

Does mammalian prey abundance explain forest-edge use by snakes?¹

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Abstract: Snakes are important predators of birds' nests, but the ecological factors that bring snakes and birds into contact are poorly known. One hypothesis is that snakes choose habitats based on abundance of alternative prey such as small mammals, with avian nest predation in those habitats arising coincidentally. At a study site in southern Illinois, we used radio telemetry to test the hypothesis that ratsnakes (*Elaphe obsoleta*) and racers (*Coluber constrictor*) preferentially use forest edges because small mammals are more abundant in edges. Diet analysis confirmed that both snake species preyed on birds and mammals. Although overall habitat use differed, both snake species preferentially used forest edges. Conversely, species of small mammals on which the snakes preyed were not more abundant (determined by live trapping) in edges, and seasonal variation in habitat use by snakes and mammalian prey abundance were not correlated. These results suggest that alternative hypotheses (e.g., abundance of nesting birds, thermoregulation) are more promising explanations for why these snakes preferentially use edges.

Keywords: diet, edge, habitat selection, predation, small mammals, snakes.

Résumé : Les serpents sont d'importants prédateurs des nids d'oiseaux mais les facteurs écologiques qui mènent au contact entre les serpents et les oiseaux sont peu connus. Une des hypothèses stipule que les serpents choisissent leurs habitats en fonction de proies alternatives tels que les petits mammifères et que la prédation sur les nids d'oiseaux dans ces habitats est une conséquence non planifiée. Dans un site d'étude au sud de l'état de l'Illinois, nous avons utilisé la télémétrie radio pour tester l'hypothèse voulant que les serpents ratiers (*Elaphe obsoleta*) et les couleuvres agiles (*Coluber constrictor*) utilisent préférentiellement les bordures de forêts parce que les petits mammifères y sont plus abondants. L'analyse de la diète a confirmé que les oiseaux et les mammifères constituent les proies des deux espèces de serpents. Même si l'utilisation générale de l'habitat n'était pas la même pour les deux espèces de serpents, les deux utilisaient préférentiellement les bordures de forêts. À l'opposé, les espèces de petits mammifères servant de proies aux serpents n'étaient pas plus abondants (tel que déterminé par le trappage vivant) dans les bordures et la variation saisonnière de l'utilisation de l'habitat par les serpents et l'abondance de leurs proies n'étaient pas corrélées. Ces résultats suggèrent que des hypothèses alternatives (e.g., abondance d'oiseaux nicheurs, thermorégulation) sont plus prometteuses pour expliquer pourquoi les serpents préfèrent les bordures.

Mots-clés : bordure, diète, petits mammifères, prédation, sélection de l'habitat, serpents.

Nomenclature: Wilson & Reeder, 1993; Greer, 1997; Phillips, Brandon & Moll, 1999.

Introduction

Ornithologists responded to declining songbird populations (Robbins *et al.*, 1989) by investigating nest predation, the most important cause of songbird nest failure (Martin, 1993). Most attention has been given to interpreting patterns of nest predation relative to habitat features such as composition and fragmentation (Chalfoun, Thompson & Ratnaswany, 2002; Stephens *et al.*, 2003). For example, predation is an important cause of nest failure in some edge habitats (Andren & Angelstam, 1988; Burkey, 1993; King, Degraaf & Griffin, 1998; Batory & Baldi, 2004). To date, the ecology of nest predators is inferred only from predation patterns. Better understanding of factors that bring nest

predators and birds in contact, however, is possible only by studying predators directly (Chalfoun, Thompson & Ratnaswany, 2002; Larivière, 2003; Stephens *et al.*, 2003). Studies that have videotaped nest predation have identified snakes as important nest predators (Thompson, Dijk & Burhans, 1999; Morrison & Bolger, 2002; Thompson & Burhans, 2003), suggesting snakes would be a good model predator to study (Weatherhead & Blouin-Demers, 2004).

Weatherhead and Blouin-Demers (2004) proposed two general hypotheses to explain patterns of snake predation. Snakes could be attracted to particular habitats (e.g., edges) by the abundance of nesting birds, or alternatively, snakes could be attracted to those habitats for reasons unrelated to birds, with higher nest predation a coincidental result. Non-avian factors that could attract snakes to particular habitats include properties conducive to thermoregulation (Blouin-Demers & Weatherhead, 2001a,b) and abundance of alter-

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native prey such as small mammals. We consider the latter alternative here. Our goal was to document habitat use by two snake species known to prey on both small mammals and birds' nests, to identify mammal species preyed on by these snakes, and to determine whether habitat associations of mammalian prey explained habitat use by snakes.

The hypothesis that snakes are attracted to edges by the abundance of small mammals is not well tested. Of the studies that have examined use of habitat edges by small mammals (reviewed by Chalfoun, Thompson & Ratnaswany, 2002), few have found small mammals associated with edges. Only two studies have examined habitat use by both snakes and small mammals in this context. Blouin-Demers and Weatherhead (2001a) found that a strong association with edges by *Elaphe obsoleta* (black ratsnake) in Ontario, Canada was not matched by small mammals and concluded that thermal considerations most likely explained edge preference by the snakes. Chalfoun, Ratnaswany, and Thompson (2002) also found that snakes were associated with edges and that small mammals were not. They included all snake species in their analyses, however. Using data only for species likely to prey on both birds' nests and mammals, snakes showed no edge association, although data were extremely limited (13 observations).

We combined intensive radio tracking of two snake species and extensive small mammal trapping to test the hypothesis that snakes are attracted to areas where small mammals are abundant. One of the snake species we studied was *Elaphe obsoleta*, the same species studied by Blouin-Demers and Weatherhead (2001a). They conducted their study in Ontario near the northern limit of the species' distribution, whereas we studied ratsnakes in the central part of their range in Illinois, so our study provides an opportunity to assess the generality of their results. In particular, a more benign thermal environment in Illinois may make thermoregulation less important to habitat selection by ratsnakes, thus making prey abundance more likely to influence habitat selection.

Methods

SNAKE SAMPLING AND ANALYSIS

We conducted this study from April to September 2003 at the Cache River State Natural Area, Johnson County, in southern Illinois. The study area was approximately 3 × 4 km and contained a mosaic of mature deciduous forest and old fields in various stages of succession. The snakes studied were *Elaphe obsoleta* and *Coluber constrictor* (racer), both of which have been documented to prey on both birds' nests and mammals (Klimstra, 1959; Fitch, 1963; Weatherhead, Blouin-Demers & Cavey, 2003). Both species often make movements of > 400 m within 48 h (G. Carfagno, unpubl. data), so all habitat types were accessible to all snakes.

We captured most snakes in the spring as they emerged from communal hibernacula and other snakes opportunistically during the summer. Radio transmitters (Model SI-2T, Holohil Systems Inc., Carp, Ontario, Canada) were surgically implanted by a veterinarian using methods described by Blouin-Demers and Weatherhead (2001a). Transmitters weighed either 8 or 12 g and never exceeded 3% of a

snake's mass. Snakes captured during the study were held for several days to obtain fecal samples. We used the methods of Weatherhead, Blouin-Demers, and Cavey (2003) to identify diet items from snake feces; mammals were identified by hair morphology.

We located the snakes every other day from emergence in March until hibernation in October. Locations were categorized as forest, successional field, old field, or edge (within 15 m of a forest–field boundary) and mapped using GPS. We quantified available habitat at random locations. At every second unique snake location we moved in a random direction a random distance between 10 and 200 paces. We restricted analysis to snake and random locations obtained from May to July to correspond with small mammal sampling periods (see below) and to snakes with a minimum of 20 locations (range = 22–45). This sample included 13 *Elaphe* (seven male, six female) and 11 *Coluber* (six male, five female). We combined data by sex within species because our purpose here is to characterize habitat use by species.

We used compositional analysis (Aebischer, Robertson & Kenward, 1993) to determine whether snakes used habitats non-randomly, with individuals as the unit of replication. For each habitat we calculated differences between log-ratio transformed proportions of habitat use and availability. We then used MANOVA to determine if log ratio differences deviated from zero, to determine if use differed from availability. We used two-tailed *t*-tests for pairwise comparisons among the four habitats.

SMALL MAMMAL SAMPLING AND ANALYSIS

We live trapped small mammals on eighteen 500-m transects. Fifteen were arrayed in groups, with each group containing three parallel transects: one in forest edge (< 5 m from edge of the canopy), one in forest interior (about 100 m from canopy edge), and one in an adjacent field (distance from canopy edge was constrained by the size of fields but always > 25 m and usually 50–100 m). Four of the fields were late successional (dense saplings, shrubs, vines) and one was an old field (predominantly grass and forbs). We added another old-field transect and two transects deeper in forest interior. Thus, in total there were seven transects in forest interiors, four in successional fields, two in old fields, and five in forest edges. Transects in similar habitats were > 500 m apart. All transects were in areas used by snakes with transmitters.

We live trapped on each transect once per month from May through July 2003. A trapping session comprised 3 d, with traps set on day 1, checked and re-set as needed in the morning of day 2, and checked and removed on the morning of day 3. We used two Sherman (H. P. Sherman Co., Tallahassee, Florida, USA) folding aluminum traps (10 × 11.25 × 37.5 cm) set per station, 2–5 m apart, at 10-m intervals along each transect. Traps were placed to maximize capture of terrestrial small mammals (*e.g.*, along fallen logs, near the base of large trees, in runways) and baited with sunflower seeds. All small mammals captured were identified to species and weighed to the nearest g. Individuals were marked with a small fur clip to identify recaptures, with the location of the clip changed for each

trapping session. Sets of forest–edge–field transects were always trapped simultaneously.

We estimated small mammal abundance for a habitat and sampling period as the mean number (or biomass) of animals caught per transect. In the absence of any evidence to the contrary, we assumed that small mammals were equally trappable (or vulnerable to snakes) in all habitats. We compared small mammal abundance among forest, edge, successional field, and old field with repeated measures ANOVA. Separate analyses were conducted for the number of individuals and biomass (summed weights) of both all small mammals and just prey species (determined from fecal analysis). When ANOVA indicated significant differences among habitats, Tukey’s HSD was used to identify pairwise differences.

To relate snake habitat use to small mammal abundance we calculated snake use of each habitat each month expressed as percentage greater than (+ ve) or less than (- ve) the expected use based on habitat availability. We used Spearman rank correlation to determine if habitat use varied with prey biomass over these 12 samples (4 habitats × 3 months).

Results

Radio-tracking produced 517 *Elaphe* locations and 391 *Coluber* locations from May through July. No individual snake provided more than 6% of total locations per species. We sampled habitat at 145 *Elaphe* and 193 *Coluber* randomly selected locations.

Snake habitat use differed significantly from expected based on availability for both *Elaphe* (Wilks’ Lambda = 0.34, $F_{3,10} = 6.60$, $P = 0.010$) and *Coluber* (Wilks’ Lambda = 0.27, $F_{3,8} = 7.14$, $P = 0.012$). *Elaphe* used edges and forests more than old fields, whereas *Coluber* used edges and successional fields more than forests (Figure 1).

Each fecal sample contained identifiable remains of only a single prey type. Samples containing mammals had only a single species or genus represented. Only mammalian and avian prey were represented in the 24 *Elaphe* samples, comprising 58% and 42% of samples, respectively. Of the *Elaphe* fecal samples containing mammals, seven had *Peromyscus* spp., four had *Microtus* spp., one had *Ochrotomys nuttalli*, one had *Zapus hudsonius*, and one was unidentifiable. Thirty-nine percent of the 23 *Coluber* samples contained mammalian prey, 17% contained avian prey, and 44% contained other taxa (insect, reptilian, and amphibian). Of the *Coluber* fecal samples containing mammals, six had *Peromyscus* spp., two had *Microtus* spp., and one had *Ochrotomys nuttalli*.

We captured 1477 individuals of 11 species of mammals (*Blarina carolinensis*, 623; *Peromyscus leucopus*, 590; *P. maniculatus*, 16; *Ochrotomys nuttalli*, 29; *Microtus ochrogaster*, 92; *Synaptomys cooperi*, 39; *M. pinetorum*, 34; *Zapus hudsonius*, 8; *Oryzomys palustris*, 3; *Tamias striatus*, 34; *Glaucomys volans*, 9). Habitats differed in the biomass of small mammals ($F_{3,14} = 3.5$, $P = 0.04$). Successional fields had less biomass than forest interior, but no other habitats differed from each other (Table I). Biomass of all small mammals also varied over sampling periods ($F_{2,28} = 34.5$,

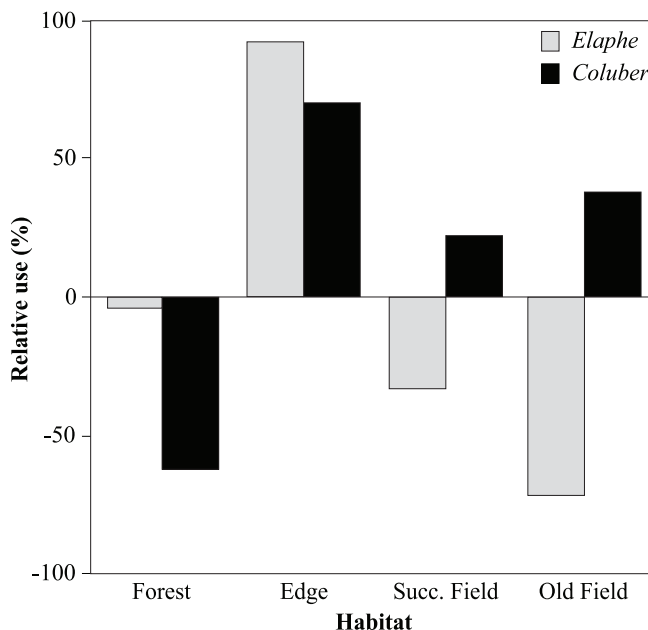


FIGURE 1. Use of habitats by ratsnakes (*Elaphe*) and racers (*Coluber*) expressed as a percentage of the expected use based on availability (positive values mean greater use than expected, negative values less use than expected).

TABLE I. Estimated abundance of small mammals by habitat and trapping period. Each entry is the mean (\pm SD) per transect within a given habitat and month. Prey values are based on species considered probable prey for *Elaphe* and *Coluber* based on diet analysis.

	Forest <i>n</i> = 7	Edge <i>n</i> = 5	Successional field <i>n</i> = 4	Old field <i>n</i> = 2
MAY				
Total <i>n</i>	22.4 \pm 9.1	15.4 \pm 3.6	8.3 \pm 2.9	9.5 \pm 7.8
Total biomass (g)	483 \pm 243	332 \pm 148	161 \pm 53	262 \pm 210
Prey <i>n</i>	17.9 \pm 7.4	12.4 \pm 5.1	6.0 \pm 2.4	9.0 \pm 8.5
Prey biomass (g)	360 \pm 152	250 \pm 105	141 \pm 54	261 \pm 210
JUNE				
Total <i>n</i>	40.9 \pm 9.8	37.6 \pm 8.2	37.8 \pm 9.7	22.0 \pm 14.1
Total biomass (g)	814 \pm 200	753 \pm 119	577 \pm 137	668 \pm 474
Prey <i>n</i>	24.7 \pm 4.7	21.0 \pm 4.8	16.8 \pm 0.5	20.5 \pm 13.4
Prey biomass (g)	501 \pm 90	462 \pm 95	388 \pm 57	609 \pm 402
JULY				
Total <i>n</i>	43.3 \pm 11.2	40.2 \pm 9.3	36.8 \pm 4.0	45.0 \pm 8.5
Total biomass (g)	828 \pm 266	913 \pm 264	489 \pm 53	1181 \pm 381
Prey <i>n</i>	26.7 \pm 8.7	22.8 \pm 5.3	10.5 \pm 2.5	34.5 \pm 12.0
Prey biomass (g)	541 \pm 173	462 \pm 110	253 \pm 34	1086 \pm 413

$P < 0.001$), with no interaction between time and habitat ($F_{6,28} = 2.1$, $P = 0.09$). We excluded *B. carolinensis*, *T. striatus*, *G. volans*, and *O. palustris* to estimate biomass of small mammal prey because diet analysis indicated the snakes preyed primarily on voles and mice. Habitats also differed in the biomass of prey species ($F_{3,14} = 6.3$, $P = 0.006$). Old fields had greater prey biomass than successional fields and edges, and forests had greater prey biomass than successional fields, but no other habitats differed from each other. Biomass of prey species varied over sampling periods ($F_{2,28} = 30.9$, $P < 0.001$), with an interaction between sampling period and habitat ($F_{6,28} = 5.5$,

$P = 0.001$) likely due to a greater increase in biomass in old fields than in other habitats in later sampling periods (Table I). Analyses based on numbers of prey were qualitatively similar to those based on biomass.

We found no evidence that snakes varied their use of habitats in response to biomass of small mammal prey (*Elaphe*: $r_s = -0.21$, $P = 0.48$; *Coluber*: $r_s = 0.15$, $P = 0.61$, Figure 2). Note that because observations within a month were not independent (use of the fourth habitat type depended on combined use of the other three), reported P values are underestimated. Results were qualitatively unchanged when we used numbers rather than biomass of small mammals or all small mammals rather than prey species.

Discussion

Both snake species exhibited a clear preference for edge habitat. Based on overall habitat use, *Elaphe* could be characterized as a forest species that preferentially uses edges between forest and field, whereas *Coluber* is a successional-field snake that preferentially uses edges between field and forest. Both snake species included birds and small mammals in their diets, with *Coluber* also including other vertebrates and insects. Thus, both species satisfied the prerequisite for this study of associating positively with forest–field edges and preying on both birds and mammals.

We found no evidence that the snakes' use of edge habitat was a consequence of small mammals being more abundant in edges. Small mammal abundance varied among habitats, but the tendency was for prey species to be less rather than more abundant in edges compared to old fields,

similar in abundance in edges and forest interior, and slightly (but not significantly) more abundant in edges than in successional fields. Direct comparison of snake habitat use by month relative to small mammal abundance showed no association, despite substantial variation in both variables that would have allowed a pattern to be detected if it existed.

Blouin-Demers and Weatherhead (2001a) found that *Elaphe* in Ontario also preferentially used edges despite small mammals not being more abundant in edges. Some snakes do select habitats based on abundance of mammalian prey, however. Madsen and Shine (1996) showed *Liasis fuscus* habitat use changed seasonally in response to *Rattus colletti* distribution, and Heard, Black, and Robertson (2004) showed that *Morelia spilota metcalfei* responded similarly to *Oryctolagus cuniculus* distributions. Because both these python species live in warmer climates than the snakes we studied, however, their use of habitat may be less constrained by thermal considerations than is the case for temperate-zone snakes.

Prey distribution may also be less important for generalist predators such as *Elaphe* and *Coluber*. These species may select habitats for thermoregulatory reasons, for example, and opportunistically prey on whatever acceptable prey species are available. Alternatively, these snakes might respond to total prey abundance, where any single prey type would be a poor predictor of the snakes' habitat use. Given the importance of mammalian prey to *Coluber* and particularly to *Elaphe*, however, the latter hypothesis should still have produced some association between snake habitat use and mammal abundance.

Failure to support the hypothesis that snakes that prey on birds' nests are attracted to particular habitats (e.g., edges) by the abundance of small mammals (another prey type) means that efforts to understand the factors that bring birds and snakes into contact can focus on alternative hypotheses. This conclusion is strengthened by the fact that our results for *Elaphe* were consistent with those of Blouin-Demers and Weatherhead (2001a), despite the two studies being conducted in different parts of the snake's range. Alternative explanations for why snakes and birds come into contact include snakes being attracted to nesting birds themselves or to habitats appropriate for thermoregulation, with the latter hypothesis appearing the most likely (Blouin-Demers & Weatherhead, 2001a; Weatherhead & Blouin-Demers, 2004). It remains to be determined whether our conclusion applies to other snake species. The large ranges of *Elaphe* and *Coluber* and their documented importance as avian nest predators (Weatherhead & Blouin-Demers, 2004), however, suggest the conclusion should apply to much of eastern North America.

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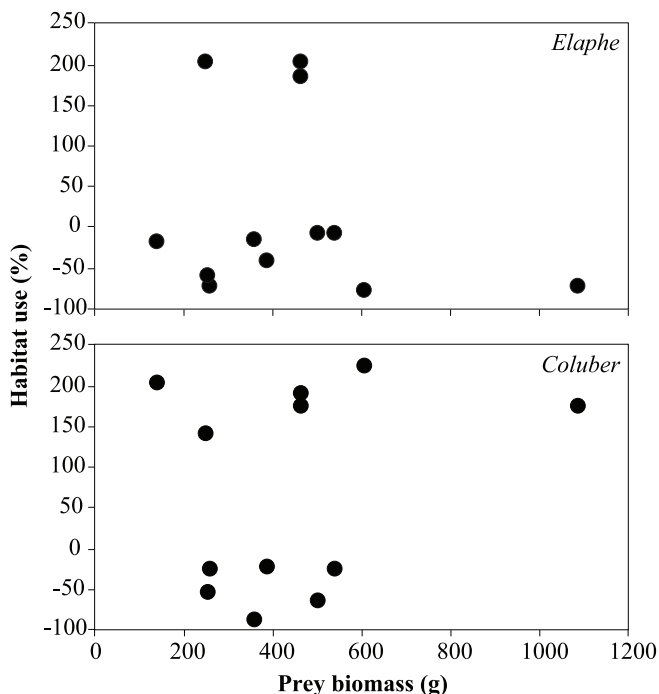


FIGURE 2. Scatterplots of habitat use by ratsnakes (*Elaphe*) and racers (*Coluber*) expressed as a percentage of the expected use based on availability, relative to abundance of small mammals, with a point for each of the four habitats for each of the three months sampled.

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