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

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ABSTRACT: The Eastern Kingsnake (*Lampropeltis getula*) is an important component and predator in herpetofaunal communities, but many of its populations have declined precipitously in the last few decades, particularly in the southeastern USA. Here, we describe an intensive mark–recapture study of *L. getula* conducted from 1974–1978 in a canal bank–water hyacinth community at Rainey Slough in southern Florida, where we also quantitatively sampled their primary prey, other species of snakes. The best-fit model for *L. getula* was an open population with a high daily capture probability (0.189) and low apparent annual survival (0.128) that were offset by high recruitment and positive population growth rates, suggesting a high turnover rate in the population. Mean population size varied annually from 11–19 adult kingsnakes with a total predator biomass of 8.20–14.16 kg in each study year. 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 0.13–0.26 of the sampling days. When above ground adults of *L. getula* exhibited a unimodal (mid-day) activity pattern, and mean cloacal body temperatures progressively increased as individuals emerged from burrows, basked, moved, and engaged in courtship activities. 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 to forage.

Based on recapture data, male *L. getula* at Rainey Slough lost an average of 39.3% of their body mass from 10 October through 15 April of each study year, whereas females lost only 3.4% in the same period. Body condition indices for both sexes improved substantially in the intervening months. We hypothesize that relative to females, male kingsnakes expend more

energy on reproductive behaviors, incur substantial metabolic costs associated with spermatogenesis and elevated testosterone levels, and may become aphagic during the spring reproductive season.

At Rainey Slough only snakes were detected in the diet of kingsnakes and those included both upland (*Coluber constrictor*) and wetland-dependent (*Regina alleni* and *Nerodia* sp.) species, the latter of which were consumed in the water hyacinth community. Concurrent sampling of potential snake prey in the hyacinths (*n* = 261) and on canal banks (*n* = 90) revealed ten species that varied in use of the two sampled habitats and in body size with most individuals (97.7%) weighing less than the mean body mass of predaceous kingsnakes. A range-wide analysis confirmed that squamates and reptile eggs dominate the diet of *L. getula*, particularly in Florida. At Rainey Slough kingsnakes were not limited by the available snake prey base: the density of six species of semi-aquatic snakes in water hyacinths averaged 3534 individuals/ha with a mean annual biomass of 135.8 kg/ha, and predator biomass was only 2.2–3.9% of prey snake biomass. Based on measured metabolic rates of a congener (*L. californiae*), we estimated that the kingsnake population consumed 36.82–63.58 kg/yr, or about 10.0–17.3% of the standing crop of snakes in the water hyacinth community. The extent to which the *L. getula* population at Rainey Slough may have regulated snake prey populations and size structure in the 1970s was unclear.

In follow-up surveys of the canal banks and water hyacinths at Rainey Slough from 2006–2010 no kingsnakes were found. Semi-aquatic snake densities in the water hyacinths were 77.2% lower (807.4/ha) than in the 1970s and consisted of only three species, indicating that factors other than kingsnakes now regulate these species in this system. Compared to the

enigmatic declines and extirpation of *L. getula* populations elsewhere in its range, 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 obvious and 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 years (Blanchard 1921; 11 recognized species), the recent application of molecular phylogenetics suggests at least 21 extant species of *Lampropeltis* (Ruane et al. 2014), with 5 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 *L. 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 (see Discussion), 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 is Florida, where many populations are in serious decline (see below), the species is phenotypically (historically, five named subspecies) and genetically diverse (Krysko and Jedd 2006), and as such, may warrant distinct population status (U.S. Department of the Interior 1996) listing under the U.S. Endangered Species Act.

This study summarizes three years of intensive capture–mark–recapture work on a population of *L. 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). Using modern statistics, we provide a detailed 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) confirm that this *L. getula* population has been extirpated, as have many others in the southeastern USA (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 the Eastern Kingsnake 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

Lampropeltis getula kingsnakes and their prey were studied from 1974–1978 in a 2.71-ha 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 to 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 time of this study, live oak–cabbage palm 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, dirt roadbed (S.R. 731) oriented in a N–S direction. The canals (1.1 km in total length) were connected below a 43-m wooden bridge that crossed Rainey Slough near its center and conveniently divided the study site into five areas: NE, NW, SE and SW 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 side slopes of the canals averaged 2: 1 (horizontal: vertical) in slope and varied from 3–4 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. Winter frosts killed back the slope vegetation in late December of 1976 and 1977, but not until mid-February 1978. By June of each year, vegetation on the canal banks had regrown, making observations difficult until the next freeze and dieback. Weather data used in our study were taken from records maintained at the Archbold Biological Station (ABS), located 23.8 km NNE of Rainey Slough.

Field Sampling

The herpetofauna of the Rainey Slough water hyacinth community was quantitatively sampled on 21 events (1–3 days each) from November 1974 through April 1977, primarily with a 0.56 m^2 hyacinth sieve described by Godley (1984). In addition, the canal banks at Rainey Slough were systematically searched for snakes on 38 days (14 of which were contemporaneous with hyacinth sampling) from November 1975 through May 1978. Systematic searches involved walking the length of each canal bank to detect snakes, their burrows, and shed skins. Detailed descriptions of the study area and hyacinth sampling methods were provided elsewhere (Godley 1980, 1984).

In general, *L. getula* and other reptiles captured during searches of the canal banks were sexed, measured (snout–vent length = SVL and total length = TL), weighed to the nearest g, permanently marked (Blanchard and Finster 1933), and released at the capture location on the same day or on the next visit to the site. Most reptiles collected in hyacinth samples also were measured and weighed, but they were preserved for future study. To obtain estimates of fasting body mass and to identify prey, we forced all *L. getula* with detectable food in their stomachs to regurgitate in the field or allowed each to defecate in the laboratory prior to release. Cloacal body temperature (T_b), shaded substrate temperature (T_s), ambient temperature (T_a, measured 3 cm above substrate) and burrow temperature (T_h) were taken with a Schultheis quick-reading thermometer. Other frequently recorded data included date/time of capture (standardized to Eastern Standard Time = EST), 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 more closely match thermal regimes and hydrological conditions at Rainey Slough, certain data were combined into seasons (winter = D, J, F; spring = M, A, M; summer = J, J, A; fall = S, O, N) and analyzed accordingly. Total search time, observations without capture, shed skins, and dead-on-road (DOR) specimens also were noted.

Follow-up surveys of Rainey Slough were conducted four decades later on seven 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 one to six individuals on all sampling dates. The water hyacinth community also was sampled quantitatively 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 mark-recapture methods to estimate annual abundance and survival. We used Jolly-Seber open population mark-recapture models to estimate annual abundance, survival, recruitment, and population growth rates of *L. getula* using Bayesian methods with data augmentation (Royle et al. 2007: Kéry and Schaub 2011). We defined annual study years to include only searches conducted between 10 October and 15 May of 1975–1976, 1976–1977, and 1977–1978, when 59 of 61 *L. getula* captures occurred. In this study all individual *L. getula* (n = 34) were captured at least once 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 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 (ϕ) constant across years. The superpopulation parameterization of the model we used required that recruitment (γ) varied among years (Royle and Dorazio 2008; Halstead et al. 2011; Kéry and Schaub 2011). The four models we evaluated were $p_{\bullet}\gamma_t\phi_{\bullet}$, $p_t\gamma_t\phi_{\bullet}$, $p_{\bullet}\gamma_t\phi_t$, and $p_t\gamma_t\phi_t$.

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 pseudo-individuals that were not present on the site. This approach is analogous to determining site occupancy (MacKenzie et al. 2002). We placed a U (0,1) prior on p and ϕ and a Dirichlet (1,1,1) prior on γ. 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 (DIC), which is interpreted in the same manner as Akaike's Information Criterion (Spiegelhalter et al. 2002). We ran all models using Markov Chain Monte Carlo (MCMC) methods as implemented in JAGS 3.4.0 (Plummer 2014) through R version 3.2.1 (R Core Team 2015) using the package runjags (Denwood 2015).

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 upon 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 (R-hat < 1.002 for all monitored parameters).

We examined the morphology, microhabitat use, and T_b of *L. getula* using standard statistical techniques. We used an exact binomial test to determine if the sex ratio of *L. getula* differed from 1:1, and a *t*-test to examine sexual size dimorphism in SVL and in body mass. 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 E vs. W banks and N vs. S 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_s as a covariate to control for differences in substrate temperature among observations. We used T_s rather than T_a as a covariate because individuals were usually in contact with the substrate and T_s was more strongly correlated with T_b than was T_a. T_s and T_a were also correlated ($r = 0.77$, $P < 0.001$), and it seemed unlikely that using T_a rather than T_s 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 study years by calculating the percent 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 percent mass loss per day. To examine body condition, we calculated a body condition index (BCI) as: BCI = (Body mass/SVL^3) x 10^5 (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 used AIC to evaluate the strength of evidence for different linear models (hypotheses) within each model set.

Only other snake species were detected as prey of *L. 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, potential prey were sampled by removing hyacinths from belt transects (see Godley 1980, for details). The 107 m^2 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. We used R 2.7.2 (R Core Team 2015) for all analyses except the mark–recapture analysis.

RESULTS

Population Structure and Size

Between November 1975 and May 1978, a total of 34 *L. getula* kingsnakes 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. The sex ratio of first-captured individuals was 1.13:1

(18 males, 16 females; 95% Confidence Interval [CI] = 0.54–2.36). Males were significantly longer in SVL than females (male mean = 1262 mm, female mean = 1085 mm; 95% CI of difference = 38–316 mm), but did not have significantly greater body mass (male mean = 853 g, female mean = 608 g; 95% CI of difference = -21–510 g). No individuals less than 800 mm SVL (immature; Krysko 2002) were observed. Model $p_{\bullet}\gamma_t\phi_{\bullet}$ was selected as the best-fit model (Table 1). Eastern Kingsnake p was 0.189 (mode; 95% Highest Posterior Density Interval [HPDI] = 0.129–0.259), and ϕ was 0.128 (0.020–0.345). Low apparent survival was offset by high recruitment (Fig. 1), resulting in a 0.969 probability of increasing abundance (B) 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 alive at Rainey Slough during the three years of the study was 45 (37–59).

Seasonal Activity

Seasonal activity of *L. 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 following sampling event (i.e., sampling without replacement on that day); and (3) as described below, *L. getula* used burrows in the canal banks particularly during winter and spring months, limiting their above-ground exposure to detection to 13–26% of the sampling days. Nevertheless, some meaningful patterns were obvious.

Table 2 summarizes the total number of live *L. 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 ($\rho = 0.57$, $P = 0.052$), and the greatest number of both occurred from January through May. At this site, shed skins lasted about a month in the field, and the relatively high number seen on 19 June 1976 (5) 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-h, sampling success was 8.3, 7.9 and 6.7-fold higher, respectively, from 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, Eastern Kingsnakes were closely associated with burrows in the canal banks, at least during winter and spring. Of the 64 observations of individual *L. 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 above ground and following them to a burrow down which they attempted to escape, (2) releasing a snake at its capture site and repeating the above observation, 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 *L. 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 some time ago. Burrows made by other species, including the Round-tailed Muskrat (*Neofiber alleni*), Marsh Rice Rat (*Oryzomys palustris*), Eastern Mole (*Scalopus aquaticus*), mice, shrews, and crayfish (*Procambarus* sp.) were 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 *L. getula*, 13 *Nerodia fasciata* (Southern Watersnake), 1 *N. floridana* (Florida Green Watersnake), 5 *Farancia abacura* (Red-bellied Mudsnake), and 1 *Coluber constrictor* (North American Racer). 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 to 1.2 m tunnel that was 20–30 cm below the surface. Four burrows contained a single kingsnake and one adult (SVL = 1240 mm) occupied a burrow with a 1560 mm 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.).

Many of the burrows known to harbor *L. getula* kingsnakes 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 the 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* adults were seen and sheds 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 three years 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 *L. getula* also entered the water hyacinth community rather than the nearby burrow. As described below, *L. getula* kingsnakes at Rainey Slough fed principally on semi-aquatic 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 SW corner of the bridge ($n = 21$), adult *L. getula* were non-randomly distributed among the four canal banks ($G = 61$, df = 3, $P < 0.001$). Individual kingsnakes were found equally on E- (NE = 2, SE = 27) and W-facing (NW = 3, SW = 14) canal banks (binomial probability of observation on E canal = 0.435, 95% CI = 0.316–0.560), but more were found S than N of the bridge (binomial probability of observation S of bridge = 0.928, 95% CI = 0.839–0.976). In addition, 10 of 18 recaptured *L. getula* kingsnakes were recorded from the SW 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 S of the bridge. Observations of live adults and shed skins among canal banks were associated, whether the SW bridge site was considered a separate location or not.

The use of rodent burrows as retreats by kingsnakes also affected their vertical distribution on the canal banks. Twenty of 28 individuals of *L. getula* recorded from the levee (road shoulder) portion of the canal banks were seen emerging from or found near a burrow at the SW 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 and observations of *Sigmodon hispidus* were made. To bask on shaded W-facing side slopes, adult *L. getula* often climbed onto tussocks of grass near their burrow. Kingsnakes observed on the levee or on E-facing slopes did not show this basking behavior.

Movements

During the study, 61% (11 of 18) of the marked male *L. 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 significantly correlated for males ($\rho = 0.12$, $P = 0.647$), females ($\rho = -0.41$, $P = 0.273$) or both sexes combined ($\rho = 0.018$, $P = 0.931$), so we examined distance moved between successive captures and the rate of movements separately. The mean distance moved between successive captures was 91 m (95% CI = 64–118 m) and was not affected by sex or SVL (Table 3). Similarly, the rate of movement did not vary by sex or SVL (mean distance moved per day = 5.1 m [1.5–8.8 m]); Table 3). Three *L. getula* (two males and one female) moved ≥ 100 m in one week or less.

No individuals of *L. getula* that were marked N or S 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

The Eastern Kingsnake at Rainey Slough apparently is diurnal, at least during winter and spring (Fig. 5). Including multiple observations of the same individuals, *L. getula* adults had a unimodal pattern of activity and were observed above ground between 0845 and 1725 h ($n = 78$). Most individuals ($n = 51$, 65.3%) were basking, which peaked in morning hours (Fig. 5). Individual *L. getula* were seen emerging from burrows ($n = 11$, 14.1%) between 0845 h and 1305 h; later observations of emergence were limited to days when the mornings were cold and/or cloudy, and some kingsnakes 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 percent exposure was not correlated with T_b ($\rho = -0.023$, $P = 0.904$). 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 *L. getula* whose stage of shed cycle was recorded, 23 (51%) were shedding when encountered above ground, with no difference between the sexes (females = 42%; males = 58%; $\beta_{male} = 0.315$, $z = 0.592$, $P = 0.554$). Marked individuals were found shedding at intervals as short as 16, 28, and 42 days.

Temperature data for 29 adult *L. 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, T_b 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 – -1.8ºC), but no other significant differences in behavior among individuals were noted. The lowest T_b of an emerging *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 their bodies wedged into a burrow (female first). No significant differences in the proportion of 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 percent of mass lost per day for individual *L. getula* was best explained by sex (Table 5), and males lost mass at a much greater rate than females (female mean = -0.018% per day, male mean = -0.21% per day, 95% CI of difference = -0.42–0.025). Consequently, between 10 October and 15 April males lost on average 39.3% of their body mass and females 3.4% of their mass. Subsequent recaptures, though few, indicated that snakes regained the lost weight over the remaining spring and summer (Fig. 7).

The BCI of individuals was best explained by sex (Table 6), and females had greater body condition than males (female mean = 0.043, male mean = 0.039, 95% CI of difference = -0.0066 – -0.00047). The within-study year change in BCI was best explained by the number of days elapsed between measurements of individuals (Table 7); we found no significant difference in the rate of BCI change between males and females (female mean = -0.00014 BCI units per day, male mean = -0.00089 BCI units per day, 95% CI of difference = -0.0024–0.00034).

Predator–Prey Relationships

Only three (4.8%) of 62 total captures of kingsnakes at Rainey Slough contained detectable prey (one each in March, October, and November), all of which were snakes eaten by females. One female contained two *Regina alleni* (Striped Crayfish Snake; 14.0% and 19.4% of the kingsnake's body mass), another one *R. alleni* (6.0% of body mass), and the third a *Nerodia* sp. of undetermined size and a *C.constrictor* (39.7% of body mass). Water hyacinth rootlets were found in the first and third of these kingsnakes, indicating that at least one of the two prey items in both individuals was consumed in the water hyacinths. One punitive kingsnake stool found at the bridge den site contained remains of a *Nerodia* sp. of undetermined size and a *C. constrictor* estimated to be 128 g (17.4 % of mean mass of kingsnakes at this site). Two male kingsnakes basking at the bridge site on different days in February briefly tongue-flicked and pursued *N. fasciata,* that was moving nearby, but returned to a coiled, basking position in < 1 min.

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 an adult Eastern Kingsnake at Rainey Slough (0.745 kg, Fig. 8). The remaining eight larger snakes included five *F. abacura,* two *Agkistrodon picivorous* (Cottonmouth)*,* one *N. floridana*, and one *N. fasciata* (Fig. 9). Of the ten species of potential snake prey, two were collected only in water hyacinths (*Seminatrix pygaea* [Black Swampsnake] and *R. alleni),* four only on canal banks (*A. picivorous, C. constrictor, Micrurus fulvius* [Harlequin Coralsnake], and *Pantherophis alleghaniensis* [Eastern Ratsnake]), and four in both habitats (*N. fasciata, N. floridana, F. abacura*, and *Thamnophis sauritus* [Eastern Ribbonsnake]). The density of potential snake prey in the hyacinth community was significantly greater in winter than all other seasons, similar in spring and fall, and significantly lower during the summer (Fig. 10). The number of kingsnakes observed per searcher-h by month (Table 2) was not correlated with the total number of potential snake prey observed on canal banks by month (ρ = 0.035, *P* = 0.914), nor with the density of semi-aquatic snake prey observed by month (ρ = 0.440, *P* = 0.175).

Rainey Slough in the Intervening Four Decades

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 Rainey Slough (J.S. Godley, personal observation). When examined in June 1981 the

NE and SE canals had been re-excavated and the extracted material deposited along the SE and SW 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 N and improved pasturelands to the S.

No kingsnakes or their sheds were found in 2006–2010 on the canal banks or in the water hyacinths. The 223 m^2 of sampled water hyacinths yielded three species of semi-aquatic snakes (1 *N. fasciata,* 13 *N. floridana, and* 4 *R. 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, M. fulvius*, and *C. constrictor*.

DISCUSSION

Population Size and Structure

Here, we frame the population ecology of *L. 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 *L. getula* species complex with adequate samples (Blanchard 1921; Fitch 1949; Hansen 1982; Mitchell 1994; Palmer and Braswell 1995; Minton 2001; but see Jenkins et al. 2001 and Faust and Blomquist 2011), 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 (1178 mm) was similar to that (ca. 1180 mm) in the Lake Okeechobee (= LOP, 80 km ESE of Rainey Slough) population 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 Dade County (= SDCP, 180 km SSE) study site, 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, 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 LOP and SDCP combined, Krysko (2002) reported that 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 ca. 15 juvenile kingsnakes (< 40 cm SVL) in about 2 h beneath large rocks on a canal bank in Krysko's (2002) LOP study site, a microhabitat that did not exist at Rainey Slough. Juvenile *L. 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 *L. 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. The between-study year apparent survival rate of this population (0.16 [0.02–0.34]) was much lower than many other late-maturing temperate colubrids (Parker and Plummer 1987; Breininger et al. 2012; Hyslop et al. 2012), perhaps because of 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).

To our knowledge, no published estimates of survivorship or population size exist for any other population of *L. getula* kingsnakes (but see Hansen [1982] and Anguiano and Diffendorfer [2015] for *L. californiae,* 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 kingsnakes along canal banks from January through May, Fig. 1 in Krysko (2002) indicates an encounter rate of about 0.74 individuals/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* kingsnakes would leave their burrows to move along canal banks in sugarcane fields near LOP, and 25–30 individuals could be collected in one afternoon, a weather event in which we did not sample. On single days along the canal banks of S.R. 441 on Paynes Prairie, Alachua County, Florida, Kauffeld (1957) and two colleagues in April 1936 collected about 20 *L. getula* (mostly under mats of cut grass) and Carr (1940) collected eight in one day (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. Clark (1949) and two assistants collected 50 individuals of *L. holbrooki* in 5 h in the late 1920s in Louisiana. These records emphasize the apparent historic number and ecological significance of kingsnakes in the herpetofaunas of at least the southeastern USA.

Seasonal and Daily Activity Patterns

As described below, activity patterns of kingsnakes in the *L. getula* species complex throughout its transcontinental 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 semi-fossorial species, as well as their daily pattern of activity.

On the canal banks of Rainey Slough, *L. getula* kingsnakes were detectable primarily in winter and spring (Table 2). Systematic searches of canal and levee banks for kingsnakes at LOP and in SDCP 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 SDCP, March–April at LOP and Rainey Slough (Krysko 2002; present study); Georgia: April and May (Linehan et al. 2010); South and North Carolina: May and June (Gibbons and Semlitch 1987; Palmer and Braswell 1995); Tennessee: May (Jenkins et al. 2001); California: April and May in southern coastal region (Hansen 1982; Hubbs 2009; Anguiano and Diffendorfer 2015), but May and June in inland valleys and foothills (Fitch 1949); and New Mexico: delayed to July with advent of rainy season (Price and LaPointe 1990; Degenhardt 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 Semlitch 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 *L. getula* spent above ground and were subject to capture: (1) the study population consisted of large (> 800 mm SVL), conspicuous 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 above ground behavior (Fig. 5) during which time the bodies of most kingsnakes were partially or completely exposed from cover; and (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.

Averaged over the entire activity season during daylight hours, radio-tracked *L. getula* kingsnakes (*n* = 9) in New Jersey were concealed (underground and/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 were located in burrows (mostly mole tunnels) in 60% of the observations (Trauth et al. 2004). Radio-tracked individuals of *L. californiae* (*n* = 34) were underground in 76% of 2684 locations (Anguiano and Diffendorfer 2015). None of these authors reported seasonal variation in above-ground activity except that associated with hibernation. However, radio-tracked individuals of a northern population of Prairie Kingsnakes, *L. c. calligaster*, (n = 10) exhibited a spring peak in above-ground activity in Illinois, but in the daytime were underground 73% of the total activity season (Richardson et al. 2006). Collectively, these values are similar to that reported for *L. getula* adults at Rainey Slough during winter–spring ($1 - p$ = 81.1% [74.1–87.0%]).

During winter and spring both males and females of *L. 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 radio-telemetry studies cited above also are similar in many respects. Together they indicate that kingsnakes usually returned to their home ranges from the previous year, established these home ranges quickly following emergence from hibernation, 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 activity 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* individuals).

At least during the winter and spring, kingsnakes at Rainey Slough 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 *L. getula* kingsnakes living in hot, arid environments (Gates 1957; Hansen 1982; Werler and Dixon 2000; Price and LaPointe 1990; Degenhardt et al. 1996; Hubbs 2009). In the only radio-telemetry study that sampled at night, Howze and Smith (2012) found *L. getula* kingsnakes 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 warmer 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 *L. 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 densities fluctuating from 10 to 25/ha in flatwoods in Florida (Layne 1974) and from 8 to 65/ha in old fields in Georgia (Odum 1955). With only about 0.8 ha of unmowed 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 man-made canal banks at Rainey Slough likely represented the only suitable communal over-wintering 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 *L. getula* kingsnakes.

Steen and Smith (2009) suggested that adult *L. 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 one day 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 occurs 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 *L. getula* and *L. californiae*.

Nearly every published source of information on kingsnakes of *L. getula* and its closely related congeners (Pyron and Burbrink 2009a) characterizes their preferred habitat as bottomland, moist, or near water (21 citations), and Kauffeld (1957) stated "selection of moist habitats by kingsnakes is partly because food snakes are abundant." Eleven studies described the species swimming or in water: Carr (1940) 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* kingsnakes 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 *L. getula* snakes 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 kingsnakes 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 *L. getula* 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_s on 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 *L. 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 a T_b within their preferred range (Fig. 6).

From 10 October through 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 and 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 *L. getula* greatly exceeds that reported for snakes hibernating in dens for extended periods (200+ days) 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 (ca. -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 above ground, in T_b (Table 4), or in movements (Table 3), perhaps because of small sample sizes. However, in another study male *L. 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 the spring mating season. Male individuals of *C. 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 (54:32) in encounter rates during the breeding season on canal banks in south Florida, as did Linehan et al. (2009) in Georgia. The museum specimens examined by Blaney (1977, Table 1) from throughout the range of the *L. getula* species complex he studied also were biased towards males (464:319), with most individuals of both sexes likely collected in the spring (see above). These studies suggest that adult male kingsnakes are more active above ground than females during the spring reproductive season and expend relatively more energy in reproductive behaviors (mate searching, courtship and combat) during this period. It is also possible that male *L. getula,* like Adders (Olsson et al. 1997), also incur substantial metabolic costs associated with spermatogenesis and elevated testosterone levels. The few records of feeding in this population (3 of 62 captures) were all from females, and two females showed substantial weight gains in the spring (Fig. 7), suggesting feeding events. We palped no eggs in females during this study, but some likely were gravid. 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 *L. getula* in the water hyacinths and on the canal banks of Rainey Slough provides insight into prey selection and availability, both factors potentially regulating the local population size of kingsnakes, and the concomitant use of available habitats in this seasonally fluctuating, semi-tropical environment by both the predator and its prey.

The only prey detected in kingsnakes at Rainey Slough was other snakes. Credible records of feeding in the wild throughout the range of *L. getula* (Table 8) are dominated by reptiles (snakes, lizards, eggs of other squamates and turtles), which accounted for 86.4% of the 110 kingsnakes with prey and 88.4% of the 181 individual prey items. At Rainey Slough, snakes likely comprise the bulk of the diet of *L. 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, 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); (3) although most semi-aquatic turtles known from Glades County, Florida (Krysko et al. 2011) were collected at Rainey Slough (including *Apalone ferox, Chelydra serpentina, Kinosternon baurii, K. subrubrum, Pseudemys floridana, P. nelson,* and *Sternotherus odoratus*), they accounted for only 1.1% of the sampled water hyacinth herpetofauna and their nests were uncommon on the canal banks (J. S. Godley, personal observation); and (4) small mammals also were uncommon and consisted primarily of *Sigmodon 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* that have relatively small heads (ca. 3% of SVL in adults; Blaney 1977).

Relative to the adult kingsnake population at Rainey Slough, the body-size distribution of potential snake prey (Fig. 9) was strongly skewed towards smaller snakes (65% ≤ 40 g) that included most individuals of the numerically dominant *S. pygaea* and *R. alleni* (32.4% and 27.1% of 351 total snakes, respectively), as well as *T. sauritus, M. fulvius*, 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, *C. constrictor* and *A. piscivorus* only seen on canal banks) and age classes of others (e.g., only adult *N. fasciata, N. floridana*. and *F.abacura* appeared to over-winter 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 *L. getula*] likely evaded capture by the 0.56-m^2 hyacinth sieve and smaller individuals of all species were more difficult to detect on canal banks).

The seven snake prey found in *L. getula* kingsnakes at Rainey Slough included three *R. alleni*, two *Nerodia* sp., and two *C. constrictor*, and these prey ranged from 6.0 to 37.9% of the predatory kingsnake's body mass. All ten snake species collected at this site are known prey of *L. getula* (Table 8) and likely were consumed if of appropriate size. It is likely that kingsnakes at this site consumed much smaller (and numerically abundant) snakes and these prey were undetectable by palping the stomach. Table 8 suggests that *L. getula* adults commonly eat prey that individually are very small: of the ___ prey items for which a mass ratio could be estimated, ___ (___%) were < 2% of kingsnake body mass. Although in the lab California Kingsnakes (*L. californiae*) can successfully consume and digest snakes that are longer and weigh more than themselves (1.06: 1 mass ratio, Jackson et al. 2004), in the field the largest snake prey of which we are aware was a 107 cm total length (TL) adult *L. getula* that ate a 111 cm TL adult *Pantherophis alleghaniensis* (Table 8) with an estimated mass ratio of 0.86:1 (Kaufman and Gibbons 1975). Prey constriction coupled with head-first ingestion, biomechanical adaptations for eating elongate prey (Jackson et al. 2004), and venom-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 mean size of the *L. getula* population ranged from 11–19 adults (Fig. 2) that averaged 0.745 kg in body mass (Figs. 8, 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 (J. S. Godley, unpublished). Thus, for the entire 2.71-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: 1), 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 a California Kingsnake (*L. californiae*) consumed 25% of its body mass in prey every 12 days of the active season. Assuming similar consumption rates from April through November and a rate of 35% of this value for the cooler transition months of December through March (Table 2 of Secor and Nagy 1994; S.M. Secor, personal communication), the average *L. getula* adult 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 *L. getula* 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 by a lizard and snake predator, respectively. An extensive correlative study in the southeastern USA (Steen et al. 2014) identified a strong negative relationship between the relative abundances of kingsnakes (*L. 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 densities in the hyacinths in the 1970s (3534/ha) decreased 77.2% (807.4/ha) by 2006–2010 in the absence of what was a dense *L. getula* population, indicating that other factors now regulate semi-aquatic snake populations in this system.

Finally, several lines of evidence indicate that at Rainey Slough*,* the *L. getula* population historically was dependent on the migration of potential snake prey in response to the pronounced wet–dry season in this region, where 61% of the total annual rainfall occurs between June and September (ABS rainfall records, 1938–2014). The density of semi-aquatic snake prey in the canals at Rainey Slough was strongly correlated with season (Fig. 10) and water levels (Godley 1980 and personal observation). With the advent of summer rains in June, the marshes of Rainey Slough re-flood, the density of semi-aquatic snakes in the water hyacinths declines dramatically (e.g., in *R. alleni*, 30 times lower in the summer than in the winter; Godley 1980), and *L. getula* kingsnakes seemingly disappear from the canal banks (Table 4 and Krysko 2002). Semi-aquatic 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 semi-aquatic 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 semi-aquatic 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). Semi-aquatic 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 an *L. getula* kingsnake at from Rainey Slough was on 25 January 1984; an adult was observed basking on the NW canal bank (ABS files; F.E. Lohrer, personal communication). Our surveys of canal banks and water hyacinths at Rainey Slough over seven days 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 from January through May (Table 2) would have yielded 17.0 observations of live *L. getula* and 5.1 sheds of kingsnakes. We assume the population is extirpated and suspect this event likely occurred before 1990.

The collapse and disappearance of *L. getula* populations across much of its range in the southeastern USA (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 other snake and reptile species (e.g., Gibbons et al. 2000; Gardner et al. 2007; Reading et al. 2010). The extirpation of kingsnakes of *L. getula* is particularly vexing because some populations in seemingly well-managed habitats, such as Conecuh National Forest in Alabama (Steen et al. 2014), Apalachicola National Forest in Florida (Krysko and Smith 2005), and at 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 (Ichauway and Albany, Georgia; Stapleton et al. 2008).

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 *L. getula* locality (Godley 1982) also made this population vulnerable to collecting pressure. The invasive red imported fire ant (*Solenopsis invicta*), which has been implicated as a potential cause for declines in *L. getula* populations (see above citations) and many other species (see reviews in Wojcik et al. 2001; Allen et al. 2004; Tschinkel 2006), reached Glades County by 1971 and had fully infested the County by 1975 (Callcott and Collins 1996). However, fire ants also were and are abundant in the sugarcane/canal banks of the LOP (Krysko and Smith 2005) and *L. getula* kingsnakes remain common there where human access and collecting is tightly controlled (Enge 2005 and personal communication). Finally, we have no evidence that environmental contamination, disease and parasitism, or climate change (Gibbons et al. 2000) affected *L. getula* populations at Rainey Slough. What we do know is that which was once an Eden for Eastern Kingsnakes has now vanished (Barbour 1945).

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Table 1.—Open population Jolly-Seber model selection results for adult *Lampropeltis getula* at Rainey Slough, Florida, 1975–1978. Models are listed in order of decreasing evidence.

Model	Bayesian p-value	DIC	ΔDIC
$p_{\bullet}\gamma_{t}\phi_{\bullet}$	0.523	135.1	0.0
$p_{t}\gamma_{t}\phi_{\bullet}$	0.470	136.8	1.7
$p_{\bullet}\gamma_{t}\phi_{t}$	0.497	136.9	1.8
$p_{t}\gamma_{t}\phi_{t}$	0.449	137.6	2.5

Table 2.—Monthly activity of adult *Lampropeltis getula* at Rainey Slough, Florida, as measured by the total number of different individuals summed over sampling days (Live Obs.), total number of shed skins, and three estimates of sampling success: Live Obs./total # sampling days (Obs./Day), Live obs./total # searcher-days (Obs./searcher-days), and Live Obs./total # searcher-h (Obs./Searcher-h).

Month	Live Obs.	Shed Skins	Total Sampling Days	Obs./ Days	Total Searcher-day	Obs./ Searcher-days	Total Searcher-h	Obs./ Searcher-h
J	6	3	2	3.00	5	1.20	14.00	0.43
F	26	8	12	2.17	38	0.68	90.25	0.29
M	14	4	6	2.33	11	1.27	39.50	0.35
A	11	3	4	2.75	13	0.86	25.00	0.44
M	6	1	2	3.00	8	0.75	27.00	0.22
J	1	5	2	0.50	6	0.17	24.00	0.04
J	1	--	2	0.25	10	0.09	13.75	0.06
A	--	1	3	--	9	--	14.00	--
S	--	1	1	--	2	--	6.00	--
O	1	--	2	0.50	4	0.25	15.50	0.06
N	1	--	1	1.00	3	0.33	9.00	0.11
D	--	1	1	--	2	--	4.00	--
Total	67	27	38		121		282.00	

Table 3.—Model selection results for the influence of sex and size on movements of adults of *Lampropeltis getula* at Rainey Slough, Florida. All models contain an intercept term and individual ID as a random effect to account for multiple observations of the same individual. Models are listed in order of decreasing support.

Model	Deviance	AIC$_c$	ΔAIC$_c$	Weight
Distance between subsequent captures				
Distance = constant	294.4	298.9	0.00	0.64
Distance = sex	294.4	301.5	2.57	0.18
Distance = SVL	294.4	301.5	2.57	0.18
Movement rate (m/day)				
Movement rate = constant	168.9	173.4	0.00	0.56
Movement rate = SVL	167.8	174.9	1.41	0.28
Movement rate = sex	168.8	175.9	2.49	0.16

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 ID 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.

Model	Deviance	AIC$_c$	ΔAIC$_c$	Weight
T_b = Behavior + T_s	234.3	246.2	0.00	0.44
T_b = Behavior + Sex + T_s	227.8	247.8	1.57	0.20
T_b = T_s	239.0	248	1.77	0.18
T_b = Sex + T_s	237.8	249.3	3.11	0.09
T_b = Hour + T_s	238.4	249.9	3.71	0.07
T_b = Hour + Hour^2+ T_s	238.0	252.2	5.98	0.02
T_b = Behavior * Sex + T_s	227.0	257.0	10.77	<0.01

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

Model	Deviance	AIC$_c$	ΔAIC$_c$	Weight
Daily percent mass change = Sex	0.43	-3.84	0.00	0.53
Daily percent mass change = Null	0.54	-3.45	0.38	0.43
Daily percent mass change = Year	0.49	1.23	5.07	0.04

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 ID 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 01 October. Models are listed in order of decreasing support.

Model	Deviance	AIC_c	ΔAIC_c	Weight
BCI = Sex	-158.0	-153.8	0.00	0.27
BCI = SVL + Sex	-159.1	-152.7	1.09	0.16
BCI = SVL	-156.5	-152.3	1.52	0.13
BCI = Sex + Date	-158.5	-152.1	1.67	0.12
BCI = Year	-157.8	-151.5	2.33	0.08
BCI = SVL + Sex + Date	-159.8	-151.2	2.64	0.07
BCI = SVL + Date	-157.5	-151.1	2.71	0.07
BCI = Null	-153.1	-151.1	2.74	0.07
BCI = Date	-154.0	-150.0	4.02	0.04

Table 7.—Model selection results for the influence of sex, year, and days elapsed on within-year body condition index (BCI) change in adults of *Lampropeltis getula* at Rainey Slough, Florida. All models contain an intercept term. Models are listed in order of decreasing support.

Model	Deviance	AIC$_c$	ΔAIC$_c$	Weight
BCI change = Days elapsed	0.0085	-56.94	0.00	0.43
BCI change = Intercept	0.0104	-56.85	0.09	0.41
BCI change = Sex	0.0099	-55.82	2.21	0.14
BCI change = Year	0.0100	-53.28	5.66	0.03

FIGURE LEGENDS

FIG. 1.—Annual recruitment (*B*) in the *Lampropeltis getula* kingsnake population at Rainey Slough, Florida, in 1976 and 1977. Points represent posterior modes; error bars are 95% highest posterior density intervals.

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.

FIG. 3.—Population growth rate (λ) 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.

FIG. 4.—Distance of adult *Lampropeltis getula* from burrows known to be used by kingsnakes at Rainey Slough, Florida.

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

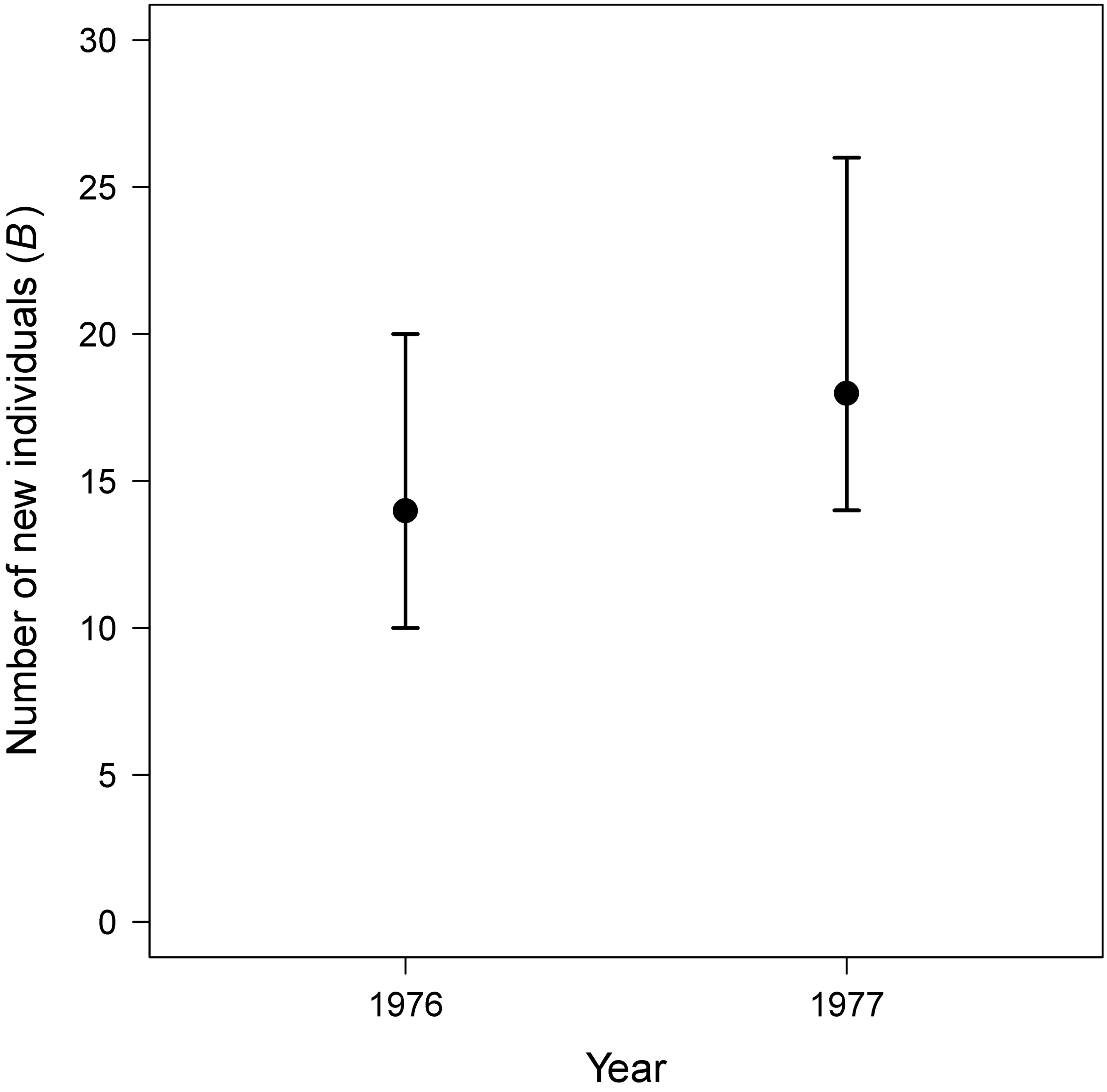
FIG. 6.—Cloacal body temperature (T_b) of *Lampropeltis getula* adults as they were emerging from a burrow (E), basking (B), moving (M), or courting (C) during daylight hours at Rainey Slough, Florida. Shown to the right are sample size, range (vertical line) and mean (bar) of T_b for each behavior.

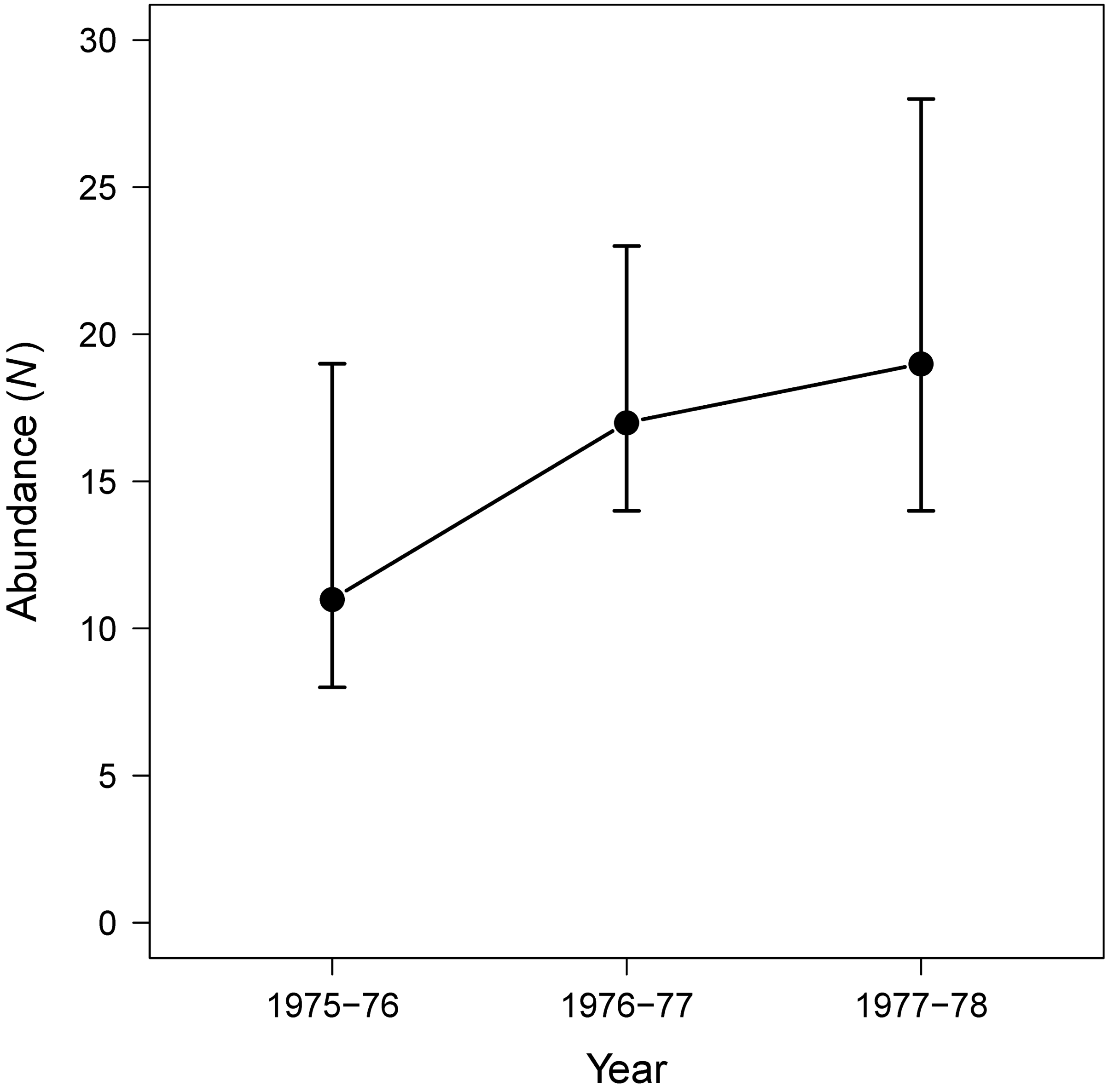
FIG. 7.—Body condition index of male (closed circles) and female (open circles) *Lampropeltis getula* adults at Rainey Slough, Florida. Lines connect individuals recaptured in same (solid) or different (dashed) study years.

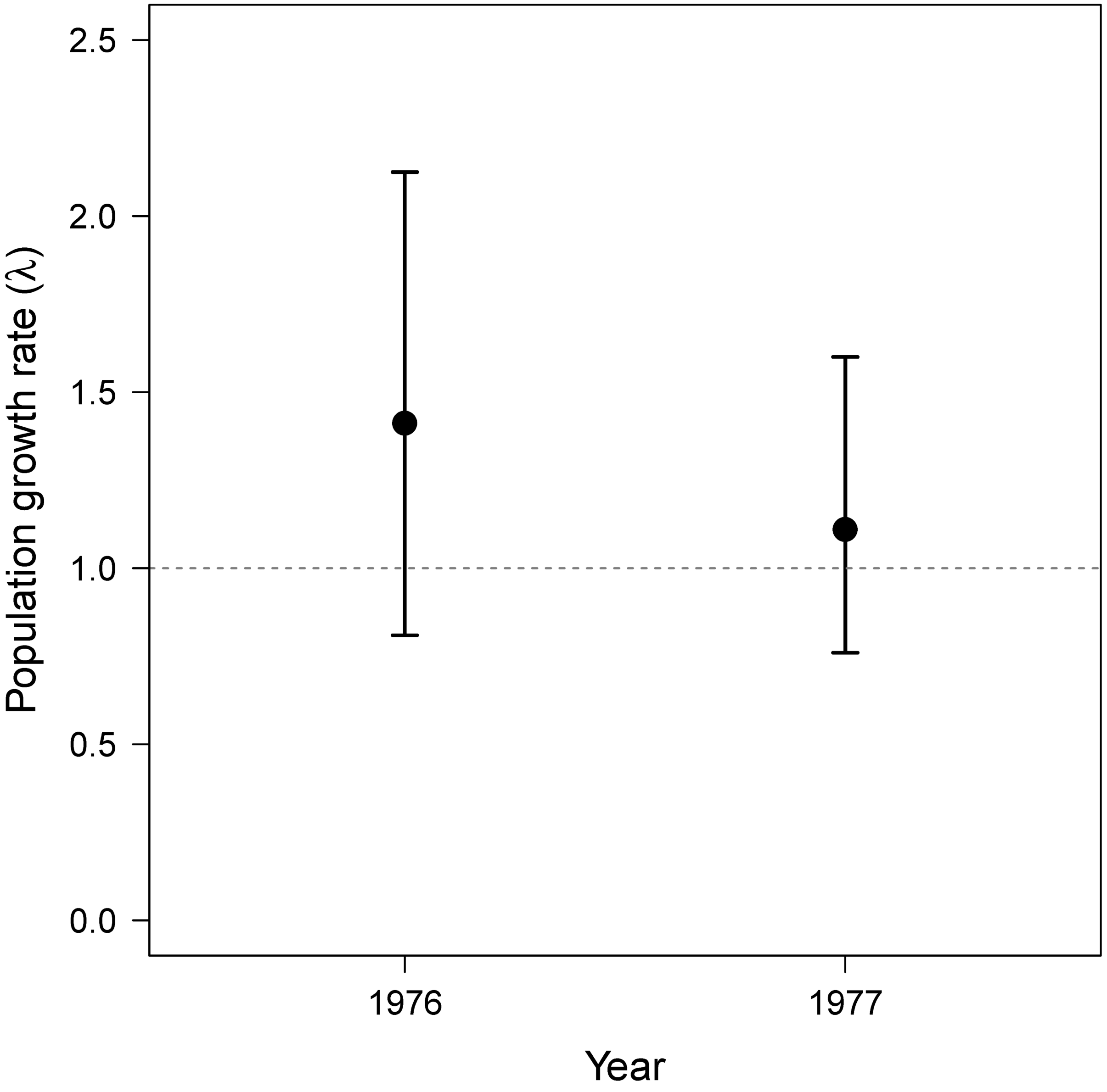
FIG. 8.—Frequency distribution of body mass (g) of first-captured *Lampropeltis getula* individuals and potential snake prey collected in water hyacinths or on canal banks at Rainey Slough, Florida, 1974–1978.

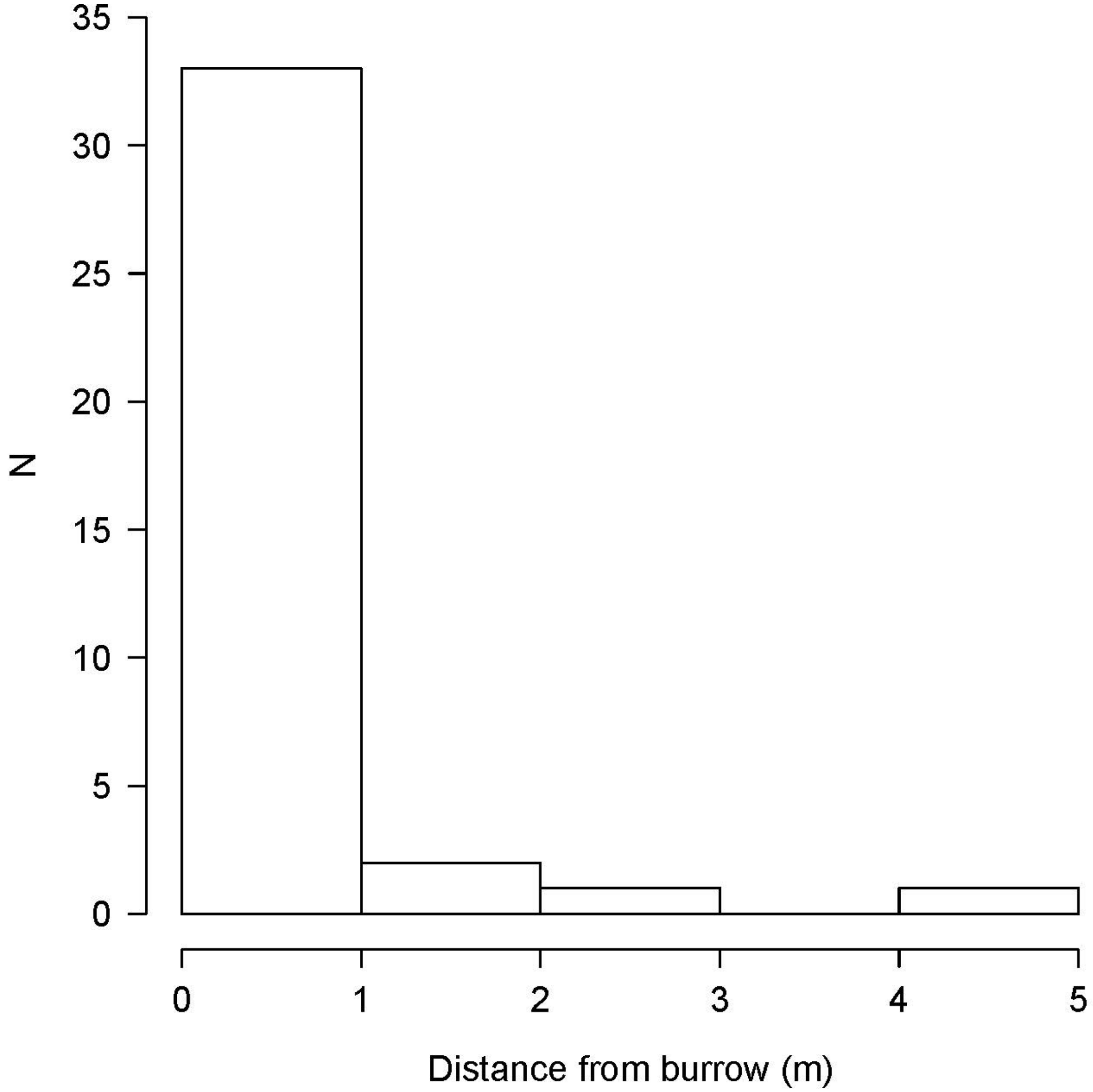
FIG. 9.—Frequency distribution of body mass (g) of first-captured *Lampropeltis getula* individuals and potential snake prey species collected in water hyacinths or on canal banks at Rainey Slough, Florida, 1974–1978.

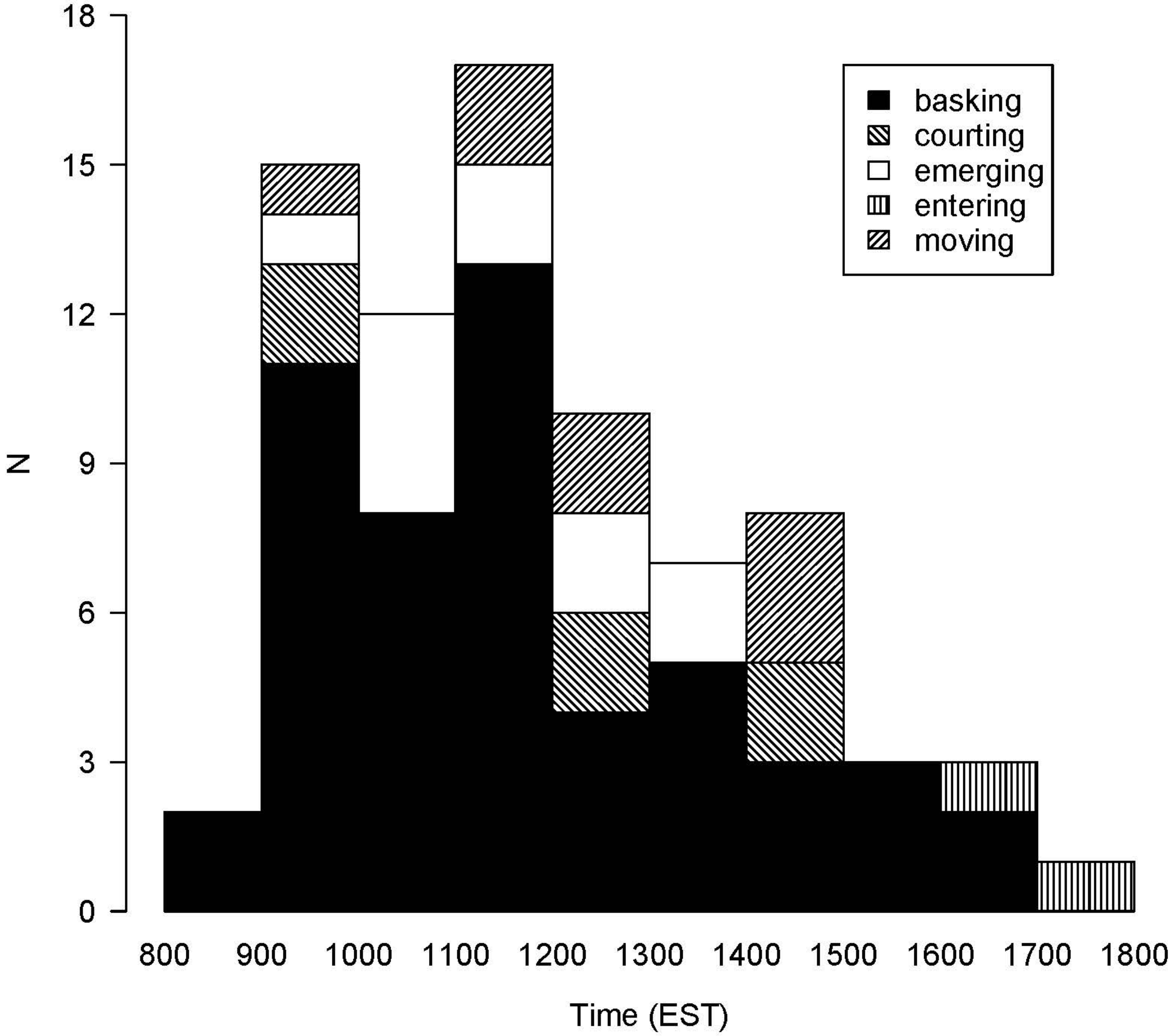
FIG. 10.—Mean density (vertical bar = 95% CI) of potential snake prey collected by season in water hyacinths at Rainey Slough, Florida, 1974–1978.

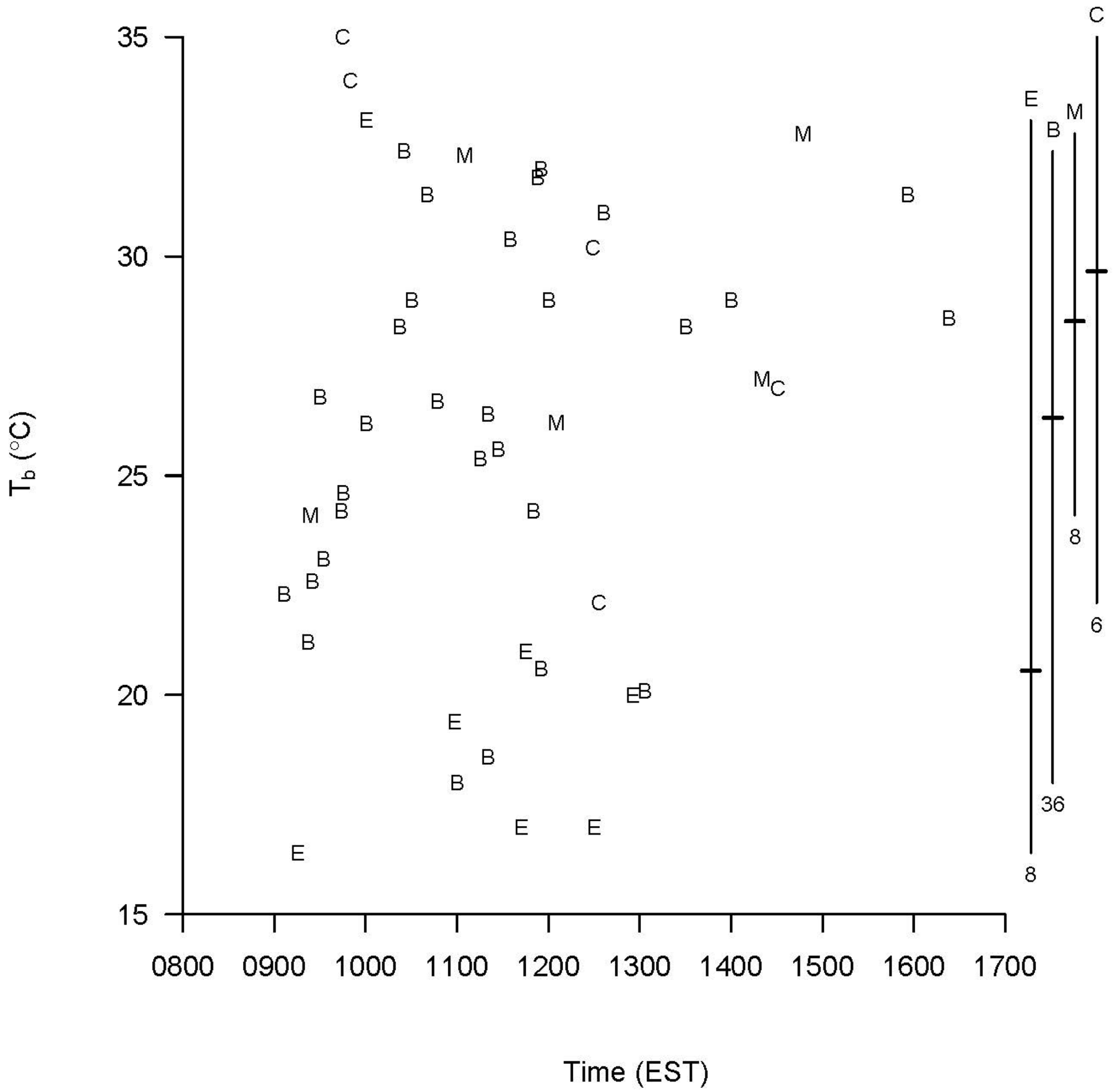

Number of new individuals (*B*)
30
25
20
15
10
5
0
1976
1977
Year

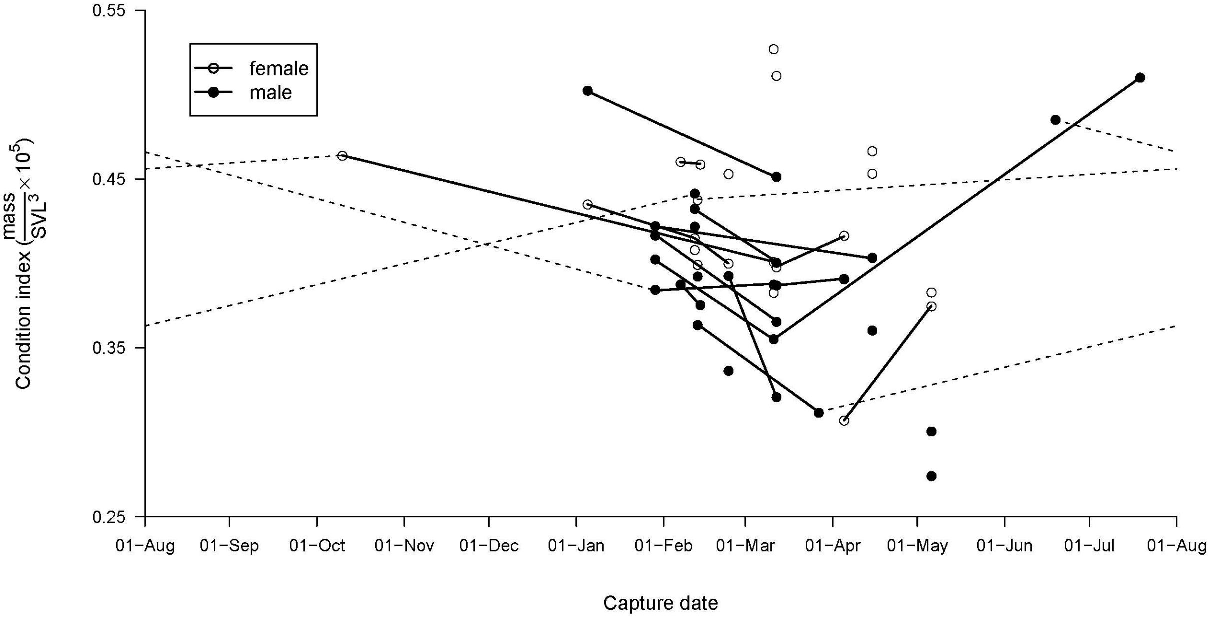

30
25
20
15
10
5
0
Abundance (*N*)
1975−76
1976−77
1977−78
Year

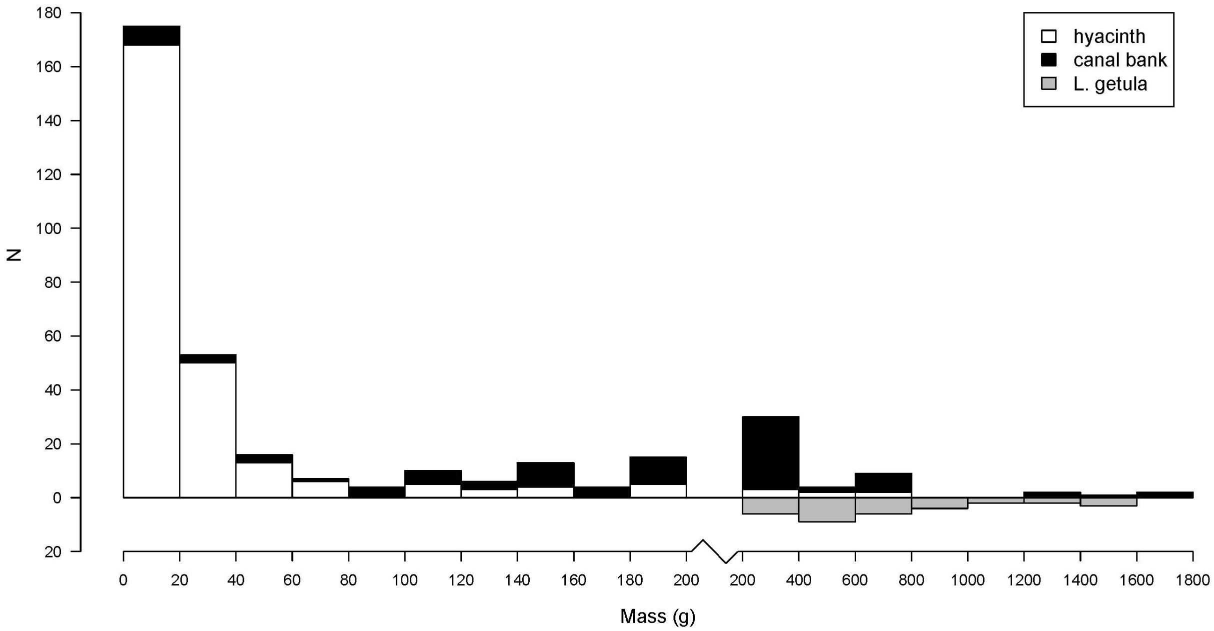

2.5
2.0
1.5
1.0
0.5
0.0
Population growth rate (λ)
1976
1977
Year

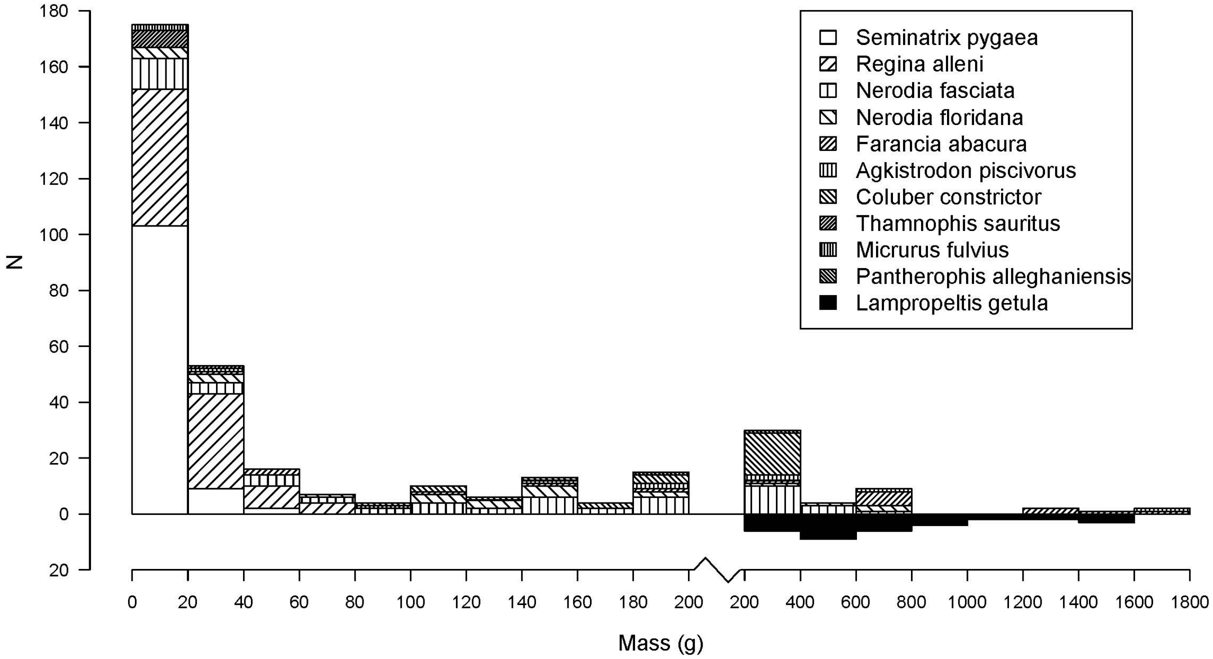

35
30
25
20
15
10
5
0
N
0
1
2
3
4
5
Distance from burrow (m)

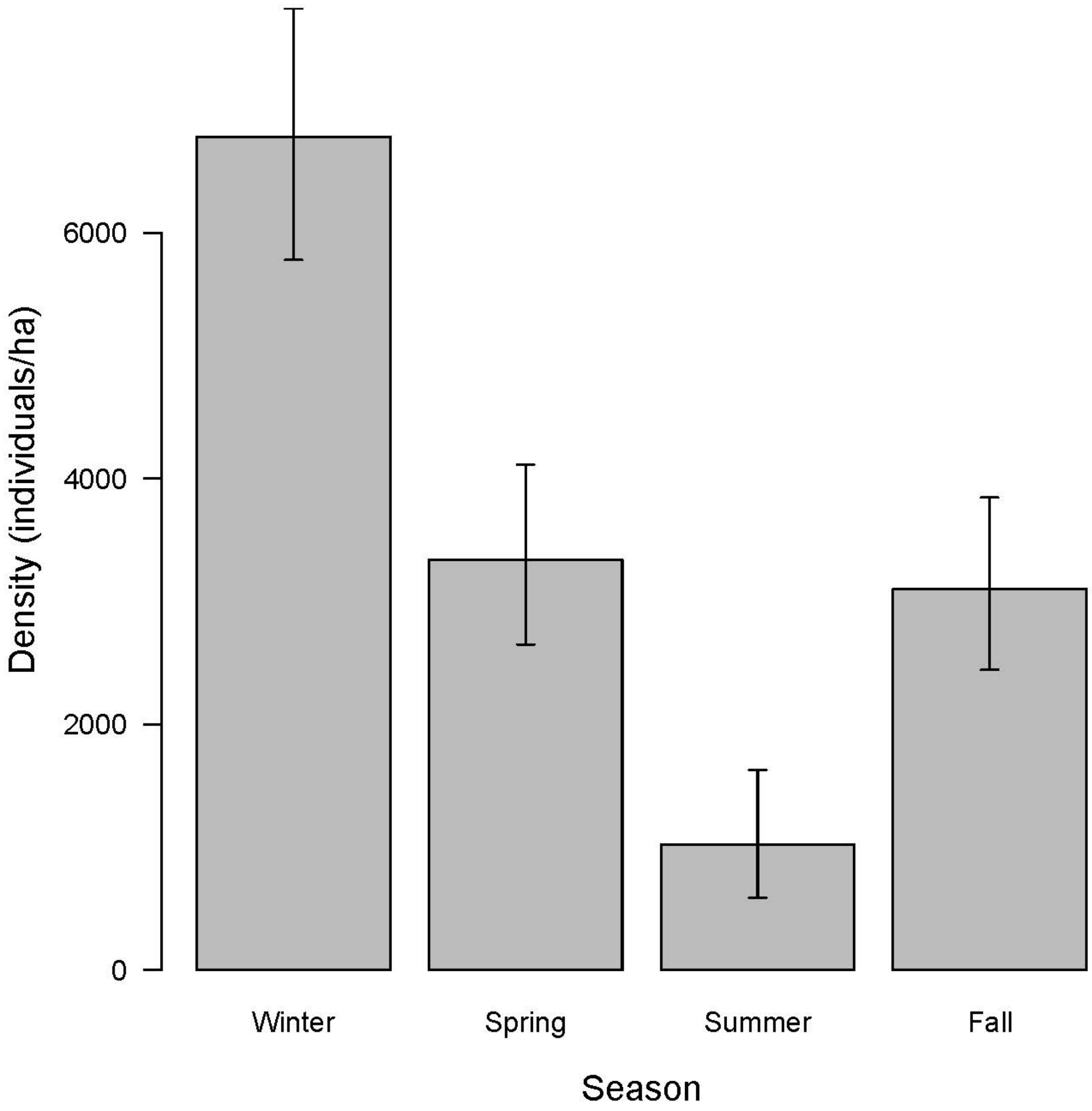

18
15
12
9
6
3
0
N
800
900
1000
1100
1200
1300
1400
1500
1600
1700
1800
Time (EST)
basking
courting
emerging
entering
moving


35
30
25
20
15
Tb (°C)
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700
Time (EST)
E
B
M
C
8
36
8
6


0.55
0.45
0.35
0.25
female
male
Condition index $\left(\frac{\text{mass}}{\text{SVL}^3} \times 10^5\right)$
01−Aug
01−Sep
01−Oct
01−Nov
01−Dec
01−Jan
01−Feb
01−Mar
01−Apr
01−May
01−Jun
01−Jul
01−Aug
Capture date


180
160
140
120
100
80
60
40
20
0
20
N
hyacinth
canal bank
L. getula
0
20
40
60
80
100
120
140
160
180
200
200
400
600
800
1000
1200
1400
1600
1800
Mass (g)


N
180
160
140
120
100
80
60
40
20
0
20
0
20
40
60
80
100
120
140
160
180
200
200
400
600
800
1000
1200
1400
1600
1800
Mass (g)
Seminatrix pygaea
Regina alleni
Nerodia fasciata
Nerodia floridana
Farancia abacura
Agkistrodon piscivorus
Coluber constrictor
Thamnophis sauritus
Micrurus fulvius
Pantherophis alleghaniensis
Lampropeltis getula


Density (individuals/ha)
0
2000
4000
6000
Winter
Spring
Summer
Fall
Season