

## CHANGES IN HABITAT USE AND MOVEMENT PATTERNS WITH BODY SIZE IN BLACK RATSNAKES (*ELAPHE OBSOLETA*)

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**ABSTRACT:** Many animals exhibit pronounced shifts in ecology (e.g., habitat use, diet) as they grow. The central goal of this study was to determine whether habitat use and movement patterns of juvenile black ratsnakes (*Elaphe obsoleta*) differed from patterns previously documented for adult ratsnakes and to determine the conservation implications of any changes identified. We found a shift in habitat use by black ratsnakes with body size; juveniles used macrohabitats and microhabitats in proportion to their availability, unlike adult black ratsnakes that have been shown to prefer forest edges at both scales. Frequency of movement declined with body size, whereas distance traveled per move increased with body size. Habitat selection and movement patterns may be a result of ontogenetic shifts in thermoregulatory behaviour associated with changes in body size, or alternatively, may reflect size-related variation in predation risk. Home range size and fidelity, and fidelity to hibernacula all increased with body size. Despite ontogenetic changes in habitat use and movement by ratsnakes, recommendations regarding critical habitat for adults of this species should be adequate to protect juveniles.

*Key words:* Body size; Home range; Juvenile; Snake; Ontogeny

BODY SIZE is one of the most influential aspects of an animal's phenotype from an ecological and evolutionary perspective (Werner and Gilliam, 1984). For instance, body size is a strong determinant of resource use and of susceptibility to predation. Most physiological processes, including energetic requirements, scale allometrically with body size (Peters, 1983; Reiss, 1989; Schmidt-Nielsen, 1984). Community ecologists have long recognized that body size plays an important role in defining a species' niche. For all these reasons, body size is subject to intense selection in nature (Blanckenhorn, 2000; Janzen, 1993; Wikelski, 2005). Interestingly, some species exhibit more intraspecific variation in body size than is commonly found between species in a community (Werner and Gilliam, 1984). This observation has led to the application of the niche concept to size-based intraspecific variation in resource use. When intraspecific size variation arises from a drastic increase in body size through ontogeny, ensuing shifts in resource use are termed ontogenetic niche shifts (Werner and Gilliam, 1984).

Although ontogenetic niche shifts usually refer to changes in diet or habitat use with

body size, in theory niche shifts could be expressed through changes in other factors, such as predation risk, motor abilities, or thermal reaction norms. Among vertebrates, ontogenetic niche shifts have been particularly well studied in fishes (e.g., Dahlgren and Eggleston, 2000; Werner and Hall, 1988) because most fishes have larval stages and, having indeterminate growth, fishes vary several fold in body size from hatching to adulthood. Although reptiles exhibit as much intraspecific size variation through ontogeny as do fishes, comparatively few studies have specifically addressed ontogenetic niche shifts in reptiles. Notable exceptions include several studies of ontogenetic shifts in diet (e.g., Clark and Gibbons, 1969; Mushinsky et al., 1982; Pough, 1973; Weatherhead et al., 2003) and habitat (Irschick et al., 2000; Stamps, 1983). Our goal was to determine whether ratsnakes exhibit an ontogenetic niche shift. Specifically, we wished to examine whether body size influences movement patterns and use of habitat in black ratsnakes (*Elaphe obsoleta*).

Movement patterns and habitat use of adult ratsnakes have been well documented (Blouin-Demers and Weatherhead, 2001a, 2002; Durner and Gates, 1993; Weatherhead and Charland, 1985; Weatherhead and Hoy-sak, 1989), but information on juveniles is

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lacking. Because ratsnakes increase 100 fold in mass from hatching to adulthood (Blouin-Demers et al., 2002), ratsnakes are a good model to examine size-based differences in habitat use and spatial ecology.

Body size influences thermoregulatory requirements of ectothermic animals because smaller individuals warm and cool more quickly than larger ones (Carrascal et al., 1992; Stevenson, 1985). Because habitat selection is largely driven by thermal ecology in ratsnakes, at least in adults (Blouin-Demers and Weatherhead, 2001b), differences in body size could result in differences in habitat use. In addition, smaller individuals are more susceptible to predation, and predation risk can affect habitat use (Keren-Rotem et al., 2006; Werner et al., 1983). Size also affects diet. Weatherhead et al. (2003) showed that only large ratsnakes include eastern chipmunks (*Tamias striatus*) in their diets, with a corresponding decrease in the abundance of smaller mammalian prey. An ontogenetic shift in prey species could lead to a shift in habitat use if different prey species use different habitats. Adult ratsnakes disproportionately use forest-edge habitat (Blouin-Demers and Weatherhead, 2001a; Weatherhead and Charland, 1985). Because size-based habitat shifts could potentially alter prior conclusions about habitat suitability for this species, our first objective was to compare adult and juvenile habitat use at both the micro and macro-habitat scales.

Ratsnakes have a prolonged adolescence, maturing only at nine or 10 yr in Canada (Blouin-Demers et al., 2002). Juveniles rarely attend communal hibernacula used by adults (Prior et al., 2001). Adult ratsnakes are faithful to home ranges, nesting sites, and communal hibernacula (Blouin-Demers and Weatherhead, 2002; Prior et al., 2001; Weatherhead and Hoysak, 1989). Dispersal is most likely to occur before sexual maturity (Greenwood, 1980; Johnson and Gaines, 1990). If small black ratsnakes are in a dispersal stage, they should move more often, move over longer distances, and travel further from hibernacula than large ratsnakes. Small ratsnakes should also show less overlap in home ranges over consecutive years and have larger home ranges than large ratsnakes. Small ratsnakes

should also be less faithful to their overwintering locations. Our second objective was to test these predictions.

Ratsnakes are threatened in Canada (Prior and Weatherhead, 1998). Because the use of distinct habitats by subgroups within the same species has to be incorporated in management plans (Law and Dickman, 1998), we consider the conservation implications of all the body size-based differences that we document.

#### MATERIALS AND METHODS

We conducted this study at the Queen's University Biological Station (44° 34' N, 76° 19' W), 100 km south of Ottawa, Ontario. The study area was approximately 10 km by 3 km and consisted of primarily second growth mixed deciduous forest with numerous natural edges along rocky outcrops, wetlands, and lakes and human-made edges associated with small hayfields and successional fields.

We caught snakes in funnel traps at fenced communal hibernacula during spring emergence (Blouin-Demers et al., 2000; Row and Blouin-Demers, 2006a) and opportunistically during the active season. Snakes were measured for snout-vent length (SVL), weighed, sexed, and marked with a passive integrated transponder tag.

For the purpose of this study, we defined a juvenile as an individual < 1050 mm SVL because this corresponds to the size of the smallest gravid female captured ( $n = 57$ ) and the size of the smallest male observed mating ( $n = 15$ , Blouin-Demers and Weatherhead, 2002). Recently, genetic parentage analyses have shown that males as small as 875 mm SVL sire young (Blouin-Demers et al., 2005). However, only approximately 15% of identified fathers were < 1050 mm SVL. Because of the uncertainty in size at maturity and because size at maturity is likely to vary between individuals, we used SVL instead of adult/juvenile as a predictor variable wherever possible. SVL increases with age, although the relationship is much stronger prior to sexual maturation (Blouin-Demers et al., 2002).

We used movement data from Blouin-Demers and Weatherhead (2002) for 82 adults that were tracked between 1996–2000 for a study of gene flow potential. We tracked an additional 45 individuals (10 adults and 35

TABLE 1.—Structural variables measured for the analysis of microhabitat use for the random locations and for the locations of juvenile black ratsnakes followed by radio-telemetry in eastern Ontario in 2003 and 2004.

Variable	Description
Drock	Distance to closest rock (> 20 cm in length) within 30 m (m)
Lrock	Length of closest rock (> 20 cm in length) within 30 m (m)
Nrock	Number of rocks within 20 m (> 20 cm in length)
Dlog	Distance to closest log (> 7.5 cm diameter) within 30 m (m)
Llog	Length of closest log (> 7.5 cm diameter) within 30 m (m)
Dmlog	Diameter of closest log (> 7.5 cm diameter) within 30 m (m)
Nlog	Number of logs within 20 m (> 7.5 cm diameter)
Canclo	Percentage canopy cover
Dedge	Distance to edge within 100 m (m)
Rock	Percentage cover of rock (within 1 m radius)
Leaf	Percentage cover of leaf litter (within 1 m radius)
Grass	Percentage cover of grass (within 1 m radius)
Shrub	Percentage cover of shrubs (height < 2 m) (within 1 m radius)
Herb	Percentage cover of herbs (within 1 m radius)
Sticks	Percentage cover of sticks or logs (height < 2 m) (within 1 m radius)
Small	Number of overstory trees of DBH 7.5–15 cm (within 10 m radius)
Medium	Number of overstory trees of DBH 15–30 cm (within 10 m radius)
Large	Number of overstory trees of DBH 30–45 cm (within 10 m radius)
Xlarge	Number of overstory trees of DBH > 45 cm (within 10 m radius)
Dunder	Distance to closest understory tree (< 7.5 cm DBH and height > 2 m) (m)
Nunder	Number of understory trees of DBH < 7.5 cm and > 2 m in height
Dover	Distance to closest overstory tree (> 7.5 m DBH, height > 2 m) (m)
Decay	Decay state of nearest overstory tree (most decayed [1]–least decayed [7])

juveniles) between 2001–2004. Radio-transmitters (Model SB-2T [5.5 g, 12 mo battery life at 20 C] and SI-2T [12.0 g, 24 mo battery life at 20 C], Holohil Systems, Carp, Ontario,) were implanted surgically under isoflurane anesthesia (Weatherhead and Blouin-Demers, 2004). Transmitters represented at most 4% of the snake's mass. Snakes were kept overnight in the laboratory and then released at their point of capture.

After release, we located snakes on foot with a telemetry receiver and a directional antenna every 2–3 days from spring emergence, or from time of implantation, until they entered their hibernacula in late September to early October. Upon locating an individual, we recorded its location using GPS ( $\pm 5$  m accuracy) and its behavior (basking/resting, or traveling) if visible, as well as whether or not it was in a tree.

In 2003–2004, we characterized habitat at each juvenile snake location ( $n = 153$ ). To minimize disturbance to the snakes, we performed habitat analyses only after the snake had moved to a new location. We classified the macrohabitat as forest, edge, or open habitat. We defined an edge as any location < 15 m from where forest met open

habitat (e.g., field, rocky outcrop, wetland) (Blouin-Demers and Weatherhead, 2001a). We measured the 15 structural variables used by Blouin-Demers and Weatherhead (2001a) and 8 additional variables that we considered potentially important to juvenile snakes (Table 1). Details of the sampling protocol are provided by Blouin-Demers and Weatherhead (2001a). We also quantified available habitat to determine if snakes were using habitat non-randomly. For each snake location, we repeated the habitat characterization procedure at a random location selected by walking a randomly determined distance (10–200 paces, or approximately 10–200 m which is a distance easily covered by a ratsnake in a day, determined from the roll of a 20-face die multiplied by 10) in a randomly selected direction (1–360°, determined by spinning the bearing dial disc on a compass).

### Analyses

We used a contingency table analysis to test if juvenile ratsnakes used macrohabitat types non-randomly. We used MANOVA to investigate microhabitat selection based on the 23 structural habitat variables. To avoid pseudoreplication, our MANOVA used means

for individual snakes. This approach, however, dramatically reduced sample size and, consequently, led to low statistical power. To confirm the pattern observed for this analysis, we also ran a MANOVA treating each observation as an independent replicate. Although this approach artificially inflates the degrees of freedom for the test, it allows for a more direct comparison with the habitat-use patterns we documented for adults in another study (Blouin-Demers and Weatherhead, 2001a). Because data were derived from multiple observations per individual, the test could be biased if individuals show high heterogeneity. In this analysis, no individual contributed more than 10% of the data for the group. This minimized the likelihood that any individual could have unduly affected group means.

We tested for the effect of SVL and sex on the mean distance an individual was from its hibernaculum during the active season, the total distance an individual traveled during the active season, and the proportion of times that an individual had moved when it was relocated. We also tested for differences in behavior when located (not visible, basking/resting, traveling).

Home ranges were calculated using 100 and 95% minimum convex polygons (MCP) as recommended by Row and Blouin-Demers (2006b). The 100% MCP incorporates all points where an individual had been located, whereas the 95% MCP uses the 95% of points closest to the harmonic mean center of the range, thereby excluding possibly atypical locations that unduly enlarge home range size. We excluded locations documented when an individual was commuting between its hibernaculum and home range. Although ratsnakes are terrestrial, they readily cross water (Blouin-Demers and Weatherhead, 2002) resulting in open water sometimes being included in MCPs. We removed water so that each MCP represents dry land area only. We calculated home ranges for individuals in a given year only if they were tracked for at least June, July, and August, when ratsnakes are most active in Ontario. We also calculated the distance between the hibernaculum and the nearest point of the 100% and 95% MCP for each individual. We calculated

the percentage fidelity to hibernacula based on all individuals followed for at least 2 winters and the percentage overlap of home ranges between years for all individuals that were radio-tracked for the length of the active season in at least two consecutive years.

We tested for interactions in all instances, but provide details only where interactions were significant. Analyses were conducted on JMP version 6 (SAS Institute) and ArcView GIS version 3.0 (Environmental Systems Research Institute) equipped with the Animal Movement Extension version 1.1 (Hooge and Eichenlaub, 1997). We inspected box plots to determine if assumptions of normality and homogeneity of variance were upheld. Significance of statistical tests was accepted at  $\alpha = 0.05$ . All means are reported  $\pm 1$  SE.

## RESULTS

### *Habitat Use*

In 2003–2004, we followed 17 juvenile ratsnakes for periods ranging from 58 to 268 days (mean  $133.4 \pm 81$  days). We characterized habitat at 153 juvenile locations and at 153 paired random locations. Contingency table analysis showed that juveniles used macrohabitats (forest, edge, and open habitats [rock outcrop, marsh, and field]) in the same proportion as their availability ( $n = 306$ ,  $R^2 = 0.01$ ,  $\chi^2_{(2)} = 4.58$ ,  $P = 0.11$ , Fig. 1).

MANOVA based on individual means for the 23 structural habitat variables showed no significant difference between the centroids for locations of juveniles and locations chosen at random ( $F_{26,144} = 0.06$ ,  $P = 0.99$ ). Repeating the MANOVA treating each observation as an independent data point did not change this conclusion ( $F_{26,279} = 1.33$ ,  $P = 0.13$ ). If juveniles are in a dispersal stage, then they could potentially be less selective at locations where they were found only once. To test this, we used MANOVA to compare locations that juveniles used only once to those used more than once and found no difference ( $F_{23,153} = 0.88$ ,  $P = 0.76$ ).

### *Movement Patterns*

For the spatial pattern analyses, we used data for 97 ratsnakes (60 females and 37 males, 162 snake-years) that were relocated

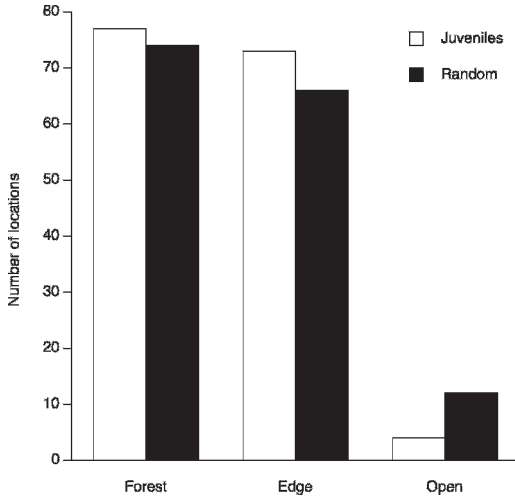


FIG. 1.—Macrohabitats used by juvenile black ratsnakes in eastern Ontario in 2003–2004.

5389 times over the period 1996–2004. All individuals were followed for at least 3 mo (June, July, August), but some were followed for up to 5 yr.

We used an ANCOVA to examine the relationship between the total distance traveled (log transformed to meet the assumption of normality) by an individual over the course of the active season and SVL, while controlling for sex. There was no significant relationship with sex ( $R^2 < 0.001$ ,  $F_{1,120} = 0.001$ ,  $P =$

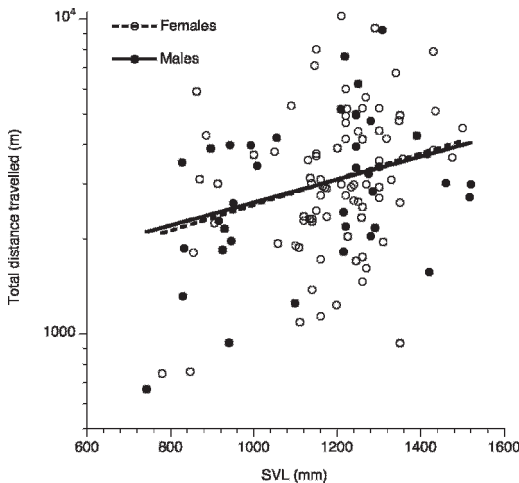


FIG. 2.—Total distance travelled (m) during the active season versus snout-to-vent length (mm) for male and female black ratsnakes radio-tracked in eastern Ontario between 1996–2004.

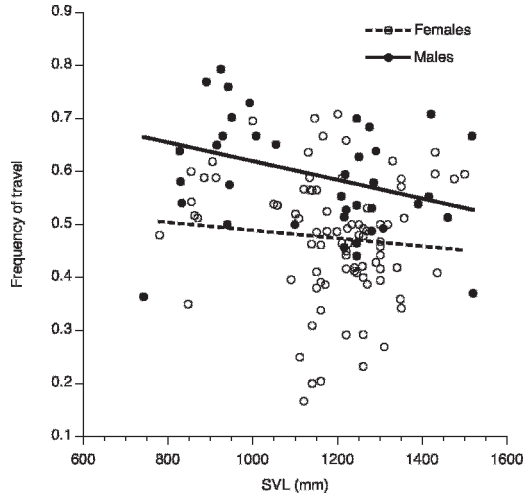


FIG. 3.—Frequency of movement versus snout-vent length for male and female black ratsnakes radio-tracked in eastern Ontario between 1996–2004.

0.99). A significant relationship with SVL ( $R^2 = 0.08$ ,  $F_{1,120} = 10.03$ ,  $P = 0.002$ ) indicated that larger snakes traveled farther over the course of the active season (Fig. 2).

To determine if smaller snakes move more often, we used ANCOVA to examine the relationship between SVL and the proportion of times that a snake had moved when relocated, while controlling for sex. A significant relationship with sex ( $R^2 = 0.16$ ,  $F_{1,120} = 24.74$ ,  $P < 0.001$ ) showed that males move significantly more often than females (59.4% and 47.6% of relocations, respectively). We also found that smaller snakes move more often than larger snakes ( $R^2 = 0.03$ ,  $F_{1,120} = 4.16$ ,  $P = 0.04$ , Fig. 3).

We used ANCOVA to determine if the mean distance an individual was from its hibernaculum during the active season was related to SVL and sex. There were no significant differences between the sexes ( $R^2 = 0.001$ ,  $F_{1,115} = 0.11$ ,  $P = 0.74$ ), but larger individuals were located further from their hibernacula than smaller individuals ( $R^2 = 0.19$ ,  $F_{1,115} = 25.99$ ,  $P < 0.001$ , Fig. 4).

We calculated home ranges for 86 individuals (54 females, 32 males, 130 snake-years). Each individual was located at least 10 times (mean =  $20.5 \pm 0.7$ ) per season. We used ANCOVA to determine if there was a relationship between SVL or sex and the area of an

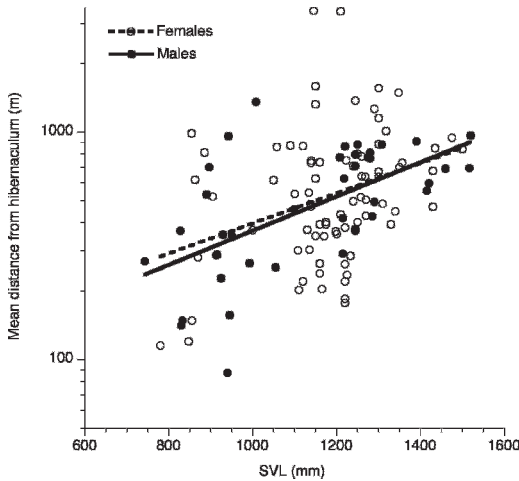


FIG. 4.—Mean distance away from hibernacula (m) versus snout-vent length for male and female black ratsnakes radio-tracked in eastern Ontario between 1996–2004.

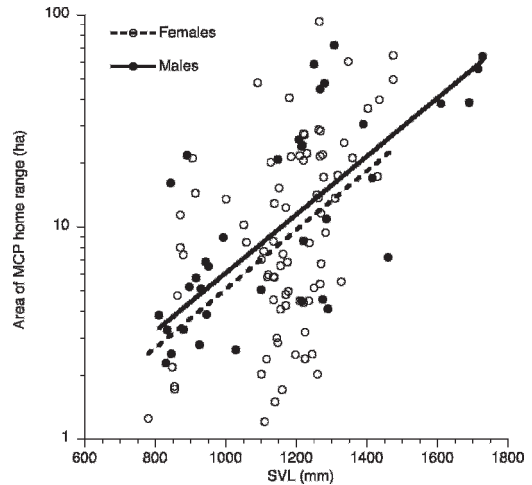


FIG. 5.—100% MCP home range size (ha) versus snout-vent length (mm) for male and female black ratsnakes in eastern Ontario. Snakes were located using radio-telemetry between 1996–2004.

individual's 100 and 95% MCP home range (log transformed to meet the assumption of normality). The area of the 100% MCP increased significantly with SVL ( $R^2 = 0.36$ ,  $F_{1,125} = 72.28$ ,  $P < 0.001$ ). Males had 100% MCP that averaged  $16.7 \pm 2.9$  ha whereas the 100% MCP of females averaged  $13.7 \pm 1.7$  ha (Fig. 5), but the difference was not significant ( $R^2 = 0.01$ ,  $F_{1,125} = 2.78$ ,  $P = 0.10$ ). We obtained qualitatively similar results using the 95% MCP except that the effect of sex was significant ( $P = 0.02$ ).

We used ANCOVA to test if distance (log transformed to meet the assumption of normality) from the hibernacula to the 100 and 95% home ranges varied with SVL and sex. There were no significant effects for distance to the 100% MCP. For distance to the 95% MCP, there was a significant interaction between size and sex ( $F_{1,125} = 4.29$ ,  $P = 0.04$ ), so we ran separate linear regressions for each sex. Home ranges of larger females tended to be further from the females' hibernacula than those of smaller females, but this relationship was not significant ( $R^2 = 0.02$ ,  $F_{1,84} = 1.42$ ,  $P = 0.24$ ). Home ranges of larger males were closer to the males' hibernacula than those of smaller males ( $R^2 = 0.09$ ,  $F_{1,42} = 4.14$ ,  $P = 0.05$ ).

We calculated the percentage overlap of 100% MCP home ranges over consecutive

years. Because our sample size was small, we only tested for the effect of SVL. Linear regression indicated that overlap tended to increase with SVL, but the relationship was not significant ( $R^2 = 0.13$ ,  $F_{1,19} = 2.93$ ,  $P = 0.10$ ).

For snakes tracked to hibernacula for at least two winters, adults were significantly more faithful to their over-wintering sites ( $R^2 = 0.18$ , Wald's  $\chi^2_{43} = 4.21$ ,  $P = 0.04$ ). Four of the 14 (28.6%) juveniles tracked for two winters between 2001–2004 switched hibernacula, whereas only 1 of the 30 (3.3%) adults tracked for two winters between 1996–2004 switched hibernacula. All adult ratsnakes tracked between 1996–2004 ( $n = 97$ ) used communal hibernacula. Eighteen of the 26 (69.2%) juveniles tracked between 2000–2004 used communal hibernacula. Of the 18 juveniles that were of unknown hibernaculum membership at the time of radio-transmitter implantation (never captured before), 10 (55.6%) subsequently went to communal hibernacula.

We used logistic regression to examine the relationship between SVL, controlling for sex, and the behavior of the snake (not visible, basking/resting, traveling) when it was located using radio-telemetry. There were significant effects of sex ( $\chi^2_2 = 14.07$ ,  $P = 0.001$ ) and of SVL ( $\chi^2_2 = 56.43$ ,  $P < 0.001$ ) on the

frequency of behaviors. Males and larger individuals were more likely to be seen (basking/resting or traveling) when located. One reason that juveniles were visible less often is that they were found in trees more often than were adults (51% vs. 37% of locations:  $\chi^2_1 = 139.96$ ,  $P < 0.001$ ).

#### DISCUSSION

Juvenile ratsnakes differed from adults in their use of habitat. At both the macrohabitat and microhabitat scales, juveniles used their habitat randomly, whereas adults are selective at both scales (Blouin-Demers and Weatherhead, 2001a). It is possible that a different pattern would emerge if juveniles were studied in a different landscape configuration. Perhaps juveniles use their habitat randomly in our study area because the habitat is very suitable for ratsnakes. Movement patterns and behavior varied with body size. Small ratsnakes moved more often but shorter distances and had smaller home ranges than large ratsnakes. Juveniles were less faithful than adults to both their home ranges and hibernation sites between years. Also, juveniles were more arboreal than adults. We first consider potential ecological explanations for these results and then their conservation implications.

Adult ratsnakes in Ontario use forest edges extensively (Blouin-Demers and Weatherhead, 2001a; Weatherhead and Charland, 1985), primarily because edges facilitate thermoregulation (Blouin-Demers and Weatherhead, 2001b). In edge habitats, individuals are able to move readily from shade to sun. Juvenile ratsnakes also need to thermoregulate, but did not preferentially use edges. Differences in body size result in juveniles heating and cooling more rapidly than adults, which could alter their thermoregulatory schedule relative to adults (Carrascal et al., 1992; Stevenson, 1985). A change in thermoregulatory schedule should not alter the suitability of edges for thermoregulation, however, so this seems unlikely to explain the ontogenetic change in habitat use.

The smaller size of juveniles seems likely to make them vulnerable to a wider range of predators. Survivorship in ratsnakes increases with body size (Weatherhead et al., 2002).

Increased predation risk might account for juveniles spending more time in trees and being less visible to observers on the ground. In a recent study of adult ratsnakes in southern Illinois, females were found to be more arboreal than males and use edges less (Carfagno and Weatherhead, 2007), similar to the juvenile-adult differences we found. It appears that female ratsnakes reduce their predation risk (associated with reproduction) by spending more time in trees, and thermoregulate by exploiting microclimates (cavities, sunspots) in the forest canopy. Thus, the interplay between predator avoidance and thermal ecology might explain the sex- and size-based switch in habitat use and arboreal behavior documented in the two ratsnake populations.

We predicted that if small ratsnakes are dispersing, then relative to large ratsnakes, small snakes should move more frequently, over longer distances and further from their hibernacula (thus have larger home ranges). Between years, juveniles should be less faithful to both home ranges and hibernacula. Some, but not all of these predictions were supported. Smaller snakes did move more often, and they were less faithful to both overwintering sites and home ranges. However, smaller snakes moved shorter distances and had smaller home ranges that were closer to hibernation sites. The failure of some of our predictions may indicate a faulty assumption about how ratsnakes disperse. Our predictions were based on the assumption that dispersal is continuous, whereas the data suggest that dispersal may be stepwise. Dispersal may result from low fidelity to home ranges and hibernation sites between years, whereas within active seasons, home range size and frequency of movement may simply be a function of body size, unrelated to dispersal. A more extensive study than ours will be required to assess this interpretation.

#### *Conservation Implications*

Although juvenile ratsnakes use forest edges less than do adults, they were still found in edges 50% of the time. Therefore, habitat use by juveniles is accounted for in previous conservation recommendations that critical habitat for ratsnakes should include

a mosaic of forest and edges (Blouin-Demers and Weatherhead, 2001a; Weatherhead and Charland, 1985). By using edges less, however, juveniles use forest interiors more. Thus, highly fragmented forest that may be beneficial for adults may be less beneficial for juveniles relative to less fragmented forest. Nonetheless, ontogenetic shifts in habitat use between juvenile and adult ratsnakes were subtle and have only a minor effect of how critical habitat for this species is defined.

The increased fragmentation of forests resulting from human activity would appear to be beneficial for ratsnakes. Having patches of suitable habitat will be insufficient to maintain a viable population, however, if those patches are not connected (Saunders et al., 1991). Blouin-Demers and Weatherhead (2002) argued that the genetic integrity of ratsnakes is susceptible to landscape fragmentation because gene flow between hibernacula populations is substantial. They proposed that habitat buffers need to be maintained around hibernacula to allow individuals from different hibernacula to come into contact during the mating season. Because ratsnakes only begin to attend communal hibernacula as juveniles and then often switch hibernacula until they become adults, appropriate habitat through which juveniles can disperse is also required. By maintaining forest habitat that connects hibernacula complexes, it is likely that habitat needs for juvenile dispersal will also be met. Again, the habitat requirements of juveniles tend to reinforce those already identified for adults.

The general picture that emerges for ratsnakes is that although there are ontogenetic changes in habitat use and movement, these do not result in substantially modified recommendations regarding critical habitat for this species. Other snake species may differ from ratsnakes, but our results at least show that habitat requirements for small and large snakes can be the same. An important caveat to include, however, is that there still remains one segment of the ratsnake population for which the habitat needs are unknown. Our reliance on radio-telemetry meant that the smallest snakes we tracked were 742 mm SVL, which means they were approximately 5 yr old (Blouin-Demers et al., 2002). Because

nothing is known regarding habitat use by ratsnakes from hatching until age 5, except the nest sites their mothers select (Blouin-Demers and Weatherhead, 2000; Blouin-Demers et al., 2004), it remains possible that specialized habitat requirements of neonate ratsnakes could still require modification of how critical habitat is defined. Until technological advances allow very small snakes to be tracked, this lacuna in knowledge will remain problematic for ratsnakes and for most other snake species.

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