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# Seasonal and Prey-size Dietary Patterns of Black Ratsnakes (Elaphe obsoleta obsoleta)

PATRICK J. WEATHERHEAD[1] AND GABRIEL BLOUIN-DEMERS[2]
*Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, K1S 5B6, Canada*

AND

KAREN M. CAVEY
*Program in Ecology and Evolutionary Biology, University of Illinois, 606 E. Healey St., Champaign, IL 61820*

ABSTRACT.—Black ratsnakes (*Elaphe obsoleta obsoleta*) prey extensively on both birds (eggs and nestlings) and mammals. There is conflicting evidence, however, regarding whether the snakes specialize on birds during the birds' nesting season or whether predation on birds is opportunistic. We tested these alternatives by determining seasonal dietary patterns from 81 fecal samples collected from black ratsnakes in eastern Ontario over 4 y. We also used these data to determine how diet varies with snake size. Birds occurred in the snakes' diet from May through August, but the occurrence of birds never exceeded that of mammals in any month. This pattern was the same as that previously reported for black ratsnakes in Kansas and supports the hypothesis that black ratsnakes prey on birds opportunistically. Relative to smaller individuals, larger ratsnakes preyed on larger species of mammals and reduced their consumption of smaller species of mammals. The reduction in the consumption of small prey by large snakes was due to diet diversification rather than specialization. However, because larger snakes continued to include small prey in their diet, predation patterns on birds and mammals suggest that ratsnakes are opportunistic predators.

## INTRODUCTION

Black ratsnakes (*Elaphe obsoleta obsoleta*) are excellent climbers and have been reported to prey on a wide variety of birds' eggs and nestlings (*e.g.*, Fitch, 1963; Stickel *et al.*, 1980; Weatherhead and Charland, 1985; Hansen and Fredrickson, 1988; Durner and Gates, 1993; Greene, 1997). Studies of nest predation suggest that black ratsnakes can be the most important nest predator in some avian communities (Chalfoun *et al.*, 2002). Nonetheless, as the species' common name suggests, black ratsnakes also prey extensively on small mammals (Fitch, 1963; Stickel *et al.*, 1980). At present, it is unclear whether the snakes achieve this catholic diet by hunting opportunistically or whether they exhibit seasonal shifts in diet, specializing on bird eggs and nestlings when birds are nesting and specializing on mammals at other times. Resolving which of these alternatives best explains the diet of black ratsnakes is important both for understanding the snakes' ecological role as avian nest predators and for understanding habitat use by black ratsnakes. Here we test these alternatives using dietary data obtained by analyzing fecal samples from black ratsnakes in eastern Ontario, Canada.

The suggestion that black ratsnakes might be specialized seasonal predators on bird nests was made by Weatherhead and Charland (1985). They found that ratsnakes in Ontario

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[1] Corresponding author: present address: Program in Ecology and Evolutionary Biology, University of Illinois, 606 E. Healey St., Champaign, IL 61820; e-mail: pweather@uiuc.edu

[2] Present address: Department of Biology, University of Ottawa, 150 Louis Pasteur, Ottawa, Ontario, K1N 6N5, Canada

preferentially used edge habitats, particularly during May and June, the nesting period for most bird species at their study site. Weatherhead and Charland (1985) speculated that the snakes could be focusing their early-season activity where nesting birds were most abundant. A more detailed analysis of habitat use by black ratsnakes in Ontario by Blouin-Demers and Weatherhead (2001a), however, found no evidence of an early season preference for edge habitat. Although the snakes preferentially used habitat edges, that preference actually increased through the active season. Such a pattern suggests no seasonal specialization on avian prey. Blouin-Demers and Weatherhead (2001a) interpreted their results as being more consistent with the snakes using edges for thermoregulatory reasons, a view supported by studies of the snakes' thermal ecology (Blouin-Demers and Weatherhead, 2001b, c). Blouin-Demers and Weatherhead (2001a) proposed that predation by black ratsnakes on avian prey is coincidental to the snakes' use of edge habitat.

A direct analysis of prey consumed by black ratsnakes in Kansas indicated that predation on birds' eggs and nestlings was opportunistic rather than specialized (Fitch, 1963), at least at that study location. Although birds occurred in 20–42% of samples of the snakes' diet from May through August, mammals comprised as much, or more, of the diet in every month. Our primary objective in this study was to analyze prey consumed by black ratsnakes to test the hypothesis that, in Ontario as in Kansas, black ratsnakes do not exhibit seasonal specialization on avian prey. Specialization would be indicated by the diet shifting from predominantly birds early in the active season to predominantly mammals later in the season. Opportunistic predation on birds would be suggested if mammals are the predominant prey throughout the active season, with birds occurring as a minor prey type during the period birds are nesting. Note that at our study site in Ontario, several bird species have breeding seasons that extend over much of the summer (*e.g.,* Weatherhead and Boak, 1986), although the pattern typical of most species is for nesting to occur almost exclusively in May and June (*e.g.,* Weatherhead and Sommerer, 2001). Therefore, even though birds' eggs and nestlings are potentially available to the snakes through most of the active season, they are much more abundant during the first half of the summer (P. J. Weatherhead, pers. obs.).

Conducting a diet analysis allowed us to meet a second objective concerning prey selection by black ratsnakes. Many snake species exhibit an ontogenetic shift in diet (reviewed by Mushinsky, 1987; Arnold, 1993). As snakes grow larger they consume larger prey. In most, but not all species, larger individuals also drop smaller prey items from their diet. Whereas the former pattern makes sense purely from the mechanics of catching and consuming large prey, the latter pattern is more interesting. For large snakes to forgo small prey items that are obviously available in their environment (as evidenced by the occurrence of small prey in the diets of small snakes), small prey must be uneconomical for large snakes (Arnold, 1993). Our goal was to determine whether black ratsnakes exhibit an ontogenetic shift in the mammalian prey they consume and, in particular, whether large snakes eliminate small prey species from their diet. Arnold's (1993) review suggests that deletion of small prey is most common in diets of piscivorous snakes, so to the extent that a prediction is possible, large ratsnakes should continue preying on small species.

## METHODS

We conducted this study from May 1997 to July 2000 at the Queen's University Biological Station (QUBS) in eastern Ontario, Canada (44°34′N, 76°19′W). Description of the study area and general study methods are provided by Blouin-Demers and Weatherhead (2001a). Snakes were captured regularly in the field and brought to the lab to be measured, have transmitters implanted, etc., as part of a long-term ecological study. Snakes were held in the

TABLE 1.—Species of mammals for which hair samples were included in the library of potential prey of black ratsnakes and their occurrence in black ratsnake fecal samples containing mammals

| Common name | Latin name | Mass (g)[1] | % occurence[2] |
|---|---|---|---|
| Star-nosed mole | *Condylura cristata* | 35–80 | 0.0 |
| Meadow vole | *Microtus pennsylvanicus* | 30–70 | 30.8 |
| White-footed mouse | *Peromyscus leucopus* | 14–30 | 9.6 |
| Deer mouse | *Peromyscus maniculatus* | 18–35 | 25.0 |
| Grey squirrel | *Sciurus carolinensis* | 340–725 | 0.0 |
| Masked shrew | *Sorex cinereus* | 3–6 | 0.0 |
| Eastern chipmunk | *Tamias striatus* | 65–125 | 34.6 |
| Northern flying squirrel | *Glaucomys sabrinus* | 115–185 | 0.0 |
| Red squirrel | *Tamiasciurus hudsonicus* | 200–250 | 3.8 |
| Meadow jumping mouse | *Zapus hudsonius* | 15–22 | 1.9 |

[1] Values obtained from Burt and Grossenheider (1976)

[2] Based on a total of 52 fecal samples that contained mammalian prey

lab in plastic containers (50 cm × 40 cm × 15 cm), which allowed us to collect fecal samples when available. We did not hold all snakes we captured until they defecated, but rather collected samples opportunistically. Over the course of the study we collected 81 fecal samples, 69 of which could be attributed to a known snake because the snake was alone in the container. The size of the "donors" ranged from 65 cm snout-vent length (SVL) to 146 cm SVL and the sex ratio was approximately even (52% female).

We extracted undigested items from the feces (hairs, feathers, teeth, egg shells). Thus, possible prey items that would be completely digested (*e.g.,* soft-bodied animals like earthworms or insects with low chitin content) would go undetected. For each sample, we recorded presence or absence of mammalian prey and avian prey (eggs shells or feathers). For mammalian prey, we used hair impressions on polyvinyl acetate to identify the species (Williamson, 1951). We used mammals obtained through trapping for another study (Blouin-Demers and Weatherhead, 2001a), from a small mammal collection at QUBS and from road kills to assemble a library of hairs of potential mammalian prey at our study site (Table 1). We could identify all potential mammalian prey species unambiguously from their hair, although this method precludes determining prey size within species. For each sample we examined at least 12 hairs selected from throughout the sample. We did not attempt to identify avian prey species from eggshell fragments and feathers.

## RESULTS

In the 81 fecal samples examined we found no evidence of amphibians and the only reptilian evidence we recorded were teeth that appeared to be from black ratsnakes. These teeth are likely to have belonged to the snake that provided the feces, having been shed or broken off and swallowed while the snake was handling its prey. Mammalian prey occurred in 64% (52/81) of the fecal samples and avian prey occurred in 30% (24/81) of samples. Most samples contained only avian remains or hair from a single species of mammal. In 6% (5/81) of samples, however, mammalian prey co-occurred with avian prey, whereas two mammalian species co-occurred in 4% (3/81) of samples. Of the three samples in which two mammal species co-occurred, two involved chipmunks and deer mice and one involved the two *Peromyscus* species. Among the mammal species in our library, we never found either of the shrew species, star-nosed moles, eastern grey squirrels or northern flying squirrels in fecal samples. However, we recorded one incident of a mature male ratsnake (131 cm SVL)

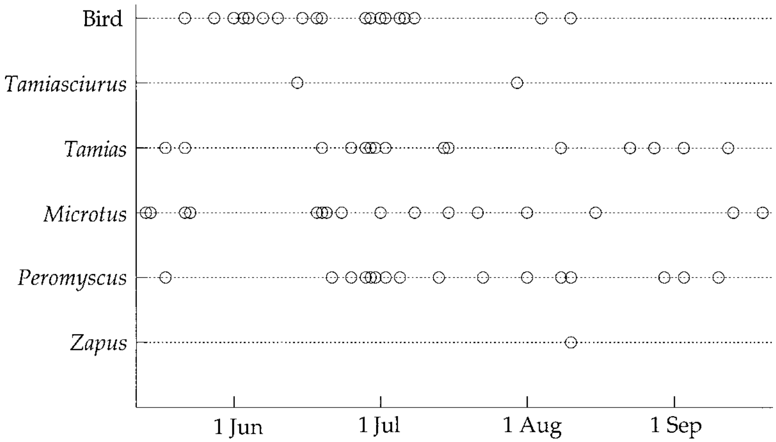

FIG. 1.—Seasonal distribution of prey consumed by black ratsnakes at the Queen's University Biological Station in eastern Ontario. Mammalian prey species are arranged in order of increasing mean mass

regurgitating an adult eastern grey squirrel and another mature male (154 cm SVL) regurgitating a juvenile eastern cottontail rabbit (*Sylvilagus floridanus*) while being transported to the lab. We found no insect remains in the fecal samples, but we have observed juvenile black ratsnakes (SVL between ca. 40 and 50 cm) feeding on moths attracted to light traps at QUBS, so insects are included in the diet of at least small ratsnakes. We often recorded vegetable matter such as seeds in fecal samples, but assume these represent instances of secondary ingestion.

Contingency table analyses indicated that the occurrence of both mammals ($\chi^2 = 9.77$, df = 4, P = 0.044) and birds ($\chi^2 = 8.67$, df = 4, P = 0.070) varied by month, although the difference for birds was not significant. Avian prey occurred in the diet primarily during the early and middle of the snakes' active season, coincident with the birds' nesting season and, therefore, mammalian prey occurred in the diet more often later in the snakes' active season (Fig. 1). Contrary to the prediction of the seasonal specialization hypothesis, mammals comprised a greater proportion of the diet than did birds in all months of the active season (paired $t = 3.43$, df = 4, P = 0.027), with a maximum occurrence of birds in the diet of 45% in June. When mammalian remains were present in feces (52/81), the species most often recorded were eastern chipmunk, meadow vole and deer mouse (Table 1). Logistic regression indicated that the occurrence of mammalian prey in feces did not vary with either the sex (Wald $\chi^2 = 0.83$, df = 1, P = 0.36) or the size (Wald $\chi^2 = 0.99$, df = 1, P = 0.32) of the snake, nor was there a significant sex by size interaction (Wald $\chi^2 = 1.04$, df = 1, P = 0.31). Similarly, the occurrence of avian prey did not vary with the sex (Wald $\chi^2 = 0.44$, df = 1, P = 0.51) or size (Wald $\chi^2 = 0.31$, df = 1, P = 0.58) of the snake, nor was there a significant sex by size interaction (Wald $\chi^2 = 0.43$, df = 1, P = 0.51).

To determine whether the size of the mammalian prey species in the diet varied with the size of the snake, we divided prey into small (deer mice, white-footed mice and jumping mouse) and large (meadow voles, red squirrels and chipmunks) species. For the 45 fecal samples that contained mammalian prey and for which the size of the snake was known, logistic regression indicated that the occurrence of large prey species in the diet increased significantly with the size of the snake (Wald $\chi^2 = 5.87$, df = 1, P = 0.015), whereas the

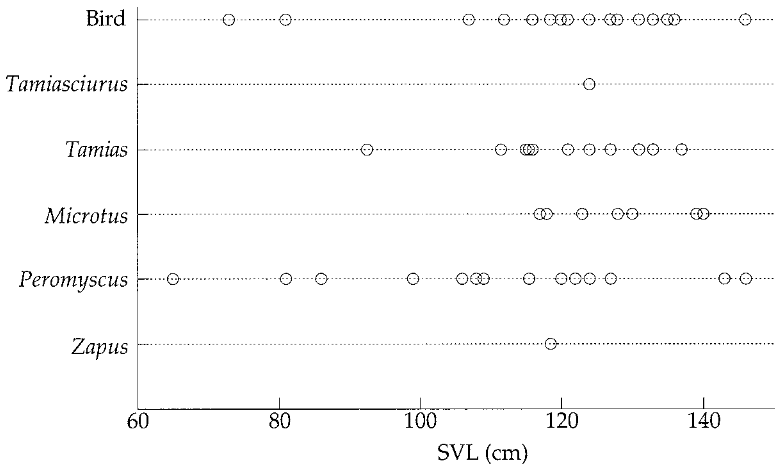

FIG. 2.—Association between prey type and snout-vent length for black ratsnakes at the Queen's University Biological Station in eastern Ontario. Mammalian prey species are arranged in order of increasing mean mass

occurrence of small prey declined significantly with the size of the snake (Wald $\chi^2 = 5.19$, df = 1, P = 0.02). A plot of prey size relative to snake size, however, reveals that large snakes still included some small prey in their diet and that the reduction in the abundance of small prey in the diet of large snakes was due to diet diversification (inclusion of large prey) and not to diet specialization (Fig. 2).

## DISCUSSION

Our results support the view from Fitch's (1963) study in Kansas that black ratsnakes are generalist foragers. Because Fitch (1963) regularly caused snakes to regurgitate stomach contents, he was able to identify amphibians and reptiles in the snakes' diet. By restricting our sampling to feces, we may have missed some diet items that leave little undigested material in the feces for identification. The picture that emerged regarding the consumption of birds and mammals, however, was remarkably similar for the two studies. In both Kansas and Ontario, birds occur in the snakes' diet from May through August, with the peak occurrence in June (42% and 45% occurrence in the respective studies). Also consistent between the studies was the failure of birds to occur in the diet more than mammals, in any month. The dietary similarity between ratsnakes in Ontario and Kansas suggests that this aspect of ratsnake ecology is evolutionarily highly stable—the study populations are more than 1500 km apart and genetic evidence suggests these populations have been isolated from each other for thousands of years (Burbrink *et al.*, 2000).

Our results, and those of Fitch (1963), suggest that black ratsnakes are aptly named, insofar as they prey primarily on mammals. These results support Blouin-Demers and Weatherhead's (2001a) view that black ratsnakes prey on birds opportunistically, despite the snakes' ability to locate and access birds' nests. This assertion is further supported by our result that avian and mammalian prey sometimes co-occurred in fecal samples. Researchers interested in the effect of forest fragmentation on nesting birds are particularly interested in how fragmentation affects nest predation (Chalfoun *et al.*, 2002). Lima (2002) recently pointed out that the study of predator-prey interactions is too often focussed only on the behavior of the prey and researchers need to pay more attention to the predator. Thus, understanding how forest fragmentation affects nest predation by black ratsnakes will require understanding how the snakes' foraging behavior is related to their use of habitat. At the northern extreme of their range, black ratsnakes preferentially use forest edges for thermoregulatory reasons (Blouin-Demers and Weatherhead, 2001a, b, c), which presumably increases nest predation in those edge habitats. There is evidence that black ratsnakes associate with habitat edges in more southern parts of their range (Durner and Gates, 1993), but the reason for that association and the consequences for nest predation remain to be determined.

Larger snakes consumed larger mammalian prey species than smaller snakes and larger snakes also reduced their consumption of smaller prey. However, the reduction in the abundance of small prey in the diet of large snakes appeared to arise from diet diversification (inclusion of large prey) rather than from diet specialization. Thus, consistent with our prediction, black ratsnakes exhibited Arnold's (1993) "ontogenic telescope" pattern where the lower limit of prey size does not increase with increasing size of the predator. This pattern is characteristic of a generalist and opportunistic predator. The fact that this pattern also seems to be characteristic of snakes that feed on animals other than fish (Arnold, 1993) is intriguing. Data on the economic consequences of specialized vs. generalized feeding relative to prey type (fish vs. non fish) are required to explain this pattern.

Finally, although the ratsnakes we studied are generalist predators collectively, that does not preclude some individual snakes from being specialists. Exploring this possibility might provide insights into individual variation in features such as home range size, movements and habitat selection (Blouin-Demers and Weatherhead, 2001a, 2002).

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