis getula* that were marked north or south of the bridge were recaptured on the opposite side of the bridge. However, 6 of 11 males (55%) and 5 of 7 females (71%) were recaptured on the opposite canal bank.
and presumably crossed the S.R. 731 roadway. Two *L. getula* were found dead on the road and presumably run over during the study; one was a marked male and the second of unknown status was found near a burrow where two *L. getula* had previously been captured and marked.

### Behavior and Thermal Ecology

During our systematic surveys at Rainey Slough, adult *Lampropeltis getula* had a unimodal pattern of activity and were observed aboveground between 0845 and 1725 h (*n* = 78), at least during winter and spring (Fig. 5). Most individuals (*n* = 51, 65.3%) were basking, which peaked in morning hours.

Individual *L. getula* were seen emerging from burrows (*n* = 11, 14.1%) between 0845 and 1305 h; later observations of emergence were limited to days when the mornings were cold and/or cloudy, and some kingsnakes (*n* = 5) ventured to the burrow mouth but never emerged under these same conditions. Adult *L. getula* that were moving (*n* = 8, 10.3%) or engaged in courtship behavior (*n* = 6, 7.7%) were encountered on warm mornings or later in the day (Fig. 5).

Only two kingsnakes were seen entering burrows without human disturbance, both in late afternoon. By 1700 h, most individuals had entered a burrow for the night.

While basking, individuals had an average of 75.2% of their body exposed from cover (*n* = 24 records), and percentage of exposure was not correlated with *T* _b_ (Spearman’s *ρ* = −0.023, *P* = 0.904). Kingsnakes emerging from burrows did so quickly with the longest recorded time from emergence to basking posture being 7 min. Individuals that were moving or courting often crossed multiple cover regimes, and generally used the more densely vegetated side slopes of the canal banks as a travel corridor. Of the 45 adult kingsnakes whose stage of shed cycle was recorded, 23 (51%) were shedding when encountered aboveground, with no difference between the sexes (females = 42%; males = 58%; β _male_ = 0.315, *z* = 0.592, *P* = 0.554). Marked individuals were found shedding at intervals as short as 16, 28, and 42 d.

Temperature data for 29 adult *Lampropeltis getula* captured 47 times at Rainey Slough are shown in Fig. 6. After accounting for differences in *T* _b_ that were caused by differences in *T* _s_ or *T* _a_ differed by behavior but not by time of day or sex (Table 4). Basking individuals had a greater *T* _b_ than emerging individuals (95% CI of difference = −7.8 to −1.8°C), but no other significant differences in behavior among individuals were noted. The lowest *T* _b_ of an emerging

<table>
<thead>
<tr>
<th>Table 3.—Model-selection results for the influence of sex and size on movements of adults of <em>Lampropeltis getula</em> at Rainey Slough, Florida. All models contain an intercept term and individual identification as a random effect to account for multiple observations of the same individual. Models are listed in order of decreasing support.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
</tr>
<tr>
<td>Distance between subsequent captures</td>
</tr>
<tr>
<td>Distance = SVL</td>
</tr>
<tr>
<td>Distance = null</td>
</tr>
<tr>
<td>Movement rate (m/d)</td>
</tr>
<tr>
<td>Movement rate = SVL</td>
</tr>
<tr>
<td>Movement rate = null</td>
</tr>
<tr>
<td>Movement rate = sex</td>
</tr>
</tbody>
</table>

* AIC *c* = Akaike’s information criterion corrected for small sample bias; SVL = snout-vent length.

**Fig. 5.**—Behavior of adult *Lampropeltis getula* related to time of day at Rainey Slough, Florida.

*L. getula* was 16.4°C, and the single individual with a high emerging *T* _b_ (33.1°C; Fig. 6) had already basked (*T* _b_ > *T* _a_ and *T* _s_). The highest *T* _b_ (35.5°C) was recorded for a male attempting to copulate with a female (34.4°C) in full sun; each snake had the anterior part of its body wedged into a burrow (female first). No differences in the proportion of

**Fig. 6.**—Cloacal body temperature (*T* _b_ ) of adult *Lampropeltis getula* as they were emerging from a burrow (circles), basking (squares), moving (diamonds), or courting (triangles) during daylight hours at Rainey Slough, Florida. Shown to the right are sample size, range (vertical line), and mean (bar) of *T* _b_ for each behavior.
males and females engaged in major behavioral activities were detected ($G = 5.55, df = 6, P = 0.48$), and the addition of sex did not improve the model fit of behavioral influence on $T_b$ (Table 4).

Winter–spring activity and low feeding rates (see below) apparently had a relatively high metabolic cost, because body condition in almost all kingsnakes decreased on subsequent captures during the same study year (Fig. 7). The percentage of mass lost per day for individual Lampropeltis getula was best explained by sex (Table 5), and males lost mass at a greater rate than females (female mean $=-0.018\%$ per day, male mean $=-0.21\%$ per day, 95% CI of difference $=-0.42$ to 0.025), though the 95% CI included zero. Consequently, between 10 October and 15 April males lost on average 39.3% of their body mass (14.0% and 19.4% of the kingsnake’s body mass); another, $R. alleni$ (6.0% of body mass); and the third, a *Nerodia* sp. of undetermined size and a *Coluber constrictor* (39.7% of body mass). The Water Hyacinth’s rootlets were found in the first and second of these kingsnakes, indicating that both individuals consumed a *R. alleni* in the Water Hyacinth. One putative kingsnake stool found at the southwest bridge site contained remains of a *Nerodia* sp. of undetermined size and a *C. constrictor* estimated to be 125 g (17.4% of mean mass of kingsnakes at Rainey Slough).

During this study, a total of 261 potential snake prey (excluding kingsnakes) were collected in the Water Hyacinths at Rainey Slough and 90 additional snakes were captured on the canal banks (Fig. 8). Snakes sampled in the hyacinth community were smaller than those sampled on the canal banks ($G = 205, df = 18, P < 0.001$). Most (97.7%) potential snake prey species weighed less than the mean body mass of adult Eastern Kingsnakes at Rainey Slough (0.745 kg; Fig. 8). The remaining eight larger snakes included five *Farancia abacura*, two *Agkistrodon piscivorus*, one *Nerodia floridana*, and one *N. fasciata* (Fig. 9). Of the 10 species of potential snake prey, 2 were collected only in Water Hyacinths (*Seminatrix pygaea* and *Regina alleni*), 4 only on canal banks (*A. piscivorus*, *Coluber constrictor*, *Micrurus fulvius*, and *Pantherophis alleghaniensis*), and 4 in both habitats (*N. fasciata*, *P. alleni*, *A. piscivorus*, and *Micrurus lemniscatus*).

### Table 4.—Model selection results for the influence of sex, behavior, and time of day on body temperature ($T_b$) of adult Lampropeltis getula at Rainey Slough, Florida. All models contain an intercept term and individual identification as a random effect to account for multiple observations of the same individual. Substrate temperature ($T_s$) was included as a covariate in all models to account for the strong influence of $T_s$ on $T_b$. Models with interaction terms also include main effects. Models are listed in order of decreasing support.

<table>
<thead>
<tr>
<th>Model</th>
<th>Distance</th>
<th>AIC</th>
<th>AAI</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_b = \text{Behavior} + T_s$</td>
<td>236.3</td>
<td>246.2</td>
<td>0.00</td>
<td>0.44</td>
</tr>
<tr>
<td>$T_b = \text{Behavior} + \text{sex} + T_s$</td>
<td>237.5</td>
<td>247.8</td>
<td>1.57</td>
<td>0.20</td>
</tr>
<tr>
<td>$T_b = T_s$</td>
<td>238.4</td>
<td>246.9</td>
<td>1.77</td>
<td>0.18</td>
</tr>
<tr>
<td>$T_b = \text{Sex} + T_s$</td>
<td>238.5</td>
<td>249.3</td>
<td>3.11</td>
<td>0.09</td>
</tr>
<tr>
<td>$T_b = \text{Hour} + T_s$</td>
<td>238.6</td>
<td>252.9</td>
<td>7.71</td>
<td>0.02</td>
</tr>
<tr>
<td>$T_b = \text{Hour} + \text{hour}^2 + T_s$</td>
<td>239.0</td>
<td>252.2</td>
<td>5.98</td>
<td>0.02</td>
</tr>
<tr>
<td>$T_b = \text{Behavior} \times \text{sex} + T_s$</td>
<td>237.0</td>
<td>257.0</td>
<td>10.77</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

* AIC = Akaike’s information criterion corrected for small sample bias.

### Table 5.—Model selection results for the influence of sex and year on percentage of mass change per day of adult Lampropeltis getula at Rainey Slough, Florida. All models contain an intercept term. Models are listed in order of decreasing support.

<table>
<thead>
<tr>
<th>Model</th>
<th>Distance</th>
<th>AIC</th>
<th>AAI</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daily % mass change = sex</td>
<td>0.43</td>
<td>-3.84</td>
<td>0.00</td>
<td>0.53</td>
</tr>
<tr>
<td>Daily % mass change = null</td>
<td>0.54</td>
<td>-3.45</td>
<td>0.38</td>
<td>0.43</td>
</tr>
<tr>
<td>Daily % mass change = year</td>
<td>0.49</td>
<td>1.23</td>
<td>5.07</td>
<td>0.04</td>
</tr>
</tbody>
</table>

* AIC = Akaike’s information criterion corrected for small sample bias.

### Table 6.—Model selection results for the influence of sex, snout–vent length (SVL), and date on body condition index (BCI) of adult Lampropeltis getula at Rainey Slough, Florida. All models contain an intercept term and individual identification as a random effect to account for multiple observations of the same individual. Date is the calendar date regardless of year, adjusted to be number of days since 1 October. Models are listed in order of decreasing support.

<table>
<thead>
<tr>
<th>Model</th>
<th>Distance</th>
<th>AIC</th>
<th>AAI</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCI = sex</td>
<td>-158.0</td>
<td>-153.8</td>
<td>0.00</td>
<td>0.27</td>
</tr>
<tr>
<td>BCI = SVL + sex</td>
<td>-159.1</td>
<td>-152.7</td>
<td>1.09</td>
<td>0.16</td>
</tr>
<tr>
<td>BCI = SVL</td>
<td>-156.5</td>
<td>-152.3</td>
<td>1.52</td>
<td>0.13</td>
</tr>
<tr>
<td>BCI = sex + date</td>
<td>-158.5</td>
<td>-152.1</td>
<td>1.67</td>
<td>0.12</td>
</tr>
<tr>
<td>BCI = year</td>
<td>-157.8</td>
<td>-151.5</td>
<td>2.33</td>
<td>0.08</td>
</tr>
<tr>
<td>BCI = SVL + sex + date</td>
<td>-159.8</td>
<td>-151.2</td>
<td>2.64</td>
<td>0.07</td>
</tr>
<tr>
<td>BCI = SVL + date</td>
<td>-157.5</td>
<td>-151.1</td>
<td>2.71</td>
<td>0.07</td>
</tr>
<tr>
<td>BCI = null</td>
<td>-153.1</td>
<td>-151.1</td>
<td>2.74</td>
<td>0.07</td>
</tr>
<tr>
<td>BCI = date</td>
<td>-154.0</td>
<td>-150.0</td>
<td>4.02</td>
<td>0.04</td>
</tr>
</tbody>
</table>

* AIC = Akaike’s information criterion corrected for small sample bias.
fasciata, N. floridana, F. abacura, and Thamnophis sauritus). The mean annual density of potential snake prey in the hyacinth community was 3525 individuals/ha (3141.5–3908.5); snake density was greatest in winter, lowest in summer, and differed among all seasons (Fig. 10). The number of kingsnakes observed per searcher-hour by month (Table 2) was not correlated with the total number of potential snake prey observed on canal banks by month (Spearman’s $r = 0.035$, $P = 0.914$) or with the density of semiaquatic snake prey observed by month ($r = 0.440$, $P = 0.175$).

Table 8 summarizes the known diet of noncaptive Lampropeltis getula from Florida and their range elsewhere. Unfortunately, most data sources did not report the number of individual prey items (particularly nest contents of turtles, squamates, mammals, and birds) consumed by each snake, so detailed analysis was limited to the number of snakes that ate particular prey types. Squamates and reptile eggs comprised 94.8% of the diet of 58 kingsnakes from Florida and 90.2% of 121 specimens outside of Florida, with snakes being the predominant prey type in both areas (62.1% and 49.6%, respectively). Identifiable species of prey included eggs of 4 turtles and 1 snake, 8 lizards, 26 snakes, 6 mammals, 2 birds (eggs and nestlings only), 1 Siren lacertina (Greater Siren), and 1 Xylophanes tersa (Tersa Sphinx Moth) larva. Although snakes were eaten more than all other prey types (Fig. 11; $\beta$ deflection difference with regions pooled = 2.659 [2.256–3.147]) and the proportion of individuals consuming snakes did not differ between the two regions (0.576 [0.062 to 1.417]), turtle eggs were more likely to be consumed in Florida than elsewhere (1.814 [0.967–2.782]), and mammals were more likely to be consumed outside of Florida than within Florida (1.927 [0.696–3.618]; Fig. 11). The difference in the proportions of individuals consuming snakes vs. mammals in Florida was greater than the difference in proportions of individuals consuming snakes vs. mammals elsewhere (2.502 [1.171–4.523]).

Using range-wide data from 90 Lampropeltis getula, prey type was not strongly associated with kingsnake size, indicating no ontogenetic shift in prey type (Fig. 12). However, incompressible turtle and bird eggs were not consumed by smaller, gape-limited kingsnakes. Based on the available sample (eight kingsnakes with eggs of four species of turtles and one bird; Colinus virginianus, Northern Bobwhite), the maximum estimated ratios of mean kingsnake lower jaw length (kingsnake SVL in centimeters in parenthesis) to egg width by prey species in ascending order were as

<table>
<thead>
<tr>
<th>Model</th>
<th>Deviance</th>
<th>AICc</th>
<th>AIC</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>BCI change = days elapsed</td>
<td>0.0085</td>
<td>−56.94</td>
<td>0.00</td>
<td>0.43</td>
</tr>
<tr>
<td>BCI change = null</td>
<td>0.0104</td>
<td>−56.55</td>
<td>0.09</td>
<td>0.41</td>
</tr>
<tr>
<td>BCI change = sex</td>
<td>0.0099</td>
<td>−55.82</td>
<td>2.21</td>
<td>0.14</td>
</tr>
<tr>
<td>BCI change = year</td>
<td>0.0100</td>
<td>−53.28</td>
<td>5.66</td>
<td>0.03</td>
</tr>
</tbody>
</table>

* AICc = Akaike’s information criterion corrected for small sample bias.
follows: *Sternotherus odoratus* = 0.625 (74), *Kinosternum subrubrum* = 0.627 (72), *Trachemys scripta* = 0.700 (114), *C. virginiana* = 0.800 (117), and *Chelydra serpentina* = 0.860 (100). Based on Krysko’s (2001: fig. 3.9) plot of ontogenetic variation in SVL to lower jaw length among *L. getula* from Florida, these estimates have a maximum error of about 20%. Although larger kingsnakes consume larger prey (Fig. 13; ln[individual prey mass] = −1.18 [−3.74 to 1.24] + 0.72 [0.27–1.15] × ln[kingsnake mass]) and are able to eat remarkably large prey relative to their mass (maximum relative prey mass = 0.86), large kingsnakes continue to eat small individual prey (ln[individual prey mass/kingsnake mass] = −1.24 [−3.69 to 1.25] + 0.28 [−0.71 to 0.17] × ln[kingsnake mass]) and exhibit an ontogenetic telescope, rather than an ontogenetic shift. The mean relative prey to kingsnake mass ratio in this sample was 0.133 (±0.029) and 12 of 43 kingsnakes consumed prey that individually were 2.0% of their body mass.

Feeding rates of male and female *Lampropeltis getula* differed seasonally. Females in the nonbreeding season (1 June–31 January) contained prey at the highest rate after

| TABLE 8.—Types of prey eaten by wild-caught Lampropeltis getula, sorted by state and decreasing latitude. Number of snakes (no. of S) indicates the number of kingsnakes that contained that prey type. Number of prey (no. of P) indicates the number of that prey type in those kingsnakes and a number in bold means the number of prey exceeds that value. |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                 | Turtle eggs     | Snakes          | Lizards         | Squamate eggs   | Mammals         | Bird eggs/nestlings | Other           | Total prey     |
|                 | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P | no. of S | no. of P |
| Maryland¹       | 1             | 1              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| West Virginia²  | 2             | 2              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Virginia²       | 1             | 1              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Virginia³       | 1             | 1              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Virginia³       | 1             | 1              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| North Carolina⁴ | 1             | 1              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| North Carolina⁵ | 2             | 2              | 3            | 4              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| South Carolina⁶ | 1             | 1              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| South Carolina⁷ | 9             | 44             |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| South Carolina⁸ | 1             | 1              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Georgia¹⁰       | 6             | 19             |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Georgia¹⁰       | 1             | 4              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Georgia¹¹       | 12            | 12             |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Florida¹²       | 1             | 2              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Florida¹³       | 1             | 2              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Florida¹³       | 1             | 2              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Florida¹³       | 1             | 2              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Other           | 21            | 74             | 60            | 66             | 14            | 14            | 2            | 10            | 17            | 19            | 7            | 26            | 1            | 1            | 121           | 210           |
| TOTAL           | 34            | 89             | 94            | 104            | 20            | 20            | 2            | 10            | 17            | 19            | 7            | 31            | 2            | 2            | 179           | 280           |

¹ Posey (1973).
² Wilson and Friddle (1946).
³ Megonsigal (1985).
⁴ Wright (1988).
⁵ Zappalorti and Mitchell (2008).
⁶ Mitchell (1994).
⁸ Groves (2014).
¹¹ Winne et al. (2007).
¹² Barrett et al. (2001).
¹³ J.D. Willson, personal communication.
¹⁴ Wright and Bishop (1915).
¹⁵ Hamilton and Pollock (1956).
¹⁶ Tamarack and Doherty (1993).
¹⁷ L.L. Smith and J.M. Howze, personal communication.
¹⁸ L. L. Smith and J.M. Howze, personal communication.
¹⁹ Carr (1940).
²₀ Durso et al. (2010).
²¹ K.L. Krysko, personal communication.
²² Present study.
²³ K.M. Euge, personal communication.
²⁴ USMN.
²⁵ FLHMNH.
controlling for seasonal capture rates (0.65 [0.35–1.10] adult females with prey per adult female captured in the nonbreeding season based on Krysko 2001), and males in the nonbreeding season had the lowest feeding rates (0.14 [0.07–0.25] adult males with prey per adult male captured in the nonbreeding season). Females substantially reduced their feeding rates during the breeding season (0.18 [0.08–0.36] adult females with prey per adult female captured in the breeding season), while males slightly increased their feeding rates during the breeding season (0.16 [0.09–0.24] adult males with prey per adult male captured in the breeding season). Females during the nonbreeding season fed at rates greater than any other sex–season group (difference between nonbreeding females and breeding females = 0.46 [0.11–0.92]; difference between nonbreeding females and nonbreeding males = 0.50 [0.18–0.95]; difference between nonbreeding females and breeding males = 0.49 [0.18–0.94]; 95% CI for all other contrasts overlapped zero).

Of the 90 kingsnakes with identifiable prey, 29 (32.2%) contained multiple prey items including 19 with turtle eggs (up to 17 eggs and 3 species per individual); 5 with 2 snakes each; 3 with 7, 8, and 8 bird eggs each, of which 2 had also consumed a snake; and 2 with 4 and 6 snake eggs each. Consumption of one or more clutches of eggs of squamates, turtles, and birds by 12 kingsnakes increased the mean prey mass ratio 4.8-fold, from 0.017 (mass of smallest identifiable individual egg in digestive tract) to 0.081, with the largest egg mass ratio being 0.181. Of the squamate prey where ingestion direction potentially was determinable, 18 were consumed head first and prey direction was indeterminable for one small Diadophis punctatus.

**Rainey Slough Four Decades Later**

No kingsnakes or their sheds were found in 2006–2010 on the canal banks or in the Water Hyacinths. Assuming identical capture probabilities in 2006–2010 as in 1974–1978, the cumulative probability of capturing a single individual Lampropeltis getula present during the seven surveys conducted in 2006–2010 would be 0.787 (0.643–0.892). The 223 m² of sampled Water Hyacinths yielded three species of semiaquatic snakes (1 Nerodia fasciata, 13 N. floridana, and 4 Regina alleni) at a total snake prey density of 807.4 snakes/ha. Snake observations on canal banks were limited to one each of N. fasciata, Micrurus fulvius, and Coluber constrictor.

**DISCUSSION**

**Population Size and Structure**

Here we frame the population ecology of Lampropeltis getula at Rainey Slough in a context designed to facilitate...
interpretation of the activity patterns, reproductive biology, and prey base of the species at this site and throughout the range of this species and its closely related congeners (Pyron and Burbrink 2009a).

The sampled population at Rainey Slough consisted of adult snakes in which males were significantly longer in SVL (16.3%) than females. Such sexual size dimorphism has been found in almost all populations of the species complex of Lampropeltis getula (sensu Pyron and Burbrink 2009a) with adequate samples (Blanchard 1921; Fitch 1949; Hansen 1952; Mitchell 1994; Palmer and Braswell 1995; Minton 2001; but see Jenkins et al. 2001 and Faust and Blomquist 2011 for L. nigra), and apparently is related to male–male combat with the proximate cause being the prolongation of the rate of growth in males after maturity (Shine 1994). The mean SVL of adults at Rainey Slough (117.5 cm) was similar to that (~118.0 cm) in the Lake Okeechobee population (80 km ESE of Rainey Slough) studied by Krysko (2002, cf. his Fig. 5), and adults in both of these populations were on the average much larger in size than those in his southern Miami-Dade County study site (180 km SSE of Rainey Slough), where collecting pressure was more intense (Krysko 2002; Krysko and Smith 2005) and prey likely limiting in that more oligotrophic environment (K. Krysko, personal communication; see also Godley 1980). At two protected sites in Tennessee, USA, Faust and Blomquist (2011) found significant differences in mean SVL (20%) and body mass (102%) between L. nigra populations <6 km apart, but no detectable differences in growth rates or BCI. They hypothesized that at these two sites L. nigra undergo an ontogenetic shift in diet from primarily snakes in juveniles to mammals in adults, and the richer mammalian prey base at one site fueled indeterminate growth rates of adults.

The absence of juvenile (<80 cm SVL) kingsnakes at Rainey Slough likely reflects sampling biases for these smaller age classes (Pike et al. 2008). At Krysko’s (2002) study sites juveniles constituted 24 of 101 live snakes and only 7 of these juveniles were observed above ground during the hours when we sampled at Rainey Slough. On 20 March 1967 one of us (JSG) collected ~15 juvenile kingsnakes (<40 cm SVL) in about 2 h beneath large rocks on a canal bank in Krysko’s (2002) Lake Okeechobee study site, a microhabitat that did not exist at Rainey Slough. Juvenile Lampropeltis nigra also were common beneath cover boards in Tennessee (Jenkins et al. 2001; Faust and Blomquist 2011).

At Rainey Slough, the best-fit model for Lampropeltis getula indicated increasing abundance of adults from 11 (8–19) in 1975–1976 to 19 (14–28) in 1977–1978 (Fig. 2). These abundance estimates correspond with a total mean annual biomass of 8.19 kg in 1975–1976 and 14.15 kg in 1977–1978. Annual apparent survival was low, as only 3 of 34 marked adults (8.8%) were captured in a subsequent study year. Nonetheless, recruitment of adult L. getula (estimated to be 14 [10–20] in 1976 and 18 [13–26] in 1977) was high enough to maintain positive population growth during the study period, suggesting a high turnover rate in the population. High annual recruitment and low apparent survival may have been driven by movements in and out of the study site at Rainey Slough. If so, most such movements likely occurred outside of our defined annual study year period (10 October–15 May), because within this period mean capture probabilities were very high (0.662–0.734) over the 3 yr. Alternatively, excessive road mortality at Rainey Slough even in the 1970s (2 DOR kingsnakes were found out of an estimated 45 [37–59] being alive during the 3-yr study) may have caused the low

![Diagram](image-url)

Fig. 13.—Relationship between the ln of mass (A) and snout–vent length (B) of Lampropeltis getula, and the ln of individual prey mass. Circles represent mean mass of individual prey items in an individual L. getula; the bold line represents the posterior mode of the line describing the predator–prey size relationship; light lines represent the 95% highest posterior density intervals of the relationship.
apparent survival rate of this population (0.12 [0.02–0.35]),
which was much lower than many other late-maturing
temperate colubrids (Parker and Plummer 1987; Brei-
To our knowledge, no published estimates of survivor-
ship or population size exist for any other population of
*Lampropeltis getula* (but see Hansen 1982 and Anguiano
and Diffendorfer 2015 for *L. californiæ*, and Hileman et al.
2015 for *L. triangulum*), although circumstantial evidence
indicates that the historic densities at Rainey Slough were
not unusual. Considering only observations of live king-
snakes along canal banks January–May, Fig. 1 in Krysko
(2002) indicates an encounter rate of about 0.74 individ-
uals/h, almost twice that reported here in the same months
(0.43/h, Table 2). Enge (2005 and personal communication)
interviewed commercial snake hunters in southern Florida,
who reported that immediately preceding a cold front
(barometric low) *L. getula* would leave their burrows to
move along canal banks in sugarcane fields near Lake
Okeechobee, and 25–30 individuals could be collected in
one afternoon, a weather event during which we did not
sample. On single days along the canal banks of S.R. 441 on
Paynes Prairie, Alachua County, Florida, Kaufield (1957)
and two colleagues in April 1936 collected about 20 *L.
getula* (mostly under mats of cut grass) and Carr (1940)
collected eight in 1 d (microhabitat and date not reported).
The S.R. 441 crossing of Paynes Prairie is about three times
longer than the S.R. 731 crossing of Rainey Slough, and the
most we collected in a single day at Rainey Slough was six
individuals. It is noteworthy that all these study sites in
Florida with seemingly high kingsnake densities were
anthropogenic in nature. However, in Louisiana, USA,
Clark (1949) and two assistants collected 50 individuals of
*L. holbrooki* in 5 h in the late 1920s in an area largely
“covered with virgin forests of pine and cypress.” These
records emphasize the apparent historic number and
ecological significance of kingsnakes in the herpetofaunas
of at least the southeastern United States.

**Seasonal and Daily Activity Patterns**

As described below, activity patterns of kingsnakes in the
*Lampropeltis getula* species complex throughout its trans-
continental range are strongly affected by seasonal variation
in temperature and rainfall. At the local scale, these
environmental features appear to shape the seasonal timing
of reproduction and the detectability of this semifossorial
species, as well as their daily pattern of activity.

On the canal banks of Rainey Slough, *Lampropeltis getula*
were detectable primarily in winter and spring (Table 2).
Systematic searches of canal and levee banks for kingsnakes
by Krysko (2002) yielded a similar seasonal pattern, with
88% of 118 adult *L. getula* observations occurring from
February through May (Fig. 4 in Krysko 2002). Throughout
their extensive ranges, adult kingsnakes in the *L. getula*
complex appear to exhibit a unimodal pattern of surface
activity that generally peaks in the spring, is correlated with
mating behavior, and is later in the year at higher latitudes
and elevations: Florida: March in southern Miami-Dade
County, March–April at Lake Okeechobee and Rainey
Slough (Krysko 2002; present study); Georgia, USA: April
and May (Linehan et al. 2010); South and North Carolina,
USA: May and June (Gibbons and Slemitch 1987; Palmer
and Braswell 1995); Tennessee: May (Jenkins et al. 2001);
California, USA: April and May in the southern coastal
region (Hansen 1982; Hubbs 2009; Anguiano and Diffen-
dorfer 2015), but May and June in inland valleys and foothills
(Fitch 1949); and New Mexico, USA: delayed to July with
advent of rainy season (Price and LaPointe 1990; Degen-
hardt et al. 1996).

Krysko (2002) suggested that kingsnakes were constrained
by high mean ambient temperatures and this response may
explain the much lower encounter rates along canal banks
and levees in south Florida from June through October.
However, kingsnakes in south Florida may rarely be active
on the canal banks in the summer and fall and may spend
more time concealed, and thus be subject to a collecting bias
(Gibbons and Slemitch 1987). At Rainey Slough winter frosts
killed back the herbaceous canal bank vegetation which grew
back by June, hiding most rodent burrows and making
kingsnakes (and their sheds) difficult to observe until the
next winter, even if present.

At our study site the mean daily capture probability (p) of
individual kingsnakes was 0.19 (range = 0.13–0.26) in the
three (10 October–15 May) study years. In addition to the
results of studies presented below, several lines of evidence
indicate that these capture probabilities closely reflect the
amount of time (days) individuals of *Lampropeltis getula*
spent aboveground and were subject to capture: (1) the
study population consisted of large (>80 cm SVL),
significant adult snakes occupying an easily sampled linear
habitat (3–4 m in width) in which most burrows used by
snakes were known; (2) basking was the most common
aboveground behavior (Fig. 5), during which time the bodies
of most kingsnakes were partially or completely exposed
from cover; (3) by repeatedly walking the same canal banks
each sampling day and inspecting known retreat sites, we
collected most snakes as they emerged from burrows or
shortly thereafter; and (4) we captured 93.9% of kingsnakes
observed aboveground.

Averaged over the entire activity season during daylight
hours, radio-tracked *Lampropeltis getula* (*n* = 9) in New
Jersey, USA, were concealed (underground or in leaf litter) in
79% of the observations (Wund et al. 2007). Ten to 12
radio-tracked kingsnakes at one site in Georgia were also
below ground 67.3–71.0% of the time, excluding repeat
locations (Linehan et al. 2010; Howze and Smith 2012). In
Tennessee, 98% of 400 *L. nigra* captures were of snakes
under cover boards (Jenkins et al. 2001) and their radio-
tracked individuals (*n* = 12) also were concealed or
underground during most tracking events (J.G. Byrd,
personal communication). Two radio-tracked *L. holbrooki*
kingsnakes in Arkansas, USA, were located in burrows (mostly mole tunnels) in 60% of the observations (Trauth et
al. 2004). Radio-tracked individuals of *L. californiæ* (*n* = 34)
were underground in 76% of 2684 locations (Anguiano and
Diffendorfer 2015). None of these authors reported seasonal
variation in aboveground activity except that associated with
hibernation. However, radio-tracked individuals of a north-
ern population of the Prairie Kingsnake, *L. c. calligaster*, (*n*
= 10) exhibited a spring peak in aboveground activity in
Illinois, USA, but in the daytime were underground 75% of
the total activity season (Richardson et al. 2006). Collectively,
these values are similar to that reported for adult *L. getula*
at Rainey Slough during winter and spring (1 - p = 81.1% [74.1–87.0%]).

During winter and spring both males and females of *Lampropeltis getula* at Rainey Slough moved frequently when active with no detectable differences between the sexes (Table 3); often they moved >100 m in a week along the canal banks and seemed intimately familiar with the burrows of conspecifics. The results of the radiotelemetry studies cited above also are similar in many respects. Together they indicate that following emergence from hibernation, kingsnakes usually returned to their summer home ranges from the previous year, and repeatedly traversed that range for the rest of the season, often returning to the same retreat locations in that and successive years (Jenkins et al. 2001; Richardson et al. 2006; Wund et al. 2007; Linehan et al. 2010; Anguiano and Diffendorfer 2015). These studies suggest that the frequency and distance of movements were relatively constant during the active season and tailed off only immediately before and after hibernation; they were not constrained by summer temperatures (but see Hansen 1982 and Anguiano and Diffendorfer 2015 for comparable data for *L. californiae*).

At least during the winter and spring, kingsnakes at Rainey Slough seemingly were diurnal (Fig. 5), typically emerging from rodent burrows in the morning and retreating to them before nightfall. Krysko (2002) also found kingsnakes to be diurnal in south Florida in these seasons, but noted that adults (and especially juveniles) occasionally were crepuscular and nocturnal during the summer months, as has been widely reported for many western populations of the kingsnakes living in hot, arid environments (Gates 1957; Hansen 1982; Werler and Dixon 2000; Price and LaPointe 1990; Degenhardt et al. 1996; Hubbs 2000). In the only radiotelemetry study that sampled at night, Howze and Smith (2012) found *Lampropeltis getula* in Georgia to be diurnal with only 1.2% of total active observations being at night during the summer months.

**Habitat Use, Behavior, and Thermal Ecology**

The previous section suggests that kingsnakes at Rainey Slough most likely were present year round, but were less conspicuous during the winter months of activity. Here, we focus on the place-based nature of this activity to explain the selective advantages of this canal-bank site to individual kingsnakes. Key ingredients appear to be readily available retreat and basking sites in close proximity to prey and potential mates.

The strong association of kingsnakes with rodent burrows at Rainey Slough is not unique to this population. Wilson and Porras (1983), Tennant (1997), and Krysko (2002) all mention rodent burrows as refugia for individuals of *Lampropeltis getula* in Florida. The use of small mammal burrows as hibernation sites and as daily retreat sites also appears to be widespread throughout this species complex (Hansen 1982; Degenhardt et al. 1996; Werler and Dixon 2000; Collins and Collins 2006; Plummer 2010; Steen et al. 2010), and in populations of *L. calligaster* as well (Fitch 1978; Ernst and Ernst 2003; Richardson et al. 2006).

*Sigmodon hispidus* was the most common rodent species at Rainey Slough and is so in most grass-dominated, upland habitats throughout its extensive range (Cameron and Spencer 1981), with fluctuating densities of 10–25/ha in flatwoods in Florida (Layne 1974) and 8–65/ha in old fields in Georgia (Odum 1955). With only about 0.8 ha of vegetated canal-bank habitat at Rainey Slough, the population size of cotton rats likely was small, but their burrows were relatively common and persisted for at least several years, providing a dependable and critical resource for kingsnakes.

The manmade canal banks at Rainey Slough likely represented the only suitable communal overwintering sites and location for frequent spring sexual encounters in the vicinity of this wetland system. Potential snake prey also was abundant at this location (see below). The extensive, closed canopy of Live Oak–Cabbage Palm hammocks that fringed Rainey Slough provided little cover or foraging habitat for cotton rats or other burrowing rodents and few basking sites for kingsnakes.

Steen and Smith (2009) suggested that adult *Lampropeltis getula* may be territorial because the overlap in home range boundaries of two radio-tracked females and four males (mean = 25%) was greater than in six male/male combinations (13%). At Rainey Slough, we found extensive spatial overlap in use of individual burrows and canal banks by both males and females, particularly in the breeding season. For example, two males and two females were captured in 1 d at the communal bridge site, and at least seven marked females and eight marked males used this site, as did nine other kingsnakes of unknown identity. However, in all nine instances where two kingsnakes used a burrow away from the bridge the same or next day, they were of opposite sex. Extensive home range overlap in adults of both sexes also occurred in several well-studied populations of *L. californiae* (Hansen 1982; Anguiano and Diffendorfer 2015). These observations suggest that intersexual interactions, not territoriality (Maher and Lott 1995), were the likely cause of this behavior in populations of *L. getula* and *L. californiae*.

Nearly every published source of information on *Lampropeltis getula* and its closely related congeners (Pyron and Burbrink 2009a) characterizes their preferred habitat as bottomland, moist, or near water (22 citations), and Kauffeld (1957: 84) stated “selection of moist habitats by kingsnakes is partly because food snakes are abundant” (but see Steen et al. 2012). Eleven studies described the species swimming or in water: Carr (1940: 85) noted “several collected in water in the middle of Payne’s [sic] Prairie,” which is 13.5 km in width. In the vicinity of Paynes Prairie, Goin (1943) also collected *L. getula* in Water Hyacinths in the months of February–May and September–October (no sampling June–August). As noted above, the total upland habitat on the canal banks of Rainey Slough used by kingsnakes was only 0.8 ha, and adults of *L. getula* readily entered the Water Hyacinth community to bask, to escape potential human predators, to pursue mates, and to forage.

Unfortunately, the daily and seasonal use by kingsnakes of Water Hyacinths in the canals or the adjacent marshes at Rainey Slough and their annual home range size remains unknown, as no snakes were radio-tracked in our study. The home range size (minimum convex polygon [MCP] method) for *Lampropeltis getula* generally radio-tracked for at least
one activity season in New Jersey was 15.6 ha (SE = 2.93; Wund et al. 2007) and in Georgia was 49.5 ha (SE = 9.6; Linehan et al. 2010). Both of these study sites contained substantial acreages of suitable adjacent uplands with small mammal burrows and other refugia. At Rainey Slough the mammal burrows used by kingsnake each night on canal banks in winter and spring were not available in the adjacent marshes and hyacinths when they were flooded the remaining months of the year. Assuming kingsnakes at Rainey Slough also used rodent burrows nightly during the warmer months, they likely had relatively smaller home range sizes.

At least during the winter and spring months, kingsnakes at Rainey Slough typically emerged from burrows in the morning on days when active (Fig. 5), often basked nearby (Fig. 4) to a \( T_b > 25^\circ C \) (Fig. 6), and retreated to these burrows before nightfall. After taking into account the effect of \( T_b \), time of day, sex, and behavior (other than the \( T_b \) of emerging individuals) had no significant effect on \( T_b \) (Table 4). This pattern of a relatively short heating phase after emergence, followed by an extended plateau phase within the preferred \( T_b \) range, and a long, slow cooling phase in the evening appears to be common in many snake species in temperate environments (Peterson et al. 1993), including the available thermal data for the Lampropeltis getula species complex (Brattstrom 1965; Bothner 1973; Sullivan 1981; Mitchell 1994; Palmer and Braswell 1995; Jenkins et al. 2001; present study). During warmer months, basking by kingsnakes probably would not be required to maintain \( T_b \) within their preferred range (Fig. 6).

During 10 October–15 April of each study year, male kingsnakes at Rainey Slough lost on average 39.3% of their body mass while females only lost 3.4% (Fig. 7, Table 5). Consequently, males had a lower BCI than females (Table 6), and did not differ significantly in mean body mass, even though they averaged 16.3% longer in SVL. The observed loss of body mass in male Lampropeltis getula greatly exceeds that reported for snakes hibernating in dens for extended periods (200+ d) in colder, more northern climates (e.g., Klauber 1956; Hirth 1966; Parker and Brown 1994), although the mean daily loss in body mass (~0.21%/day) is less than that of male adders (Viper berus) following emergence from hibernation and the reproductive season (approximately ~0.43%/day; Fig. 1 of Olsson et al. 1997).

Why did male and female kingsnakes differ so dramatically in body mass loss? During this study no sexual differences were detected in survivorship or capture probability, in behavior while aboveground, in \( T_b \) (Table 4), or in movements (Table 3), perhaps because of small sample sizes. However, male Lampropeltis nigra (Jenkins et al. 2001) had significantly (3.5 times) larger MCP home range sizes than did females and made longer movements between retreat sites (but see Wund et al. 2007); yet the proportion of each sex under cover boards did not differ, including during the spring mating season. Male individuals of L. californiae also had significantly larger MCP home ranges (four times) than females, and daily movements during the spring breeding season were twice that of females (Anguiano and Diffendorfer 2015). Hansen (1982) found similar results in another population of L. californiae and reported that adult females were proportionately heavier than adult males (BCI not calculated). Krysko (2002) found a significant adult male bias (34:32) in encounter rates during the breeding season (1 February–31 May; Van Hyning 1931; Knepton 1951; Iverson 1978; Krysko et al. 1998) on canal banks in south Florida, as did Linehan et al. (2010) in a Longleaf Pine (Pinus palustris) savannah in Georgia. The museum specimens examined by Blaney (1977: table 1) from throughout the range of the L. getula complex also were biased toward males (464:319), with most individuals of both sexes likely collected in the spring (see above). Krysko (2001 and personal communication) provided data for 325 sexed L. getula collected from Florida. His sample suggests a strong bias toward the collection of adult males during the breeding season (120 males vs. 67 females).

These studies suggest that during the spring reproductive season adult male kingsnakes are more active above-ground than females and expend relatively more energy in reproductive behaviors (mate searching, courtship, and combat) during this period. It is possible that male Lampropeltis getula, like adders (Olsson et al. 1997), also incur substantial metabolic costs associated with spermatogenesis and elevated testosterone levels. However, after controlling for sexual differences in seasonal capture rates, our range-wide analysis found that during the breeding season adult males fed more frequently than females, magnifying these metabolic costs and suggesting that increased rates of movements resulted in encounters with both more females and potential prey. The few records of feeding in our population (3 of 62 captures) were all of females, and two females showed substantial weight gains in the spring (Fig. 7), suggesting feeding events. We detected no eggs in females during this study, but some likely were gravid. In our range-wide analysis, females fed at higher rates following egg laying than any other sex–season group, and in captivity female L. getula (K.M. Enge, personal communication) and L. californiae (Zweifel 1980) breed and lay eggs almost every year. We encourage researchers with large kingsnake datasets (e.g., Winne et al. 2007; Linehan et al. 2010; Faust and Blomquist 2011; Anguiano and Diffendorfer 2015) to examine seasonal and sexual differences in BCI values.

Predator–Prey Relationships

The concomitant sampling of potential prey populations and adult Lampropeltis getula in the Water Hyacinths and on the canal banks of Rainey Slough provides insight into prey selection and availability—two factors potentially regulating the local population size of kingsnakes—and the use of available habitats in this seasonally fluctuating, semitropical environment by both the predator and its prey.

The only prey detected in kingsnakes at Rainey Slough was other snakes. At Rainey Slough, snakes likely comprise the bulk of the diet of Lampropeltis getula for several reasons: (1) snakes were very abundant in the Water Hyacinths (Fig. 10) and on the canal banks, and most individuals were of appropriate size (Figs. 8 and 9) and shape as prey; (2) elongate lizards (Plestiodon sp. and Ophisaurus sp.) were rare or absent on the canal banks (J.S. Godley, personal observation); and (3) small mammals also were uncommon and consisted primarily of Signodon
hispidus (J.S. Godley, personal observation), which as adults probably were too large (to 225 g; Cameron and Spencer 1981) and bulky to be ingested by most individuals of *L. getula*, which have relatively small heads (~3.25% of SVL in adults; Krysko 2001). Although most semiaquatic turtles known from Glades County, Florida, (Krysko et al. 2011) were collected at Rainey Slough (including *Apalone ferox*, *Chelydra serpentina*, *Deirochelys reticularia*, *Kinosternon baurii*, *K. subrubrum*, *Pseudemys floridana*, *P. nelson*, and *Sternotherus odoratus*), they accounted for only 1.1% of the sampled Water Hyacinth’s herpetofauna (likely sampling bias against turtles with the hyacinth sieves; J.S. Godley, personal observation) and their eggs probably were undetected in the diet of kingsnakes because (1) few kingsnakes contained prey when available for capture in winter and spring, (2) in Florida most of these turtle species lay eggs in summer (Banercoft et al. 1983), and (3) turtle eggs of small kinosternids that dominate the diet of *L. getula* elsewhere (Fig. 13; see below) are difficult to detect by palpation.

Our range-wide analysis of kingsnakes (Table 8; Fig. 11) suggests that geographic variation in diet is related to local variation in prey abundance. As this species consumes the same basic prey types range-wide (Table 8), differential vulnerability to capture and ingestion, prey energy content, and risk of injury or predation to kingsnakes (Arnold 1993) are unlikely to be important factors regulating diet. The higher frequency of kingsnakes consuming snakes vs. mammals in Florida relative to all other regions may be related to patterns of prey diversity in these taxa (Simpson 1964; Keister 1971), or may be something specific about kingsnakes in Florida. The Florida specimens (Table 8; n = 58 kingsnakes with prey) came from at least 33 localities widely distributed across 22 counties, suggesting this pattern is not caused by sampling bias in this state.

Several examples illustrate the site-specific importance of landscape and relative prey abundance to the diet of the Eastern Kingsnake. (1) At Ellenton Bay, South Carolina (an isolated wetland where kingsnakes and their prey base have been studied extensively), of 14 kingsnakes with prey, 6 each had consumed turtle eggs or semiaquatic snakes and *Seminatrix pygaea* was the most frequently eaten snake species (Winne et al. 2007). Within this 10-ha wetland, Congdon et al. (1986) calculated that over a 16-yr period, six turtle species had a mean total density of 1380 individuals with a biomass of 730 kg that annually produced 19.3 kg of eggs for potential consumption by kingsnakes. The species composition of semiaquatic snakes at Ellenton Bay was similar to Rainey Slough and *S. pygaea* was the most abundant species at both sites (Willson et al. 2006; Fig. 9): the estimated CMR density of *S. pygaea* adults at Ellenton Bay was >60/ha (Winne et al. 2005) and 145.6 adults/ha at Rainey Slough (J.S. Godley, personal observation). (2) At Itchauway, Georgia, radio-tracked kingsnakes (Steen et al. 2010) selected Longleaf Pine savannas at the landscape scale (wetlands similar to Ellenton Bay and Rainey Slough not present). Fourteen kingsnakes with prey contained 12 snakes (8 species; all upland-dependent), 2 mammals, and 2 clutches of bird eggs (L.L. Smith and J.M. Howze, personal communication). (3) At Krysko’s (2002) canal-bank study sites in south Florida, of 13 kingsnakes with prey, 10 contained turtle eggs, 2 had eaten a snake, and 1 a Hispid Cotton Rat. This confirms the observations of Wilson and Porras (1983: 30) that kingsnakes in south Florida living along canal banks, often adjacent to otherwise inhospitable habitat, eat “primarily turtle eggs.”

Relative to the adult kingsnake population at Rainey Slough, the body-size distribution of potential snake prey (Fig. 9) was strongly skewed toward smaller snakes (65% ≤ 40 g) that included most individuals of the numerically dominant *Seminatrix pygaea* and *Regina alleni* (32.4% and 27.1% of 351 total snakes, respectively), as well as *Thamnophis sauritus*, *Miciurus fulvus*, and juveniles of the remaining species. Differences in the size-frequency distributions of potential snake prey in the Water Hyacinths and on the canal banks primarily were attributed to (1) differential use of habitat types by some key species (e.g., *S. pygaea* and *R. alleni* restricted to Water Hyacinths, *Coluber constrictor* and *Agregistrodon piscivorus* only seen on canal banks) and age classes of others (e.g., only adult *Nerodia fasciata*, *N. floridana*, and *Farancia abacura* appeared to overwinter in rodent burrows on canal banks), and (2) size-related biases in sampling methodologies (e.g., some adults of larger-bodied species of *Nerodia* and *Farancia*, and *Lampropeltis getula*, likely evaded capture by the 0.56-m² hyacinth sieve and smaller individuals of all species were more difficult to detect on canal banks).

The seven snake prey found in *Lampropeltis getula* at Rainey Slough included three individuals of *R. alleni*, two *Nerodia* sp., and two *Coluber constrictor*, and the range of these prey items was 6.0–37.9% of the predatory kingsnake’s body mass. Ten of 11 snake species occurring at this site are known prey of *L. getula* (Carr 1940, *Agregistrodon piscivorus* and *Miciurus fulvus*; Godley 1982, *R. alleni*; Plummer and Congdon 1992, *C. constrictor*; Winne et al. 2007, *L. getula*, *N. fasciata*, *N. floridana*, and *Seminatrix pygaea*; K.M. Enge, personal communication, *Pantherophis alleghaniensis*; and K.L. Krysko, personal communication, *Thamnophis sauritus*) and presumably Eastern Kingsnakes eat *Farancia abacura* as well (see Palmer and Braswell 1995, for *F. erythrogaster*). It is likely that kingsnakes at this site consume any and all snakes of appropriate size, including much smaller (and numerically abundant) snakes that were undetectable by palpating the stomach. Figure 13 indicates that adult *L. getula* commonly eat prey that individually are very small and exhibit an ontogenetic change in prey size rather than an ontogenetic shift in prey size (Arnold 1993), the single exception being incompressible turtle and bird eggs where gape limitations prohibit smaller kingsnakes from consuming these prey types (Gartner and Greene 2008). Although in the lab juveniles of the California Kingsnake (*L. californiae*) occasionally can consume and successfully digest snakes that are longer and weigh more than themselves (1.06 mass ratio; Jackson et al. 2004), in the field the largest snake prey of which we are aware was a 107-cm TBL adult *L. getula* that ate a 111-cm TBL adult *P. alleghaniensis* (K.M. Enge, personal communication) with an estimated mass ratio of 0.86. Prey constriction coupled with head-first ingestion, biomechanical adaptations for eating elongate prey (Jackson et al. 2004), and veno-neutralizing proteins against crotalines (Weinstein et al. 1992) would allow *L. getula* to exploit the vast majority of
all size classes of upland- and wetland-dependent snake species as prey at Rainey Slough.

The snake prey base likely was not a limiting factor to the kingsnake population at Rainey Slough. During our 3-yr study the range of the mean size of the population was 11–19 adults (Fig. 2) that averaged 0.745 kg in body mass (Figs. 8 and 9) for a total predator biomass of 8.20–14.16 kg. In this same period, the density of the six snake species collected in the Water Hyacinth community (only) averaged 3534 individuals/ha (Fig. 10) with an estimated total biomass of 135.8 kg/ha. Thus, for the entire 2.7-ha Water Hyacinth community at Rainey Slough, 504.1–879.7 kg of snake prey potentially were available for consumption each year by a kingsnake, 96.3% of these snakes were of a suitable size for ingestion (mean mass ratio ≤0.86), and the total kingsnake biomass was only 2.2–3.9% of the estimated snake biomass in the Water Hyacinths. Based on measured metabolic rates, Secor and Diamond (2000) estimated that in the wild California Kingsnakes (Lampropeltis californiae) consume 25% of their body mass in prey every 12 d of the active season. Assuming similar consumption rates April–November and a rate of 35% of this value for the cooler transition months of December–March (Table 2 of Secor and Nagy 1994; S.M. Secor, personal communication), an average adult Lampropeltis getula at Rainey Slough would eat about 4.49 kg of snakes/yr, and the kingsnake population would consume 36.82–63.58 kg/yr or about 10.0–17.2% of the standing crop of snakes in the Water Hyacinth community.

The extent to which the kingsnake population at Rainey Slough may have regulated snake prey populations and size structure remains unclear. The only two experimental studies of squamate predator–prey systems (Schoener et al. 2002; Campbell et al. 2012) were on islands and both showed substantial depressions of lizard prey populations (and changes in size structure) by a lizard and snake predator, respectively. An extensive correlative study in the southeastern United States (Steen et al. 2014) identified a strong negative relationship between the relative abundances of kingsnakes (Lampropeltis getula, L. nigra, and L. holbrooki) and one of their known prey, the Copperhead (Agkistrodon contortrix); the authors suggested that kingsnake declines decreased predation pressure and caused a release of Copperhead populations in this region. However, at Rainey Slough the opposite occurred: snake prey in the Water Hyacinths declines dramatically (e.g., in Regina alleni, 30 times lower in the summer than in the winter; Godley 1980), and L. getula seemingly disappear from the canal banks (Table 4 and Krysko 2002). Semiaquatic snake prey in the Water Hyacinth community return the following fall and attain maximum densities in the winter (Fig. 10 and Godley 1980), whereas individuals of L. getula (and semiaquatic snakes) are not commonly found on canal banks until late winter (Table 2 and Krysko 2002). The snake fauna in the Everglades National Park, dominated by semiaquatic species (89.2%), exhibits mass migrations following the drying edge of water to deep-water refugia during the winter, even though upland species remain largely inactive in these same, cooler months (Bernardino and Dalrymple 1992). Similarly, Holman and Hill (1961) observed a mass, unidirectional movement of Nerodia fasciata (128 of 130 individuals) from the drying edge of Paynes Prairie into Levy Lake. From the S.R. 731 study site at Rainey Slough, the nearest other deep-water refugia were 5.2 km upstream and 2.0 km downstream (J.S. Godley, personal observation). Semiaquatic snakes that survive the spring dry-down apparently emigrate from these refugia as soon as the marshes reflood the following wet season, along with their invertebrate, fish, and amphibian prey (Godley 1980; Bernardino and Dalrymple 1992; Trexler et al. 2002; Hoch et al. 2015).

The Extirpation of Kingsnakes at Rainey Slough

The last known record of a kingsnake at Rainey Slough was on 25 January 1984 when an adult was observed basking on the northwest canal bank (ABS files; F.E. Lohrer, personal communication). Our surveys of canal banks and Water Hyacinths at Rainey Slough over 7 d from 2006–2010 under mostly ideal conditions (i.e., following a cold front with clear skies and warming temperatures) failed to detect an Eastern Kingsnake. In the 1970s similar sampling effort during January–May (Table 2) would have yielded 17.0 observations of live Lampropeltis getula and 5.1 sheds of kingsnakes. Moreover, the cumulative probability of capturing a single individual kingsnake with this sampling effort would have been 0.787 (0.643–0.892) and the probability of detecting any individual in a population would certainly have been much higher. In the 1970s, kingsnakes were detected on 17 of 18 surveys (per-survey probability of detection = 0.936 [0.772–0.997]). If similar detection probabilities are assumed for surveys conducted 2006–2010, the cumulative detection probability of kingsnakes, if they were present, would have been >0.999. We assume the population is extirpated and suspect this event likely occurred before 1990. The collapse and disappearance of populations of Lampropeltis getula across much of its range in the southeastern United States (Krysko and Smith 2005; Winne et al. 2007; Stapleton et al. 2008; Steen et al. 2014; present study) remains enigmatic, as it does globally for many snake and other reptile species (e.g., Gibbons et al. 2000; Gardner et al. 2007; Reading et al. 2010; Todd et al. 2010). The extirpation of L. getula is particularly vexing
because some populations in seemingly well-managed habitats such as Conocuh National Forest in Alabama (Steen et al. 2014), Apalachicola National Forest in Florida (Krysko and Smith 2005), and three sites in the Red Hills of northern Florida and southern Georgia (Stapleton et al. 2008) have largely disappeared. Yet, they remain common at two other nearby, maintained sites (Itchewauy and Albany, Georgia; Stapleton et al. 2008 and L.L. Smith, personal communication). Historically, the anthropogenic canal banks along the U.S. 441 crossing of Paynes Prairie (Alachua County, Florida) had catch rates of kingsnakes similar to Rainey Slough (see Discussion, Population Size and Structure). Coincidentally, the last kingsnake reported from Paynes Prairie (Krysko and Smith 2005; and Alachua County, K.L. Krysko, personal communication) and Rainey Slough was in 1984.

At Rainey Slough the primary (but correlative) cause of extirpation likely was the replacement of the wooden bridge and the paving of S.R. 731 and the subsequent, unsustainable increase in road mortality from traffic. Construction occurred during the winter and spring of 1979, when kingsnakes would have been concentrated on the canal banks. Publication of this locality for *Lampropeltis getula* (Godley 1982) also made this population vulnerable to collecting pressure. Although no trapping for small mammals was conducted in either study period, we did not observe any Hispid Cotton Rats or their burrows on the canal banks in 2006–2010. The conversion of pine flatwoods to pine plantations and improved pasturelands north and south of Rainey Slough likely had a negative impact on *Signodon hispidus*. A review of historical imagery on Google Earth, however, indicates this habitat conversion occurred sometime between 1996 and 1999, well after the last known observation of a kingsnake at this site (1984). The invasive Red Imported Fire Ant (*Solenopsis invicta*), which has been implicated as a potential cause for declines in populations of *L. getula* (see above citations) and many other species (see reviews in Wojcik et al. 2001; Allen et al. 2004; Tschinkel 2006), reached Glades County by 1975 and had fully infested the county by 1975 (Calcott and Collins 1996). However, fire ants also were and are abundant in the sugarcane fields and canal banks near Lake Okeechobee (Krysko and Smith 2005) and kingsnakes remain common there where human access and collecting is tightly controlled (Enge 2005; K.M. Enge, personal communication). Finally, we have no evidence that environmental contamination, disease and parasitism, or climate change (Gibbons et al. 2000; Todd et al. 2010) affected *L. getula* at Rainey Slough. What we do know is that which was once an Eden for the Eastern Kingsnake affected *L. getula* or climate change (Gibbons et al. 2000; Todd et al. 2010)

**Supplemental Material.** Supplemental material associated with this article can be found online at http://dx.doi.org/10.1655/HERPMONOGRAPHS-D-16-00006.S1.

**Literature Cited.**


Hower contributed unpublished data on the diet of *L. getula*: L.L. Smith confirmed the current status of populations of *L. getula* at certain sites in Georgia; and K.L. Krysko provided access to his 2001 dataset of Florida *L. getula* for analysis. S.M. Secor confirmed our estimates of prey consumption by *L. getula*: F.E. Lohrer searched ABS records for *L. getula* at Rainey Slough. Helpful comments on this manuscript were provided by C.M. Reilly, J.S. Godlely, R. Reynolds, H.W. Greene, B.D. Todd, M.B. Harvey, and two anonymous reviewers. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the US government.

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Kaufeld, C. 1957. Snakes and Snake Hunting. Hanover House, USA.


Layne, J.N. 1974. Ecology of small mammals in a flatwoods habitat in north-


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APPENDIX

Museum Specimens Examined with Prey

Lampropeltis getula.—USA: FLORIDA: Alachua County (FLMNH 1691), Brevard County (FLMNH 95469), Calhoun County (FLMNH 95471), Charlotte County (USNM 5509), Citrus County (FLMNH 80758), Columbia County (FLMNH 78086), Dixie County (FLMNH 95459), Duval County (USNM 14140), Franklin County (FLMNH 73659), Glades County (FLMNH 9272, 9273), Gulf County (FLMNH 33779), Jackson County (FLMNH 131542), Jefferson County (FLMNH 115939), Leon County (FLMNH 73420, 134853), Levy County (FLMNH 95558), Liberty County (FLMNH 73434, 105383), Miami-Dade County (FLMNH 105382, 145377, 146063, 152680), Okeechobee County (FLMNH 528), Orange County (USNM 124142), Polk County (FLMNH 95552), Wakulla County (FLMNH 144811), and Washington County (FLMNH 64715).