

# Intraspecific and interspecific variation in use of forest-edge habitat by snakes

Gerardo L.F. Carfagno and Patrick J. Weatherhead

**Abstract:** Variation in use of edge habitat among populations and species of snakes should reflect underlying causes (e.g., thermal ecology, prey availability) and consequences (e.g., predation on birds' nests) of habitat selection. We compared the habitat use of ratsnakes, *Elaphe obsoleta* (Say in James, 1823), in Illinois and Ontario and compared habitat use by ratsnakes and racers, *Coluber constrictor* (L., 1758), in Illinois. Ratsnakes in Illinois used upland forest more and forest edges less than ratsnakes in Ontario. Female ratsnakes in Illinois used edges less than males, regardless of their reproductive status. Relative to ratsnakes, racers preferred forest edges and avoided forest interior. Female racers used edges more than males, especially while gravid. These results, and most of the seasonal patterns in habitat use, were broadly consistent with variation expected from differences in thermoregulatory needs, although other factors potentially influencing habitat use cannot be ruled out. Although it has been proposed that some forest fragmentation is likely to be beneficial for ratsnakes in Canada, such fragmentation may be detrimental to ratsnakes in Illinois but beneficial to racers. Thus, relative to forest-interior species, edge-nesting birds should be more vulnerable to predation by ratsnakes in Ontario, and fragmentation should increase the vulnerability of forest birds to nest predation by racers.

**Résumé :** La variation dans l'utilisation des habitats de bordure dans les diverses populations et espèces de couleuvres devrait refléter les causes (par ex., l'écologie thermique, la disponibilité des proies) et les conséquences (par ex., la prédation sur les nids d'oiseaux) sous-jacentes de la sélection d'habitat. Nous avons comparé l'utilisation de l'habitat chez les couleuvres obscures, *Elaphe obsoleta* (Say in James, 1823) en Illinois et en Ontario et comparé l'utilisation de l'habitat chez les couleuvres obscures et les couleuvres agiles, *Coluber constrictor* (L., 1758), en Illinois. Les couleuvres obscures d'Illinois utilisent plus les forêts de terres hautes et moins les bordures de forêt que les couleuvres obscures d'Ontario. Les couleuvres obscures femelles en Illinois utilisent moins les bordures que les mâles, quel que soit leur statut reproductif. Par rapport aux couleuvres obscures, les couleuvres agiles préférèrent les bordures et évitent l'intérieur des forêts. Les couleuvres agiles femelles utilisent plus les bordures que les mâles, particulièrement lorsqu'elles sont gravides. Ces résultats, de même que la plupart des patrons saisonniers d'utilisation de l'habitat, s'accordent en général avec la variation attendue des différences dans les besoins de thermorégulation, bien qu'on ne puisse éliminer d'autres facteurs qui pourraient influencer l'utilisation de l'habitat. Bien qu'on ait proposé qu'une certaine fragmentation de la forêt puisse être favorable aux couleuvres obscures au Canada, une telle fragmentation en Illinois est peut-être défavorable aux couleuvres obscures, mais favorable aux couleuvres agiles. Ainsi, les oiseaux qui nichent en bordure des forêts devraient être plus vulnérables à la prédation par les couleuvres obscures en Ontario que ceux qui nichent à l'intérieur des forêts; la fragmentation devrait augmenter la vulnérabilité des oiseaux forestiers à la prédation des nids par les couleuvres agiles.

[Traduit par la Rédaction]

## Introduction

Habitat loss and fragmentation imperil natural communities throughout the world (Meffe and Carroll 1997; Wilson 2001). Fragmentation increases the relative amount of edge habitat, which can have important consequences for community interactions (Donovan et al. 1995; Robinson et al. 1995). Generalist predators that use edge habitat are of special concern, especially for avian populations (Yahner and Scott 1988; Andren 1992; Harrison and Bruna 1999). Nest predation is the greatest cause of nest failure in birds (Ricklefs 1969; Martin 1988; Martin 1993) and is especially significant in some edge habitats (Andren and Angelstam 1988; Burkey 1993; King et al. 1998; Batary and Baldi

2004). Therefore, avian conservation requires better understanding of habitat use by nest predators (Chalfoun et al. 2002a, 2002b; Larivière 2003; Stephens et al. 2003). Snakes have been identified as important nest predators (e.g., Thompson et al. 1999; Morrison and Bolger 2002; Thompson and Burhans 2003). Therefore, an essential step toward identifying links between habitat structure and nest predation by snakes is the determination of how snakes select and use habitat, particularly edges (Weatherhead and Blouin-Demers 2004).

Ratsnakes, *Elaphe obsoleta* (Say in James, 1823), prey extensively on nesting birds (Stickel et al. 1980; Weatherhead and Robertson 1990; Weatherhead et al. 2003) and pre-

Received 4 February 2006. Accepted 3 August 2006. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 29 November 2006.

G.L.F. Carfagno<sup>1</sup> and P.J. Weatherhead. Program in Ecology and Evolutionary Biology, University of Illinois, 606 East Healey Street, Champaign, IL 61820, USA.

<sup>1</sup>Corresponding author (e-mail: [carfagno@uiuc.edu](mailto:carfagno@uiuc.edu)).

fer edge habitat at their northern range limit (Weatherhead and Charland 1985; Blouin-Demers and Weatherhead 2001a, 2001c). Preference for edges was greatest when thermal demands were highest (egg development by females, shedding, digestion) and did not correspond to variation in abundance of mammalian prey. Edges in Ontario were thermally superior habitat because they provided access to both shaded forest and sunny fields, whereas temperatures available to snakes in forested habitat rarely approached preferred temperatures (Blouin-Demers and Weatherhead 2001b, 2001c). These results support the proposition that thermal considerations are one of the most important proximate factors determining habitat use in temperate-zone squamates (Reinert 1984; Grant 1990; Reinert 1993).

Ratsnakes in Ontario may have an important impact on edge-nesting birds through predation. However, because habitat use by reptiles should differ across a species' range, especially if behavioral thermoregulation is an important determinant of habitat use (Adolph 1990), more centrally located ratsnakes may be less restricted to edge habitat than ratsnakes at their northern range limit. Studies of geographic variation within a species also provide the opportunity to examine the plasticity of habitat selection (Reinert 1993). Thermal considerations may be less important for a population not encountering temperature extremes, and instead, habitat use may be driven more by other factors such as prey availability or predator avoidance (Reinert 1993). Therefore, our first general goal was to determine how landscape-scale habitat use by ratsnakes differs between Illinois and Ontario. Because the thermal environment in Illinois should be more benign, we predicted that if thermal ecology is an important determinant of habitat selection, ratsnakes in Illinois should use forest edges less than ratsnakes in Ontario.

A study in Maryland (also a more central location) found that ratsnakes preferentially used edges, with no change through the season (Durner and Gates 1993). However, several aspects of how that study was conducted may limit the generality of the results and may make comparisons between populations problematic. Study animals were captured along edges and in areas where they were frequently encountered by residents, potentially biasing the sample towards individuals predisposed to using certain habitat types. Analyses did not consider the proportion of time spent in habitats, but instead used only unique locations pooled across individuals, possibly underrepresenting locations used frequently or for extended periods. Another study in Illinois found no clear association of ratsnakes with edge habitat (Keller and Heske 2000), although the methods used were again different from those used in the Ontario study (Blouin-Demers and Weatherhead 2001a, 2001b). Other factors also make direct comparisons with the Ontario study difficult. Neither Durner and Gates (1993) nor Keller and Heske (2000) analyzed microhabitat use and in both studies edge was not considered as a separate habitat type; instead, use was determined by the relative proximity of snake locations to edges. We avoid these ambiguities by using a standard approach across locations and by directly testing snake use of edges relative to other habitat types.

Not all species of snakes are expected to use habitat in the same way, so edge use may also differ between ecologically similar species at the same study site (Schoener 1977;

Reinert 1984; Tracy and Christian 1986). Such interspecific differences would determine the relative impact of each species on the relevant prey populations. For example, species with greater maximum sprint speeds may have coevolved physiologies that are maximized at higher optimal body temperatures (Huey and Kingsolver 1993; Bauwens et al. 1995). To achieve those temperatures, individuals should need to spend more time in habitats that allow higher or more precise body temperatures to be realized more often. Predator avoidance or prey availability could also promote interspecific variation in habitat use (Reinert 1993). For example, species with more specialized diets could be restricted to a specific habitat relative to a generalist predator. Therefore, our second general goal was to determine how habitat use by ratsnakes differs from habitat use by racers, *Coluber constrictor* (L., 1758), at the same study site in Illinois.

Among the ecological similarities between ratsnakes and racers, both prey extensively on birds and mammals (Klimstra 1959; Fitch 1963a, 1963b; Weatherhead et al. 2003; Carfagno et al. 2006), which should reduce the importance of prey abundance for habitat use. Ratsnakes and racers occur together in Illinois in areas characterized by a mixture of forests and fields (Keller and Heske 2000). Thus, both species would have access to the edges between those habitats. The species are also similar in size and color as adults, which makes their physical properties associated with heating and cooling similar. Despite these similarities, there are several reasons to assume that racers and ratsnakes should differ in their habitat use, particularly in their use of edges.

Where they coexist, racers tend to be more visible than ratsnakes on the hottest days and in the warmest habitats, and as their name suggests, they are more active, relying on speed to avoid predators and to capture fast-moving prey (Fitch 1963b, 1999). Racers are also thought to grow and mature more quickly than ratsnakes at the same location (Turner 1977; Fitch 1999), which should favor more frequent foraging and more precise temperature control by racers to maintain nutrient assimilation rates necessary for growth and development. Given that racers should be more strongly thermophilic than ratsnakes, we predicted that racers would be more dependent on those habitats that provide the greatest opportunity for snakes to maintain higher or more precise body temperatures. Therefore, relative to ratsnakes, racers should select open habitats over forested habitats and should use forest edges more.

Habitat use by snakes may shift with changing environmental conditions (Webb and Shine 1998). As in Ontario, for example, forest edges in Illinois may be the optimal thermal habitat when the need to shuttle between shade and sun is great (Heatwole and Johnson 1979; Blouin-Demers and Weatherhead 2001b, 2001c). During warmer months, however, forested sites could allow ratsnakes to achieve preferred temperatures solely by using sun flecks or canopy gaps (Lillywhite and Henderson 1993), whereas old fields could generally become too warm for racers. Therefore, we predicted that ratsnakes in Illinois would preferentially use forest edges in the spring and fall, but would move to forested interior habitat in the summer. Contrary to the pattern expected for ratsnakes, we predicted that racers would show an increasing preference for edges in the hottest parts of the summer as open habitats became too warm.

In a preliminary analysis of ratsnake and racer habitat selection at our study site, we determined that mammalian prey abundance did not influence snake habitat use (Cargano et al. 2006). That analysis did not adequately test the hypotheses considered here, however, because data were restricted to only 3 months of one field season and microhabitat analyses were not conducted. Analysis of habitat selection at the landscape scale examines broad patterns of habitat use, whereas examination of microhabitat selection provides information about the specific features within habitats that snakes select (Shine and Fitzgerald 1996; Blouin-Demers and Weatherhead 2001a; Heard et al. 2004). Here we evaluate habitat selection at both the landscape and the microhabitat scale.

In our preliminary study we also did not consider differences in habitat use between sexes or between gravid and non-gravid females. Habitat use is likely to vary by sex or by reproductive condition (Ford and Burghardt 1993; Blouin-Demers and Weatherhead 2001a, 2001b), particularly because females should have more specific thermal needs while developing eggs. Here we test the prediction that habitat use by gravid females of both species differs from habitat use by non-gravid females and males.

## Materials and methods

### Study site and species

We avoided the impracticality of having to conduct studies of ratsnakes in two places simultaneously by taking advantage of a recent study of habitat use by ratsnakes in Ontario, at the northern limit of their distribution (Blouin-Demers and Weatherhead 2001a, 2001b, 2001c). The thermal environment differs substantially between Illinois and Ontario. The average yearly temperature for Ottawa, Ontario, is 6.6 °C with 142 frost-free days (Blouin-Demers et al. 2002), whereas southern Illinois averages 14.4 °C with over 190 frost-free days (Changnon et al. 2004). Active-season temperatures also differ, with local weather stations reporting mean summer temperatures in southern Illinois approximately 10 °C warmer than those in Ottawa. To facilitate comparisons, we followed the methods of the Ontario study as closely as possible.

We conducted our research from 2002 to 2004 at the Cache River State Natural Area in Johnson County, southern Illinois. Genetic and morphological analyses have suggested that *E. obsoleta* consists of four species, with Ontario snakes part of the eastern species and Illinois snakes part of the central species (Burbrink et al. 2000; Burbrink 2001). More recently, however, an analysis of the Ontario population studied by Blouin-Demers and Weatherhead showed that it is a mix of eastern and central species (Gibbs et al. 2006). Thus, for the purpose of this study we consider ratsnakes in Ontario and Illinois to be different populations of the same species, which we refer to simply as ratsnakes.

Both *E. obsoleta* and *C. constrictor* are members of the Colubridae, and both species are widely distributed in North America, with the central parts of their ranges occurring in Illinois (Conant and Collins 1998). Because the two species hibernate communally (Sexton and Hunt 1980), we were able to design a study involving individuals of both species from the same hibernacula. This allowed us to assume that

individuals of both species had the same habitat available to them.

### Radiotelemetry

We captured most ratsnakes and racers as they emerged from shared communal hibernacula each spring, but also opportunistically throughout the season. Hibernacula were located by radio-tracking snakes caught opportunistically during the first field season. Upon capture, snakes were sexed, measured to the nearest millimetre, and weighed to the nearest gram. Reproductive condition of females was assessed by palpation of the abdomen periodically throughout the field season and by observation of mating behavior. We classified a female as not gravid that season when we failed to observe mating behavior or the presence of eggs. However, many females (especially ratsnakes) were inaccessible to us (i.e., in tree canopies) most of the time. Therefore, we were unable to assess reproductive condition for all female ratsnakes.

Snakes had temperature-sensitive transmitters (Model SI-2T, Holohil Systems Inc., Ontario) implanted surgically using isoflurane as the anesthetic (Blouin-Demers et al. 2000) under the supervision of a wildlife veterinarian and in compliance with the University of Illinois' Animal Care and Use Committee. Transmitters were implanted only in snakes in which the transmitter mass was less than 3% of snake body mass. Snakes were provided with antibiotics and analgesics and released 3 days after surgery.

Radio-tracking procedures generally followed those of Blouin-Demers and Weatherhead (2001a, 2001b). Snakes were usually relocated every other day from spring emergence (February through March) until their return to hibernation (October through November) using a handheld receiver (Model R-1000, Communication Specialists Inc., California). Every location was flagged and mapped using a handheld global positioning system unit (Model GPS V, Garmin International Inc., Kansas). Snake position and height were recorded, and the general habitat was characterized.

### Habitat characterization

We assessed macro- and micro-habitat at randomly selected points for every other snake location to quantify habitat availability. Each point was selected at a random direction and distance (10–200 paces) from the snake location (Blouin-Demers and Weatherhead 2001a). Thus, this approach did not sample available habitat in the study area in a strictly random sense. Rather, it was a random sample of habitat actually available to each snake.

At the landscape scale, habitat at our study site consisted of a mixture of forest and open areas (e.g., fields, wetlands) with occasional old barns and other man-made structures, similar to the habitat in the study site used by Blouin-Demers and Weatherhead (2001a) in Ontario. We classified habitat into five categories. Upland forest was dominated by oaks and hickory and was located along a ridge adjacent to the Cache River floodplain. Bottomland forest was dominated by cypress and tupelo and occurred below the ridge and directly adjacent to the river, where flooding was common, especially in spring. Grasses and forbs dominated old fields. Later successional fields were dominated by woody

**Table 1.** Descriptions of structural variables and associated sampling radii used to assess microhabitat use by snakes in Illinois.

| Variable | Radius (m)      | Description*  |
|----------|-----------------|---|
| DLOG     | 30              | Distance (m) to nearest log ( $\geq 7.5$ cm diameter)                     |
| DOVER    | 30              | Distance (m) to nearest overstory tree ( $\geq 7.5$ cm dbh)               |
| DUNDER   | 30              | Distance (m) to nearest understory tree ( $< 7.5$ cm dbh, $> 2$ m height) |
| DBHOVER  | 30              | Dbh (cm) of nearest overstory tree  |
| LLOG     | 30              | Length (m) of nearest log ( $\geq 7.5$ cm diameter)                       |
| DMLOG    | 30              | Mean diameter (cm) of nearest log ( $\geq 7.5$ cm)                        |
| 7.5–15   | 10              | Number of trees $\geq 7.5$ and $< 15$ cm dbh in plot                      |
| 15–30    | 10              | Number of trees $\geq 15$ and $< 30$ cm dbh in plot                       |
| 30–45    | 10              | Number of trees $\geq 30$ and $< 45$ cm dbh in plot                       |
| $> 45$   | 10              | Number of trees $\geq 45$ cm dbh in plot                                  |
| NUNDER   | 5               | Number of understory trees ( $< 7.5$ cm dbh, $> 2$ m height)              |
| %ROCK    | 2               | Coverage (%) of rocks within plot   |
| %LEAF    | 2               | Coverage (%) of leaf litter within plot                                   |
| %LOG     | 2               | Coverage (%) of logs within plot  |
| %GRASS   | 2               | Coverage (%) of grass within plot   |
| %SHRUB   | 2               | Coverage (%) of shrubs within plot  |
| %SOIL    | 2               | Coverage (%) of bare soil within plot                                     |
| %HERBS   | 2               | Coverage (%) of herbs (non-woody) within plot                             |
| HGRDVEG  | 2               | Height (m) of ground vegetation (shrubs and herbs)                        |
| NWOODY   | 2               | Number of woody stems   |
| HCAN     | 2               | Height (m) of canopy  |
| CANCLO   | 45 <sup>†</sup> | Canopy closure (%) within cone  |
| DEDGE    | 100             | Distance (m) to nearest edge  |

\*Dbh, diameter at breast height.

<sup>†</sup>Measured in degrees.

species including shrubs, vines, and dense saplings. Finally, we defined edge habitat as the interface between closed and open canopy habitats (including forest–field and forest–river interfaces). We used a distance of 15 m from the interface to define edge habitat (Blouin-Demers and Weatherhead 2001a).

Microhabitat was quantified by collecting detailed data at every other unique snake relocation for 23 of the 28 variables (Table 1) used by Blouin-Demers and Weatherhead (2001a; their Table 1, p. 2885). We excluded rock and snag variables because these features were rare in our samples. We also did not include log variables for our racer analyses because this feature was rare in samples for that species. We excluded sites where snakes were actively traveling when found because these locations may not represent habitat selected by the snakes. We also did not include sites the snakes used occasionally that could not be adequately characterized by our sampling methods (e.g., in barns or under junk piles). When snakes were found in tree canopies, we did not sample ground-level habitat variables but instead used mean values for the group (e.g., males) in that habitat (Blouin-Demers and Weatherhead 2001a). Sites were sampled as soon as possible after snakes had moved. If a snake moved back to a site already sampled, we included that site only once in the analysis.

### Data analysis

All analyses were performed using SYSTAT<sup>®</sup> Version 10.0 (Systat Software Inc., Richmond, California). Using individual animals as replicates, we used compositional analysis to determine landscape-scale habitat preferences (Aebischer

et al. 1993), which allowed us to include all locations in the landscape-scale analysis, weighted by the amount of time individual snakes spent at each location. We calculated a composition for each snake, pooling data for snakes that were tracked in multiple years. For females that changed reproductive condition, we calculated separate compositions for the snake when gravid and when not. We calculated differences between log-ratio transformed proportions of habitat use and availability. To determine whether use differed from availability, we used MANOVA to determine whether the deviations between habitat use and availability points differed from a normal distribution centered on a mean of zero. We used *t* tests for pairwise comparisons among the five habitat types. The analysis was repeated with observations categorized by sex and reproductive condition. We also calculated compositions separately by month to test for differences across the season. Blouin-Demers and Weatherhead (2001a) analyzed microhabitat selection without weighting locations by the amount of time a snake had spent there, and by pooling data across all individuals. To allow direct comparisons between studies, we reanalyzed the raw telemetry data from their Ontario study using compositional analysis.

We used MANOVA to test for differences in microhabitat variables between sites used by ratsnakes and racers and random sites. Discriminant function analysis was used to describe differences between groups in multivariate space. The analysis was repeated with observations categorized by sex and reproductive condition. We also categorized data by time to test for differences in microhabitat use across the season. Because our observations were treated independ-

ently, with data pooled from all individuals in a group, one aberrant individual sampled repeatedly could have biased the results. However, no individual was overrepresented in our sample, with the largest sample comprising only 6.2% of the total snake microhabitat samples. We could have used mean values for each snake. However, this approach fails to make use of the substantial variation found within individuals (Reinert 1984; Blouin-Demers and Weatherhead 2001a). The alternative of using only one observation per individual would have drastically reduced our number of observations per group, thereby precluding the use of discriminant function analysis because of sample size requirements (McCarigal et al. 2000).

All variables were checked for normality and where necessary, transformations were used to improve normality. Although multivariate normality is not assured by univariate normality, the latter is assumed to be a good step towards the former (McCarigal et al. 2000). When a value for a certain variable was missing because the feature did not occur in that sample (e.g., length of nearest log when no log was present), we used the mean for the group (Blouin-Demers and Weatherhead 2001a); this occurred <15% of the time for any variable. A Box's M test failed to show homogeneity of covariance matrices, but this assumption is rarely met with large ecological data sets. However, multivariate analyses are robust when sample sizes are large and balanced (Reinert 1984).

## Results

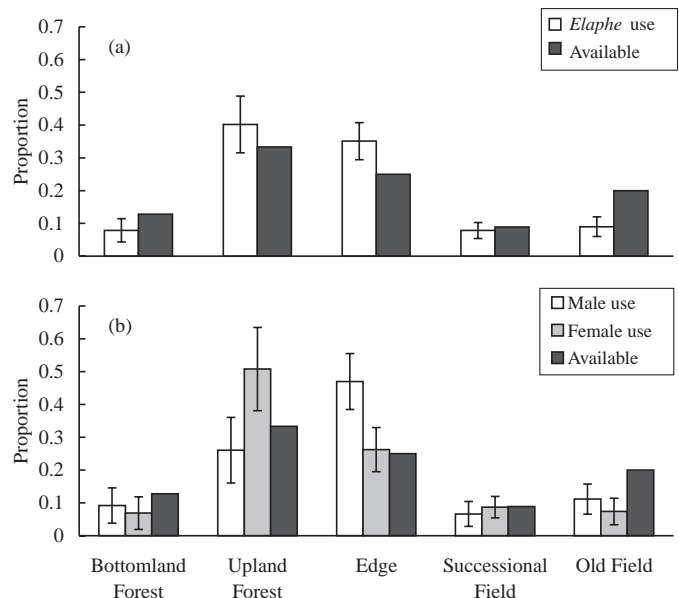
### Landscape-scale habitat selection by Ontario ratsnakes

Blouin-Demers and Weatherhead (2001a) had sufficient (>25) telemetry locations for 46 ratsnakes (15 males and 31 females), for a total of 2990 telemetry points between May and August. Sixteen females were not gravid when tracked, nine were gravid, and six were gravid one year and not the other. Habitat availability was recalculated with the exclusion of aquatic habitat because we considered this habitat unavailable to terrestrial ratsnakes. Qualitatively, compositional analysis did not change overall landscape-scale habitat use by ratsnakes in Ontario. Consistent with the results of the original analyses (Blouin-Demers and Weatherhead 2001a), edge habitat was used significantly more, and forests and open habitats less, relative to their availability. Therefore, we do not present the results of those reanalyses here and instead use Blouin-Demers and Weatherhead's (2001a) original results for comparison with our results from Illinois.

### Landscape-scale habitat selection in Illinois

We tracked 22 ratsnakes and 16 racers over the course of the 3-year study. Eighteen of the ratsnakes (nine males and nine females) and 15 of the racers (seven males and eight females) had sufficient locations (>25) to be used in the compositional analysis, for a total of 1727 ratsnake and 1419 racer telemetry points between April and September. One of the female ratsnakes was gravid while tracked and three were gravid one year and not the other; we were unable to determine the reproductive status of the other five. We recalculated compositions with data for all females combined because gravid and non-gravid females used habitat

**Fig. 1.** Proportion of habitat used (mean  $\pm$  SE) relative to availability by ratsnakes (*Elaphe obsoleta*) overall (a) and by sex (b).



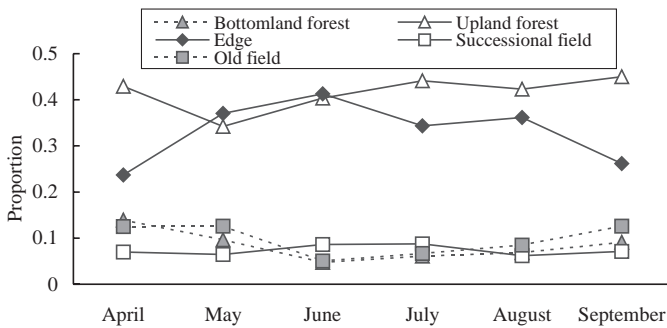
similarly (see below). Because we know females are not reproductive every year in this population and elsewhere at this latitude (e.g., Fitch 1999), we assume the unknown group comprised both gravid and non-gravid females. Racer compositions were also calculated using all females, but in this case because all female racers were gravid each year of the study. The mean number of observations per individual averaged 82.2 for ratsnakes and 94.6 for racers.

### Ratsnakes

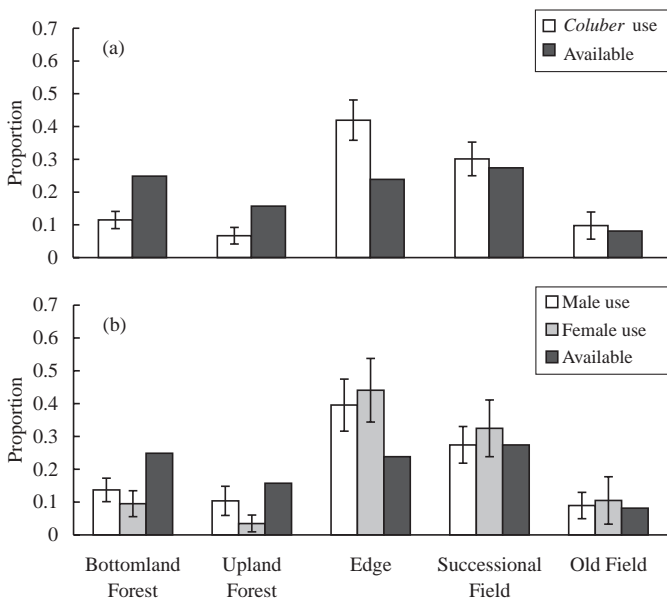
Overall, Illinois ratsnakes used edges and upland forest more and old fields and bottomland forest significantly less relative to their availability, with old fields the most strongly avoided habitat (Wilks'  $\lambda = 0.31$ ,  $F_{[4,17]} = 9.64$ ,  $P < 0.001$ ; Fig. 1a). There was no significant difference between the use of upland forest and the use of edge habitat by ratsnakes ( $t = -0.90$ ,  $P = 0.38$ ), though edge habitat was preferred over all other habitat types (all  $P < 0.04$ ), whereas upland forest was not significantly preferred over other habitat types (all  $P > 0.11$ ). Qualitatively, known gravid and non-gravid females both used upland forest more than expected based on availability, whereas all other habitats were used less relative to their availability. When analyzed by sex using all female locations, selectivity at the macrohabitat scale remained significant for males ( $P = 0.006$ ) and was marginally significant for females ( $P = 0.06$ ). The general trends differed between the sexes, with males more strongly preferring edges over all other habitats (all  $P < 0.05$ ) and females showing no preference for edges relative to upland forest ( $t = 0.36$ ,  $P = 0.73$ ; Fig. 1b).

Ratsnake habitat use varied across the season (Fig. 2). Ratsnakes used edges most in late spring (May and June) and upland forest most in early spring and later in the summer. Sex differences in habitat use were consistent across the season, with females using upland forests more than edges and males using edges more than forests.

**Fig. 2.** Mean monthly habitat use by ratsnakes (*E. obsoleta*) over the course of the active season.



**Fig. 3.** Proportion of habitat used (mean ± SE) relative to availability by racers (*Coluber constrictor*) overall (a) and by sex (b).

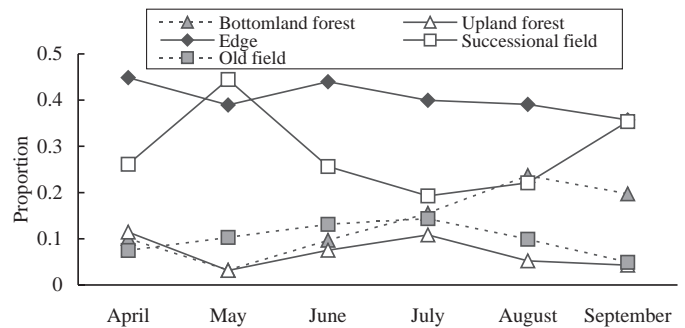


**Racers**

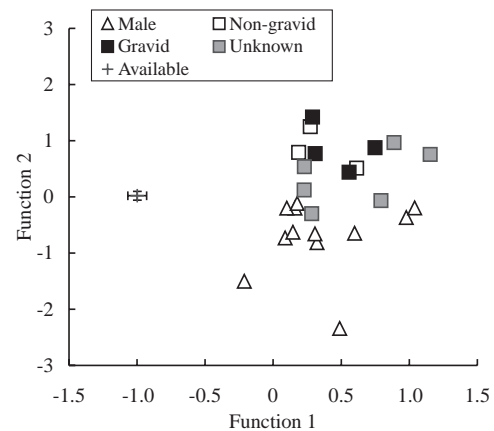
Overall, racers used edges more, and both bottomland and upland forest significantly less, relative to their availability (Wilks'  $\lambda = 0.23$ ,  $F_{[4,11]} = 9.31$ ,  $P = 0.002$ ; Fig. 3a). There was no significant difference between the use of successional fields and the use of edge habitat by racers ( $t = -1.66$ ,  $P = 0.12$ ), though relative to availability, edge habitat was significantly preferred over all other habitat types (all  $P < 0.02$ ). Successional fields were also significantly preferred over both forested habitats (all  $P < 0.02$ ). By sex, selectivity at the macrohabitat scale remained significant for females ( $P = 0.03$ ) but not for males ( $P = 0.36$ ), although general trends were consistent with the overall results (Fig. 3b). Both sexes preferred edges over both forested habitats (all  $P < 0.04$ ), but males only weakly preferred edges over upland forest ( $t = -2.02$ ,  $P = 0.09$ ). Successional habitat tended to be preferred over both forested habitats by females (all  $P < 0.07$ ) and over upland forest by males ( $t = 2.32$ ,  $P = 0.06$ ).

Racer habitat use also varied across the season (Fig. 4). Successional field use peaked strongly in May and at the end of the active season. Edge use remained strong throughout the season but declined slightly through the summer, concurrent with an increase in the use of bottomland forest.

**Fig. 4.** Mean monthly habitat use by racers (*C. constrictor*) over the course of the active season.



**Fig. 5.** Relative positions along the first two discriminant functions of individual ratsnakes (*E. obsoleta*) grouped by reproductive condition, compared with microhabitat availability (mean ± SE). See Table 2 for factor loadings on discriminant functions.



By sex, habitat use differed early in the season, with females more strongly preferring edges and avoiding forests relative to males. The sexes became more similar after June, coincident with the end of the reproductive season.

**Microhabitat selection in Illinois**

We quantified microhabitat characteristics for all 22 ratsnakes (i.e., including three males and one female of unknown reproductive status not used in the landscape-scale analysis because of the short period that they were tracked) and the 15 racers. We had a total of 372 snake (211 male and 161 female) and 180 random locations for ratsnakes, and 402 snake (245 male and 157 female) and 197 random locations for racers.

**Ratsnakes**

Overall, snake-selected microhabitats differed significantly from random locations (Wilks'  $\lambda = 0.67$ ,  $F_{[23,528]} = 11.22$ ,  $P < 0.001$ ). Microhabitat used by males, non-gravid females, gravid females, and females of unknown status and microhabitat of random locations differed significantly (Wilks'  $\lambda = 0.42$ ,  $F_{[92,2080]} = 5.48$ ,  $P < 0.001$ ). All groups differed significantly from each other (all  $F > 3.47$ , all  $P < 0.001$ ; Fig. 5). The first discriminant function accounted for 49.8% of the total variation among groups and separated snake locations from random locations. We interpreted the first function as a gradient from forested to more open hab-

**Table 2.** Factor loadings of variables used to assess microhabitat availability and use by ratsnakes (*E. obsoleta*) by reproductive condition and by sex.

| Variables* | By reproductive condition |            | By sex     |            |
|------------|---------------------------|------------|------------|------------|
|            | Function 1                | Function 2 | Function 1 | Function 2 |
| DLOG       | 0.10                      | 0.55       | 0.14       | 0.48       |
| DOVER      | -0.98                     | -0.39      | -1.01      | -0.31      |
| DUNDER     | -0.44                     | -0.11      | -0.41      | -0.23      |
| DBHOVER    | 0.28                      | 0.10       | 0.30       | 0.03       |
| LLOG       | 0.17                      | -0.27      | 0.17       | -0.27      |
| DMLOG      | 0.07                      | 0.33       | 0.07       | 0.33       |
| 7.5-15     | -0.24                     | -0.09      | -0.24      | -0.10      |
| 15-30      | -0.18                     | -0.08      | -0.16      | -0.16      |
| 30-45      | -0.19                     | -0.31      | -0.19      | -0.34      |
| >45        | 0.07                      | 0.04       | 0.03       | 0.20       |
| NUNDER     | -0.11                     | 0.02       | -0.09      | -0.05      |
| %ROCK      | 0.13                      | -0.58      | 0.12       | -0.57      |
| %LEAF      | -0.03                     | -0.48      | -0.06      | -0.35      |
| %LOG       | 0.65                      | -0.04      | 0.66       | -0.09      |
| %GRASS     | 0.31                      | -0.70      | 0.30       | -0.73      |
| %SHRUB     | 0.37                      | -0.39      | 0.37       | -0.47      |
| %SOIL      | 0.14                      | 0.14       | 0.13       | 0.16       |
| %HERBS     | 0.42                      | -0.66      | 0.37       | -0.48      |
| HGRDVEG    | 0.09                      | -0.25      | 0.09       | -0.29      |
| NWOODY     | -0.10                     | 0.14       | -0.08      | 0.12       |
| HCAN       | -0.52                     | 0.34       | -0.51      | 0.33       |
| CANCLO     | 0.25                      | -0.18      | 0.26       | -0.22      |
| DEDGE      | -0.02                     | 0.51       | 0.01       | 0.43       |

\*See Table 1 for definitions of variables.

itats (Table 2). Snake locations in general were closer to overstorey trees with taller canopies and had greater log ground cover than random sites. Along this axis, all groups were significantly different from random locations (all  $F > 57.11$ , all  $P < 0.001$ ) but not from each other (all  $F < 2.03$ , all  $P > 0.16$ ), with unknown females farthest from random locations and marginally different from both known non-gravid females ( $F = 3.06$ ,  $P = 0.08$ ) and males ( $F = 3.48$ ,  $P = 0.06$ ).

The second discriminant function separated male locations from all other snake groups, with all groups differing significantly along this axis (all  $F > 7.30$ , all  $P < 0.007$ ), except for known gravid and non-gravid females ( $F = 0.10$ ,  $P = 0.76$ ). The interpretation of this second function is not as clear (Table 2). Locations of all female groups were farthest from edges and had less rock ground cover. Locations used by non-gravid females and females of unknown status had greater leaf litter ground cover and were closer to logs than male locations. However, male locations were similar to locations of females of unknown status: both locations had greater herbaceous ground cover, and locations of females of unknown status had less grass ground cover than all other groups. Overall, males were most similar to females of unknown status, while known gravid and non-gravid females scored similarly, though known non-gravid females were most different from males. Because three of the four known gravid females were also the sole known non-gravid females, the similarity between these groups suggests that differences among individuals were greater than those within individuals, even when an individual's

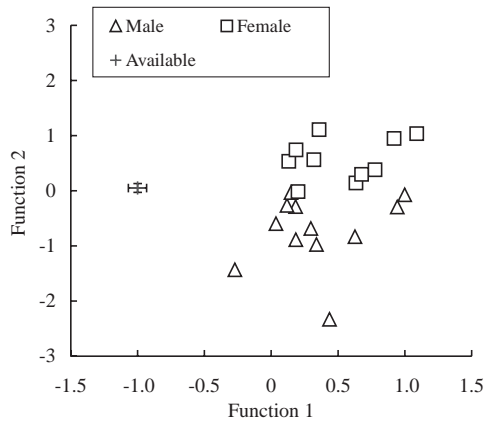
reproductive condition changed (e.g., gravid one year and not the next).

Given this variation among females, we reanalyzed the data by sex, combining data for all females. Microhabitat used by males, microhabitat used by females, and random locations differed significantly (Wilks'  $\lambda = 0.55$ ,  $F_{[46,1054]} = 8.06$ ,  $P < 0.001$ ; Fig. 6). All groups differed significantly from each other (all  $F > 5.63$ , all  $P < 0.001$ ). The first discriminant function accounted for 68.5% of the total variation among groups and separated snake locations from random locations. Snake locations were generally closer to overstorey trees with taller canopies and had greater log ground cover than random sites (Table 2). Along this axis, both sexes were significantly different from random locations (all  $F > 203.53$ , all  $P < 0.001$ ) but not from each other ( $F = 1.40$ ,  $P = 0.24$ ).

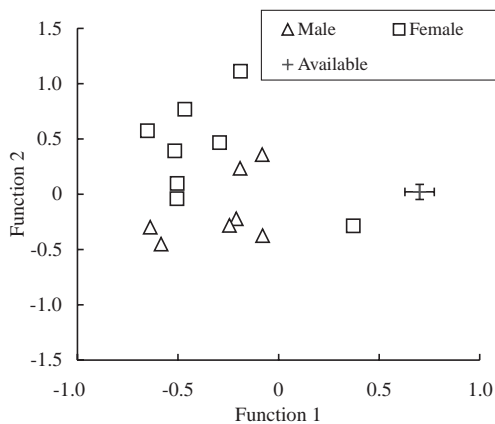
The second discriminant function separated the sexes from each other and from random locations, with all groups differing significantly (all  $F > 28.49$ , all  $P < 0.001$ ). Males and females were at opposite extremes along this axis. Female locations were farther from edges and closer to logs with sparser grass, herb, shrub, and rock ground cover. Male locations had the opposite characteristics: closer to edges and farther from logs with greater grass, herb, shrub, and rock ground cover (Table 2).

Ratsnake locations varied significantly across the season (Wilks'  $\lambda = 0.74$ ,  $F_{[46,694]} = 2.42$ ,  $P < 0.001$ ). Locations from early in the season (March through May) differed significantly from those in mid-season (June through July; Wilks'  $\lambda = 0.76$ ,  $F_{[23,265]} = 3.63$ ,  $P < 0.001$ ) and late season

**Fig. 6.** Relative positions along the first two discriminant functions of individual ratsnakes (*E. obsoleta*) grouped by sex, compared with microhabitat availability (mean  $\pm$  SE). See Table 2 for factor loadings on discriminant functions.



**Fig. 7.** Relative positions along the first two discriminant functions of individual racers (*C. constrictor*) grouped by sex, compared with microhabitat availability (mean  $\pm$  SE). See Table 3 for factor loadings on discriminant functions.



(August through October; Wilks'  $\lambda = 0.71$ ,  $F_{[23,166]} = 3.02$ ,  $P < 0.001$ ). However, mid-season locations were not significantly different from late-season locations (Wilks'  $\lambda = 0.93$ ,  $F_{[23,241]} = 0.84$ ,  $P = 0.68$ ). With observations divided by month, the first discriminant function accounted for 82.5% of the total seasonal variation. As the season progressed, snakes increased their use of sites that were farther from logs and had taller canopies, larger trees, and more grass but less leaf, herb, and shrub ground cover. These changes are consistent with increased use of upland forest relative to edge habitat. Microhabitat remained significantly different between the sexes throughout the season (all  $F > 2.57$ , all  $P < 0.001$ ).

### Racers

Overall, snake-selected microhabitats differed significantly from random locations (Wilks'  $\lambda = 0.81$ ,  $F_{[20,578]} = 7.00$ ,  $P < 0.001$ ). Microhabitat used by males, microhabitat used by females, and random locations differed significantly (Wilks'  $\lambda = 0.78$ ,  $F_{[40,1154]} = 3.90$ ,  $P < 0.001$ ). Both sexes were significantly different from random locations (all  $F > 5.18$ , all  $P < 0.001$ ) but did not differ from each other ( $F =$

1.05,  $P = 0.41$ ; Fig. 7). The first discriminant function accounted for 87.2% of the total variation among groups and separated snake locations from random locations. We interpreted the first function as a gradient from forested to more open successional habitat (Table 3). Snake sites had more open canopies, were closer to more understory trees, and had more herbaceous and log ground cover than random sites. Along this axis, both sexes were significantly different from random locations (all  $F > 106.25$ , all  $P < 0.001$ ), but not different from each other ( $F = 0.87$ ,  $P = 0.35$ ).

The second discriminant function separated the sexes from each other and from random locations, with all groups differing significantly along this axis (all  $F > 5.23$ , all  $P < 0.02$ ). Males and females were at opposite extremes along this axis. We interpreted the second function as a gradient from interior successional fields to edge habitat (Table 3). Female locations were closer to forest edges, with a lower density of small trees and shorter ground vegetation. Male locations had the opposite characteristics: farther from edges, with a greater density of small trees and taller ground vegetation.

Racer locations varied significantly across the season (Wilks'  $\lambda = 0.75$ ,  $F_{[40,760]} = 2.96$ ,  $P < 0.001$ ). Locations early in the season (March through May) differed significantly from those in mid-season (June through July; Wilks'  $\lambda = 0.78$ ,  $F_{[20,309]} = 4.40$ ,  $P < 0.001$ ) and late season (August through October; Wilks'  $\lambda = 0.78$ ,  $F_{[20,210]} = 2.99$ ,  $P < 0.001$ ). Mid-season locations also differed significantly from late-season locations (Wilks'  $\lambda = 0.84$ ,  $F_{[20,222]} = 2.06$ ,  $P = 0.006$ ). With observations divided by month, the first discriminant function accounted for 65.0% of the total seasonal variation. As the season progressed, snakes increased their use of sites with denser canopies and greater leaf litter ground cover. These changes are consistent with increased use of bottomland forest and edge habitat relative to successional fields. There were no significant differences between sexes when examined seasonally (all  $F < 0.88$ , all  $P > 0.30$ ).

### Interspecific comparisons

Microhabitat used by ratsnakes, microhabitat used by racers, and random locations differed significantly (Wilks'  $\lambda = 0.60$ ,  $F_{[40,2258]} = 16.37$ ,  $P < 0.001$ ). All groups differed significantly from each other (all  $F > 12.28$ , all  $P < 0.001$ ; Fig. 8). The first discriminant function accounted for 64.2% of the total variation among groups and separated ratsnake locations from racer locations, which were intermediate between ratsnake locations and random locations but more similar to random locations. However, all groups differed significantly from each other (all  $F > 21.36$ , all  $P < 0.001$ ). We interpreted the first function as reflecting variance in preference for forested habitat (Table 3). Compared with racer and random locations, ratsnake locations were closer to the largest trees and had greater canopy heights and log ground cover.

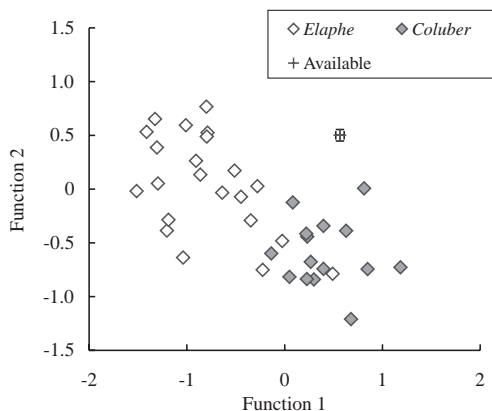
The second discriminant function separated racer locations from ratsnake locations, which were intermediate between racer locations and random locations but more similar to random locations. However, all groups differed significantly from each other (all  $F > 25.67$ , all  $P < 0.001$ ). We interpreted the second function as reflecting variance in

**Table 3.** Factor loadings of the variables used to assess microhabitat availability and use by racers (*C. constrictor*) by sex, and availability and use by racers relative to ratsnakes.

| Variables* | Racers (by sex) |            | Racers vs. ratsnakes |            |
|------------|-----------------|------------|----------------------|------------|
|            | Function 1      | Function 2 | Function 1           | Function 2 |
| DOVER      | 0.26            | 0.25       | 0.90                 | 0.02       |
| DUNDER     | 0.76            | -0.01      | 0.27                 | 0.68       |
| DBHOVER    | 0.01            | -0.34      | -0.59                | 0.28       |
| 7.5-15     | 0.33            | -0.51      | 0.27                 | 0.22       |
| 15-30      | -0.21           | -0.13      | 0.02                 | -0.03      |
| 30-45      | 0.24            | 0.00       | 0.02                 | 0.33       |
| >45        | -0.06           | 0.35       | 0.05                 | -0.08      |
| NUNDER     | 0.51            | 0.00       | 0.27                 | 0.24       |
| %ROCK      | 0.11            | -0.16      | -0.11                | 0.11       |
| %LEAF      | -0.18           | 0.00       | 0.19                 | -0.17      |
| %LOG       | -0.73           | -0.18      | -0.51                | -0.55      |
| %GRASS     | -0.16           | 0.19       | -0.22                | -0.16      |
| %SHRUB     | -0.35           | -0.44      | -0.24                | -0.36      |
| %SOIL      | -0.15           | -0.13      | -0.09                | -0.12      |
| %HERBS     | -0.46           | -0.02      | -0.21                | -0.46      |
| HGRDVEG    | -0.10           | -0.52      | -0.13                | -0.03      |
| NWOODY     | -0.08           | 0.45       | 0.10                 | -0.09      |
| HCAN       | -0.09           | -0.17      | 0.49                 | -0.11      |
| CANCLO     | 0.69            | 0.07       | -0.24                | 0.36       |
| DEDGE      | 0.23            | -0.64      | -0.12                | 0.23       |

\*See Table 1 for definitions of variables.

**Fig. 8.** Relative positions along the first two discriminant functions of individual ratsnakes (*E. obsoleta*) and racers (*C. constrictor*), compared with microhabitat availability (mean  $\pm$  SE). See Table 3 for factor loadings on discriminant functions.



preference for successional habitat (Table 3). Compared with ratsnake and random locations, racer locations were associated with more open canopies, were closer to understory trees, and had greater shrub and herbaceous ground cover. Racer locations had sparser log ground cover than ratsnake locations, but more log ground cover than random locations.

The two species also differed in the extent to which they were arboreal. Pooling all locations, ratsnakes were found in trees (>3 m high) significantly more often than racers, which were most often found on the ground ( $\chi^2_{[3]} = 913.31$ ,  $P < 0.001$ ; Fig. 9). Even when analyses were restricted to locations within forest, ratsnakes were still found in trees more

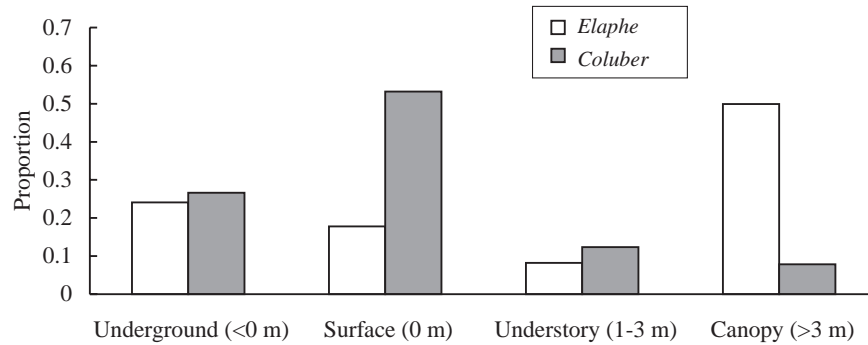
often than racers (61.0% vs. 6.6%). Within species, female ratsnakes were significantly more arboreal than males (52.1% vs. 44.8%); males were more often below ground (27.6% vs. 20.6%;  $\chi^2_{[3]} = 23.42$ ,  $P < 0.001$ ). Male and female racers did not differ in their use of trees ( $\chi^2_{[3]} = 4.58$ ,  $P = 0.21$ ).

## Discussion

### Ratsnake latitudinal comparison

Ratsnakes in southern Illinois can best be described as an upland forest species that also uses forest edges. This was supported both by our landscape analysis and by the microhabitat features with which ratsnakes were associated. Preference for edges in our study was weaker than found at the species' northern range limit. At the landscape scale in Illinois, upland forest and edges were equally preferred over open habitats. At the microhabitat scale, ratsnake locations in both Illinois and Ontario were closer to trees and had more log ground cover, indicative of the preference for forests, whereas only in Ontario, microhabitat locations were closer to edges (Blouin-Demers and Weatherhead 2001a). Thus, ratsnakes in both populations appear to select similar microhabitat, except that Ontario ratsnakes select locations closer to edges. The association of ratsnakes in Ontario with edges is consistent with the expectation that they rely more on edges for thermoregulation (Blouin-Demers and Weatherhead 2001a, 2001c). Ours is the first direct test of behavioral differences across latitudes and is consistent with results from studies of reptiles across altitudinal gradients (e.g., Hertz and Huey 1981; Adolph 1990; Gvozdik 2002).

Our results for edge use differ from results previously reported from our study site (Carfagno et al. 2006). In addition,

**Fig. 9.** Mean height above ground of ratsnake (*E. obsoleta*) and racer (*C. constrictor*) telemetry locations.

tion to those analyses being restricted to 3 months of one active season, habitats were classified differently. Because bottomland (avoided) and upland (preferred) forest types were combined in those analyses, preference for edges was increased relative to preference for forest habitat. The more inclusive current analyses still showed forest edge habitat to be important for ratsnakes in southern Illinois, but not more than upland forest interior. The lack of an overall edge preference that we documented is consistent with Keller and Heske's (2000) results from Illinois but differs from Durner and Gates' (1993) study of ratsnakes in Maryland. These results are not directly comparable, however, because neither of those studies quantified edge as a specific habitat type. This is especially problematic in fragmented landscapes, where the extent of fragmentation might influence the degree to which snake locations in forest are proximate to edges.

Although Illinois ratsnakes used edges less than their Ontario counterparts, consistent with Illinois having a more moderate thermal environment, ratsnakes in Illinois still frequently used edges. However, it is unclear whether this use is associated with thermoregulation. The seasonal patterns of edge use were equivocal. In Ontario, edge use increased through the season (Blouin-Demers and Weatherhead 2001a). In Illinois, ratsnakes used upland forest to the greatest extent relative to edges early and late in the season. During these times, however, snakes are moving to or from their hibernation sites, which were predominantly in interior upland forest. More consistent with thermoregulation, edge use peaked during May and June, when environmental temperatures remain variable and the need to thermoregulate should still be high. Later in the summer, snakes used edges less but then failed to increase edge use in the fall as environmental temperatures became more variable. Alternatively, the peak in edge use during May and June could correspond to an increase in the number of nesting birds within edges. Testing this hypothesis will require data on habitat-specific abundance of nesting birds and nest predation rates at our study site.

Use of edges by female ratsnakes was definitely not consistent with the thermal ecology hypothesis. If snakes used edges for thermoregulation, then gravid females should have used edges most because their need to thermoregulate should have been greatest, as was seen in the Ontario population (Blouin-Demers and Weatherhead 2001a). However, it was males that showed the greatest affinity for edges both at the landscape and the microhabitat scale, whereas females (both gravid and non-gravid) used upland forest more. We

found weak evidence for divergence of habitat use by gravid females relative to non-gravid females, though we were able to compare only a small sample of females of known reproductive condition. If most females of unknown status were non-gravid, it would explain the lack of a seasonal shift in habitat use by females. However, this would also indicate that males and females use habitat differently. Although gravid female snakes regularly use habitat differently from males, habitat divergence between males and non-gravid females is rare (Reinert 1993). Greater preference for edges by male ratsnakes relative to females may indicate that something other than thermal considerations is responsible. Sex differences in habitat use can be a result of sex differences in diet associated with extreme sexual size dimorphism (e.g., Houston and Shine 1993). However, sexual dimorphism is not extreme in ratsnakes (Blouin-Demers et al. 2002). If male ratsnakes have larger home ranges than females, this could result in more habitat types being included when habitat patches are small. For example, given that ratsnakes in Illinois are predominantly an upland forest species, a smaller female home range would include primarily forest, whereas a larger male home range could include other habitats, including forest edges. In Ontario, male ratsnakes tend to have larger home ranges than females (Weatherhead and Hoysak 1989; Blouin-Demers and Weatherhead 2002), and the same is true in Illinois (G. Carfagno, unpublished data). Testing this hypothesis will require studying ratsnakes where the scale of habitat patches is larger than at our study site.

Thermal considerations could still affect how gravid female ratsnakes select habitats, although in ways different from those further north. Forest interiors may have more retreat sites (e.g., tree cavities), which could provide reliable, optimal thermal conditions for gravid females (Webb and Shine 1998; Kearney 2002). More frequent use of canopy locations could also provide females access to a gradient of temperatures unavailable on the forest floor. Ratsnakes could maintain appropriate temperatures by shuttling among branches, similar to the shuttling behavior proposed for edge locations at their northern range limit (Blouin-Demers and Weatherhead 2001a). Spending more time in the canopy or in tree cavities could also reduce predation risk for females, because carrying eggs can compromise a female's ability to escape from predators (Seigel et al. 1987; Charland and Gregory 1995; Brown and Shine 2004). All these factors would also apply to ratsnakes in Ontario, but forest canopy there may be less thermally suitable than edges because of the cooler climate.

### Comparison of ratsnakes and racers

Racers in southern Illinois can best be described as an edge-habitat species that avoids forest interior. This was supported both by our landscape analysis and by the microhabitat features with which racers were associated. Compared with ratsnakes in Illinois, racers preferred edge habitat, whereas the forested habitats were the most strongly avoided. On a landscape scale, racers preferred edges over all habitats except successional fields; both edges and successional fields likely provide the greatest access to variation in microclimates. Our results are consistent with racers being known as open habitat specialists (Plummer and Congdon 1994; Fitch 1999) but are contrary to another study in Illinois that showed a lack of edge preference, albeit with very small samples (Keller and Heske 2000). Because edges are so important for racers relative to ratsnakes in southern Illinois, this difference in edge preference may reflect an interspecific difference in thermoregulatory precision (Huey and Slatkin 1976; Hertz 1992). Racers may be more confined to the habitats that most readily facilitate thermoregulation (forest edges and successional fields), analogous to the behavior seen in ratsnakes at their northern range limit (Blouin-Demers and Weatherhead 2001a).

Seasonal patterns of edge use by racers were consistent with this use being associated with thermoregulation. During May and late in the season, racers used successional fields to the greatest extent relative to edges. During these periods, racers are likely to experience relatively lower temperatures, so successional fields could provide them with greater local-scale thermal heterogeneity to facilitate thermoregulation (Sartorius et al. 2002). Racers used forest edges more in mid-summer, when environmental temperatures in open habitats may have become too warm. Additionally, the increased use by racers of bottomland forest through the summer may reflect an increased ability to meet thermal requirements in closed canopy habitats as temperatures increased. However, the low use of successional fields relative to edges in April is contrary to our prediction, but could indicate a lack of sufficient vegetative cover in that habitat type early in the season that would increase predation risk (Charland and Gregory 1995). Finally, sex differences in edge use by racers were also consistent with use being associated with thermoregulation. Females used edges more than males at both the landscape and the microhabitat scale, particularly early in the season, when females were gravid.

Overall, intraspecific and interspecific patterns of habitat use were broadly consistent with thermal ecology being an important determinant of how and why snakes select habitat. However, confirmation of this hypothesis will require documenting how the snakes' body temperatures vary among habitats, both absolutely and relative to body temperatures that could be realized in each habitat. Furthermore, although the abundance of mammalian prey appears not to influence habitat use (Carfagno et al. 2006), availability of avian prey and habitat-specific variation in predation risk remain possible, and thus far unexplored, factors that could affect habitat use by ratsnakes and racers.

### Broader implications

Our results have implications for both nest predation by snakes and the effects of habitat fragmentation on ratsnakes

and racers. Whereas Blouin-Demers and Weatherhead (2001a) suggested that a mosaic of smaller forest fragments would benefit ratsnakes in Ontario by facilitating thermoregulation, our results show that this may not be applicable for all populations. In Illinois, male ratsnakes used forest edges and interiors equally, whereas females selectively used forest interiors. Therefore, for ratsnakes in Illinois, ideal habitat seems likely to be continuous forest with limited edge, not a fragmented and reforested landscape. However, increased forest fragmentation and maintenance of old fields at different levels of succession would produce more appropriate habitat for racers.

Because both ratsnakes and racers in southern Illinois use edges, edge-nesting birds may be especially threatened by predation. Generalist predators (such as snakes) that use habitats within an agricultural matrix have the greatest potential to affect forest bird populations with increasing fragmentation (Andren 1992). Forests in Illinois show high rates of nest predation throughout (Robinson and Robinson 2001), and this is especially true for more fragmented areas (Marini et al. 1995; Heske et al. 2001) such as our study site. Decreasing the amount of forest edge in Illinois would reduce nest predation by racers but could ultimately increase predation by ratsnakes because more continuous forests seem likely to be beneficial to ratsnakes, particularly through their effects on females.

### Acknowledgements

We thank G. Blouin-Demers for allowing us to use his data; K. Bugle, A. Hagen, R. Kelly, and E. Tetauer for assisting with fieldwork; J. Whittington for assisting with surgeries; L. Jones and the US Fish and Wildlife Service for allowing us to use their field station; J. Waycullis and the Illinois Department of Natural Resources for logistical support; the University of Illinois and The Nature Conservancy for financial support; and two anonymous reviewers for comments that improved the manuscript.

### References

- Adolph, S.C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology*, **71**: 315–327. doi:10.2307/1940271.
- Aebischer, N.J., Robertson, P.A., and Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, **74**: 1313–1325. doi:10.2307/1940062.
- Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology*, **73**: 794–804. doi:10.2307/1940158.
- Andren, H., and Angelstam, P. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology*, **69**: 544–547. doi:10.2307/1940455.
- Batary, P., and Baldi, A. 2004. Evidence of an edge effect on avian nest success. *Conserv. Biol.* **18**: 389–400. doi:10.1111/j.1523-1739.2004.00184.x.
- Bauwens, D., Garland, T., Castilla, A.M., and Van Damme, R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution*, **49**: 848–863. doi:10.2307/2410408.
- Blouin-Demers, G., and Weatherhead, P.J. 2001a. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forest. *Ecology*, **82**: 2882–2896. doi:10.2307/2679968.

- Blouin-Demers, G., and Weatherhead, P.J. 2001b. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology*, **82**: 3025–3043. doi:10.2307/2679832.
- Blouin-Demers, G., and Weatherhead, P.J. 2001c. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes (*Elaphe obsoleta obsoleta*). *J. Anim. Ecol.* **70**: 1006–1013. doi:10.1046/j.0021-8790.2001.00554.x.
- Blouin-Demers, G., and Weatherhead, P.J. 2002. Implications of spatial and movement patterns for gene flow in black rat snakes (*Elaphe obsoleta*). *Can. J. Zool.* **80**: 1162–1172.
- Blouin-Demers, G., Weatherhead, P.J., Shilton, C.M., Parent, C.E., and Brown, G.P. 2000. Use of inhalant anesthetics in three snake species. *Contemp. Herpetol.* [serial online], 2000(4). Available from <http://www.cnah.org/CH/ch/2000/4/index.htm>.
- Blouin-Demers, G., Prior, K.A., and Weatherhead, P.J. 2002. Comparative demography of black rat snakes (*Elaphe obsoleta*) in Ontario and Maryland. *J. Zool.* **256**: 1–10.
- Brown, G.P., and Shine, R. 2004. Effects of reproduction on the antipredator tactics of snakes (*Tropidonophis mairii*, Colubridae). *Behav. Ecol. Sociobiol.* **56**: 257–262.
- Burbrink, F.T. 2001. Systematics of the eastern ratsnake complex (*Elaphe obsoleta*). *Herpetol. Monogr.* **15**: 1–53. doi:10.2307/1467037.
- Burbrink, F.T., Lawson, R., and Slowinski, J.B. 2000. Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. *Evolution*, **54**: 2107–2118. doi:10.1554/0014-3820(2000)054[2107:MDPOTP]2.0.CO;2. PMID:11209786.
- Burkey, T.V. 1993. Edge effects in seed and egg predation at two neotropical rainforest sites. *Biol. Conserv.* **66**: 139–143.
- Carfagno, G.L.F., Heske, E.J., and Weatherhead, P.J. 2006. Does mammalian prey abundance explain forest-edge use by snakes? *Ecoscience*, **13**: 293–297.
- Chalfoun, A.D., Ratnaswamy, M.J., and Thompson, F.R., III. 2002a. Songbird nest predators in forest–pasture edge and forest interior in a fragmented landscape. *Ecol. Appl.* **12**: 858–867.
- Chalfoun, A.D., Thompson, F.R., III, and Ratnaswamy, M.J. 2002b. Nest predators and fragmentation: a review and meta-analysis. *Conserv. Biol.* **16**: 306–318. doi:10.1046/j.1523-1739.2002.00308.x.
- Changnon, S.A., Angel, J.R., Kunkel, K.E., and Lehmann, C.M.B. 2004. Climate atlas of Illinois. Illinois State Water Survey, Champaign, Ill.
- Charland, M.B., and Gregory, P.T. 1995. Movements and habitat use in gravid and nongravid female garter snakes (Colubridae: *Thamnophis*). *J. Zool. (Lond.)* **236**: 543–561.
- Conant, R., and Collins, J.T. 1998. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin Company, New York.
- Donovan, T.M., Lamberson, R.H., Kimber, A., Thompson, F.R., III, and Faaborg, J. 1995. Modeling the effects of habitat fragmentation on source and sink demography of Neotropical migrant birds. *Conserv. Biol.* **9**: 1396–1407. doi:10.1046/j.1523-1739.1995.09061396.x.
- Durner, G.M., and Gates, J.E. 1993. Spatial ecology of black rat snakes on Remington Farms, Maryland. *J. Wildl. Manag.* **57**: 812–826.
- Fitch, H.S. 1963a. Natural history of the black rat snake (*Elaphe o. obsoleta*) in Kansas. *Copeia*, 1963: 649–658. doi:10.2307/1440967.
- Fitch, H.S. 1963b. Natural history of the racer, *Coluber constrictor*. *Univ. Kans. Publ. Mus. Nat. Hist.* **15**: 351–468.
- Fitch, H.S. 1999. A Kansas snake community: composition and changes over 50 years. Krieger Publishing Company, Malabar, Fla.
- Ford, N.B., and Burghardt, G.M. 1993. Perceptual mechanisms and the behavioral ecology of snakes. *In Snakes: ecology and behavior.* Edited by R.A. Seigel and J.T. Collins. McGraw-Hill, New York. pp. 117–164.
- Gibbs, H.L., Coreyl, S.J., Blouin-Demers, G., Prior, K.A., and Weatherhead, P.J. 2006. Hybridization between mtDNA-defined phylogeographic lineages of black ratsnakes (*Pantherophis* sp.). *Mol. Ecol.* **15**: 3755–3767. PMID:16842423.
- Grant, B.W. 1990. Trade-offs in activity time and physiological performance for thermoregulating desert lizards, *Sceloporus merriami*. *Ecology*, **71**: 2323–2333. doi:10.2307/1938643.
- Gvozdkik, L. 2002. To heat or to save time? Thermoregulation in the lizard *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient. *Can. J. Zool.* **80**: 479–492.
- Harrison, S., and Bruna, E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*, **22**: 225–232. doi:10.1111/j.1600-0587.1999.tb00496.x.
- Heard, G.W., Black, D., and Robertson, P. 2004. Habitat use by the inland carpet python (*Morelia spilota metcalfei*: Pythonidae): seasonal relationships with habitat structure and prey distribution in a rural landscape. *Austral Ecol.* **29**: 446–460.
- Heatwole, H., and Johnson, C.R. 1979. Thermoregulation in the red-bellied blacksnake, *Pseudechis porphyriacus* (Elapidae). *Zool. J. Linn. Soc.* **63**: 83–101.
- Hertz, P.E. 1992. Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology*, **73**: 1405–1417. doi:10.2307/1940686.
- Hertz, P.E., and Huey, R.B. 1981. Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. *Ecology*, **62**: 515–521. doi:10.2307/1937714.
- Heske, E.J., Robinson, S.K., and Brawn, J.D. 2001. Nest predation and neotropical migrant songbirds: piecing together the fragments. *Wildl. Soc. Bull.* **29**: 52–61.
- Houston, D., and Shine, R. 1993. Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *J. Anim. Ecol.* **62**: 737–748.
- Huey, R.B., and Kingsolver, J.G. 1993. Evolution of resistance to high temperature in ectotherms. *Am. Nat.* **142**: S21–S46. doi:10.1086/285521.
- Huey, R.B., and Slatkin, M. 1976. Cost and benefits of lizard thermoregulation. *Q. Rev. Biol.* **51**: 363–384. doi:10.1086/409470. PMID:981504.
- Kearney, M. 2002. Hot rocks and much-too-hot rocks: seasonal patterns of retreat-site selection by a nocturnal ectotherm. *J. Therm. Biol.* **27**: 205–218.
- Keller, W.L., and Heske, E.J. 2000. Habitat use by three species of snakes at the Middle Fork Fish and Wildlife Area, Illinois. *J. Herpetol.* **34**: 558–564. doi:10.2307/1565271.
- King, D.I., Degraaf, R.M., and Griffin, C.R. 1998. Edge-related nest predation in clearcut and groupcut stands. *Conserv. Biol.* **12**: 1412–1415. doi:10.1046/j.1523-1739.1998.97199.x.
- Klimstra, W.D. 1959. Foods of the racer, *Coluber constrictor*, in southern Illinois. *Copeia*, 1959: 210–214. doi:10.2307/1440390.
- Larivière, S. 2003. Edge effects, predator movements, and the travel-lane paradox. *Wildl. Soc. Bull.* **31**: 315–320.
- Lillywhite, H.B., and Henderson, R.W. 1993. Behavioral and functional ecology of arboreal snakes. *In Snakes: ecology and behavior.* Edited by R.A. Seigel and J.T. Collins. McGraw-Hill, New York. pp. 1–48.
- Marini, M.A., Robinson, S.K., and Heske, E.J. 1995. Edge effects on

- nest predation in the Shawnee National Forest, southern Illinois. *Biol. Conserv.* **74**: 203–213. doi:10.1016/0006-3207(95)00032-Y.
- Martin, T.E. 1988. Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology*, **69**: 74–84. doi:10.2307/1943162.
- Martin, T.E. 1993. Nest predation and nest sites. *Bioscience*, **43**: 523–532. doi:10.2307/1311947.
- McCarigal, K., Cushman, S., and Stafford, S. 2000. *Multivariate statistics for wildlife and ecology research*. Springer-Verlag, New York.
- Meffe, G.K., and Carroll, C.R. 1997. *Principles of conservation biology*. 2nd ed. Sinauer Associates, Inc., Sunderland, Mass.
- Morrison, S.A., and Bolger, D.T. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia*, **133**: 315–324. doi:10.1007/s00442-002-1040-3.
- Plummer, M.V., and Congdon, J.D. 1994. Radiotelemetric study of activity and movements of racers (*Coluber constrictor*) associated with a Carolina bay in South Carolina. *Copeia*, 1994: 20–26. doi:10.2307/1446666.
- Reinert, H.K. 1984. Habitat separation between sympatric snake populations. *Ecology*, **65**: 478–486. doi:10.2307/1941410.
- Reinert, H.K. 1993. Habitat selection in snakes. In *Snakes: ecology and behavior*. Edited by R.A. Seigel and J.T. Collins. McGraw-Hill, New York. pp. 201–240.
- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* **9**: 1–48.
- Robinson, S.K., and Robinson, W.D. 2001. Avian nesting success in a selectively harvested north temperate deciduous forest. *Conserv. Biol.* **15**: 1763–1771. doi:10.1046/j.1523-1739.2001.00226.x.
- Robinson, S.K., Thompson, P.R., Donovan, T.M., Whitehead, D.R., and Faaborg, J. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science (Washington, D.C.)*, **267**: 1987–1990.
- Sartorius, S.S., do Amaral, J.P.S., Durtsche, R.D., Deen, C.M., and Lutterschmidt, W.I. 2002. Thermoregulatory accuracy, precision, and effectiveness in two sand-dwelling lizards under mild environmental conditions. *Can. J. Zool.* **80**: 1966–1976. doi:10.1139/z02-191.
- Schoener, T.W. 1977. Competition and the niche. In *Biology of the Reptilia*. Edited by C. Gans and D.W. Tinkle. Academic Press, New York. Vol. 7. pp. 35–136.
- Seigel, R.A., Huggins, M.M., and Ford, N.B. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. *Oecologia*, **73**: 481–485. doi:10.1007/BF00379404.
- Sexton, O.J., and Hunt, S.R. 1980. Temperature relationships and movements of snakes (*Elaphe obsoleta*, *Coluber constrictor*) in a cave hibernaculum. *Herpetologica*, **36**: 20–26.
- Shine, R., and Fitzgerald, M. 1996. Large snakes in a mosaic rural landscape: the ecology of carpet pythons *Morelia spilota* (Serpentes: Pythonidae) in coastal Eastern Australia. *Biol. Conserv.* **76**: 113–122. doi:10.1016/0006-3207(95)00108-5.
- Stephens, S.E., Koons, D.N., Rotella, J.J., and Willey, D.W. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biol. Conserv.* **115**: 101–110.
- Stickel, L.F., Stickel, W.H., and Schmid, F.C. 1980. Ecology of a Maryland population of black rat snakes (*Elaphe o. obsoleta*). *Am. Midl. Nat.* **103**: 1–14. doi:10.2307/2425033.
- Thompson, F.R., III, and Burhans, D.E. 2003. Predation of songbird nests differs by predator and between field and forest habitats. *J. Wildl. Manag.* **67**: 408–416.
- Thompson, F.R., III, Dijak, W., and Burhans, D.E. 1999. Video identification of predators at songbird nests in old fields. *Auk*, **116**: 259–264.
- Tracy, C.R., and Christian, K.A. 1986. Ecological relations among space, time, and thermal niche axes. *Ecology*, **67**: 609–615. doi:10.2307/1937684.
- Turner, F.B. 1977. The dynamics of populations of squamates, crocodylians, and rhynchocephalians. In *Biology of the Reptilia*. Edited by C. Gans and D.W. Tinkle. Academic Press, New York. Vol. 7. pp. 157–264.
- Weatherhead, P.J., and Blouin-Demers, G. 2004. Understanding avian nest predation: why ornithologists should study snakes. *J. Avian Biol.* **35**: 185–190. doi:10.1111/j.0908-8857.2004.03336.x.
- Weatherhead, P.J., and Charland, M.B. 1985. Habitat selection in an Ontario population of the snake, *Elaphe obsoleta*. *J. Herpetol.* **19**: 12–19. doi:10.2307/1564415.
- Weatherhead, P.J., and Hoysak, D.J. 1989. Spatial and activity patterns of black rat snakes (*Elaphe obsoleta*) from radiotelemetry and recapture data. *Can. J. Zool.* **67**: 463–468.
- Weatherhead, P.J., and Robertson, I.C. 1990. Homing to food by black rat snakes (*Elaphe obsoleta*). *Copeia*, 1990: 1164–1165. doi:10.2307/1446506.
- Weatherhead, P.J., Blouin-Demers, G., and Cavey, K.M. 2003. Seasonal and prey-size dietary patterns of black ratsnakes (*Elaphe obsoleta obsoleta*). *Am. Midl. Nat.* **150**: 275–281. doi:10.1674/0003-0031(2003)150[0275:SAPDPO]2.0.CO;2.
- Webb, J.K., and Shine, R. 1998. Thermoregulation by a nocturnal elapid snake (*Hoplocephalus bungaroides*) in southeastern Australia. *Physiol. Zool.* **71**: 680–692. PMID:9798255.
- Wilson, E.O. 2001. *The diversity of life*. Penguin, London.
- Yahner, R.H., and Scott, D.P. 1988. Effects of forest fragmentation on depredation of artificial nests. *J. Wildl. Manag.* **52**: 158–161.