

## HABITAT USE BY BLACK RAT SNAKES (*ELAPHE OBSOLETA OBSOLETA*) IN FRAGMENTED FORESTS

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**Abstract.** Declining nest success of forest birds in fragmented habitat has been attributed to increased nest predation. Better understanding of this problem and potential solutions to it require information on why nest predators are attracted to habitat edges. Toward this end we investigated habitat use by black rat snakes (*Elaphe obsoleta obsoleta*), an important avian-nest predator in eastern deciduous forests. We radio-tracked 52 black rat snakes for periods of 3–41 mo from 1996 to 1999. All black rat snakes exhibited a strong preference for edge habitats. Consistent with edges being used because they facilitate thermoregulation, gravid females associated more strongly with edges than did males and nongravid females, and sites used by snakes when shedding were significantly associated with habitat edges. Gravid females lost an average of >20% of their body mass, while nongravid females and males did not lose mass, suggesting that edges were not used because they offered high success in foraging. Similarly, an increase in use of edge habitat through the season by all rat snakes was inconsistent with the snakes being attracted principally to hunt: avian prey would have been more abundant in spring when birds were breeding, and the density of small mammals in edges did not vary seasonally. Also, snakes moved longer distances and were found traveling more often when located in forests. Because our results collectively are most consistent with the hypothesis that rat snakes use edges for thermoregulatory reasons, the negative impact of the snakes on nesting birds may be coincidental; the snakes primarily use edges for reasons other than foraging but opportunistically exploit prey they encounter there. Rat snakes appeared to respond to the edge structure rather than to how the edge was created (natural vs. artificial). Thus, fragmentation of forests by humans has created habitat structurally similar to that preferred by rat snakes in their natural habitat, thereby inadvertently increasing contact between the snakes and nesting birds.

**Key words:** black rat snake; breeding birds; ecdysis; edge effects; *Elaphe obsoleta obsoleta*; fragmentation; habitat use; Ontario Canada; nest predation.

### INTRODUCTION

Habitat loss and fragmentation are the two main threats to biodiversity (Wilson 1992). Habitat loss has direct consequences for species abundance and diversity because it reduces the available living space. The consequences of fragmentation are more complex and depend upon the degree of fragmentation, the shape and spatial arrangement of the fragments, and the composition of the separating habitat (Andreassen et al. 1998). One consequence of habitat fragmentation is an increase in the proportion of edge habitat in the landscape, which in turn can affect ecosystems by modifying ecological relationships such as predator–prey interactions (Donovan et al. 1995, Robinson et al.

1995). Here we investigate the extent of, and reasons underlying, use of habitat edges by black rat snakes (*Elaphe o. obsoleta*), and consider the implications of these results for the role of black rat snakes as important nest predators of forest birds.

Most research on forest fragmentation has focused on species that are adversely affected, often using birds as the model system (Murcia 1995, McCollin 1998, Tewksbury et al. 1998). Habitat fragmentation is thought to be one of the key factors responsible for the decline of many forest-bird species (Bolger et al. 1991, Donovan et al. 1995). These declines may result from forest fragments becoming too small to be suitable for forest-interior species or because nesting success is lower in fragmented forest. The decline in nest success may be a function of fragmentation enhancing the density or success of generalist and edge-associated predators (Yahner and Scott 1988, Andrén 1992, Harrison and Bruna 1999) or of increasing brood parasitism (Brittingham and Temple 1983, Robinson et al. 1995). Nest predation is the most significant cause of nest failure in birds (Ricklefs 1969, Martin 1988) and has been demonstrated to increase dramatically with proximity to some edges (Andrén and Angelstam 1988, Burkey 1993, King et al. 1998). However, the rea-

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son that predation is higher in some habitat edges remains poorly understood.

More detailed information about the use of habitat edges by predators is a prerequisite for understanding the interrelation between landscape configuration and the importance of predation in local animal communities (Angelstam 1986, Paton 1994, Tewksbury et al. 1998, Heske et al., *in press*). To meet the goal of increasing our understanding of the relation between habitat edges and predation, we chose black rat snakes as the subject of our research. Snakes have been identified as important nest predators (Loiselle and Hoppes 1983, Robinson et al. 1995, Fritts and Rodda 1998), and *Elaphe obsoleta* is particularly well known in this regard (Fitch 1963, Jackson 1970, 1978, Stickel et al. 1980, Weatherhead and Robertson 1990). Second, previous work has shown that black rat snakes preferentially use edges (Weatherhead and Charland 1985, Durner and Gates 1993). Third, as we outline below, there are several clearly testable alternative hypotheses for why black rat snakes might prefer habitat edges. Thus, black rat snakes provide an opportunity to identify the ecological factors that might explain observed patterns of habitat use.

One reason that black rat snakes might prefer habitat edges is that more avian prey is available in those habitats. If so, then higher predation on birds' nests in edge habitat would be a direct consequence of more birds nesting in that habitat, and/or their nests being more accessible to snakes in edge habitat. Increased density of birds near forest edges has been documented at our study site (J. Jones, *personal communication*), consistent with what has been documented elsewhere (Gates and Gysel 1978, Paton 1994). We tested this hypothesis indirectly by examining seasonal patterns of habitat use by black rat snakes. If rat snakes are attracted to edges to hunt for birds' eggs and nestlings, then use of edges should be most pronounced in May and June when the vast majority of birds in our study area are nesting (Weir 1989).

An alternative version of the foraging hypothesis is that black rat snakes are attracted to edges to hunt for prey other than birds. Of the 97 food items Fitch (1963) identified from stomachs of black rat snakes, 23 (24%) were birds and 65 (67%) were small mammals. Thus, rat snakes might be attracted to edges because small mammals are more abundant. If black rat snakes use edges for foraging on small mammals, we predicted that small mammal densities should be higher in edges than in other habitats, and any seasonal variation in mammal densities should be mirrored by seasonal variation in use of edges by rat snakes. A corollary of both foraging hypotheses is that snakes should gain more mass while in edges compared to other habitats, consistent with foraging success in edges being higher. Also, because rat snakes are active hunters, if they are in edges primarily to forage, they should be more active

in edges than in other habitats, but their movement patterns should be short and localized.

Weatherhead and Charland (1985) proposed that black rat snakes prefer habitat edges in Ontario (the northern extreme of the snakes' range) because greater exposure to sun along edges facilitates thermoregulation. Ectothermic animals obtain heat from their environment and therefore regulate their body temperature by adjusting microhabitat use and timing of activity (Huey et al. 1989, Krohmer 1989, Grant 1990). Thermoregulation is probably the single most important proximate factor in habitat use and timing of activity of terrestrial squamates (Grant 1990, Reinert 1993), with the probable exception of tropical species (Shine and Madsen 1996). Several predictions follow from this thermoregulation hypothesis. First, in addition to a general preference for edges by all individuals, those snakes with a greater need to maintain optimal body temperatures should use edges more. Gravid females of many viviparous snake species thermoregulate more precisely than nongravid females and males (Charland and Gregory 1990, Cobb and Peterson 1991, Schwarzkopf and Shine 1991, Brown and Weatherhead 2000). Although the same type of behavior has been suggested to occur in oviparous species (Shine and Madsen 1996), it has not been formally documented. We predicted that, prior to egg-laying, gravid female rat snakes should use habitat edges more extensively than do nongravid females and males. Similarly, when snakes shed their skins (ecdysis), they maintain higher body temperatures (Gibson et al. 1989, Peterson et al. 1993). Therefore, we also predicted that sites used for ecdysis should occur disproportionately along habitat edges, and in this case, we expected males, nongravid females, and gravid females all to use these sites.

Another reason that rat snakes might be attracted to edges is that these habitats offer greater protection from predation. This hypothesis also predicts that gravid females should use edge habitat more than other snakes (Cooper et al. 1990, Charland and Gregory 1995). However, in this case their preference for edges is predicted to be a consequence of their impaired mobility (Seigel et al. 1987), which makes them more vulnerable to predators. If gravid females use edges to avoid predators, then we predicted that they should be concealed more than other snakes when in edges.

An additional goal of our study was to quantify the snakes' use of natural edges (e.g., boundaries between marsh and forest) and artificial edges (e.g., boundaries between forest and cleared field). The two previous studies of habitat use by black rat snakes (Weatherhead and Charland 1985, Durner and Gates 1993) were conducted in landscapes where the total availability of edge habitat had been increased substantially by human activity (e.g., forest clearing for agriculture). Although both studies showed that black rat snakes preferred edge habitats, that preference could have been an artifact of the artificially fragmented study areas. Deter-

mining whether the snakes differentiate between natural and artificial edges will provide additional insight into why the snakes use edges and may suggest ways in which that use could be modified. Both previous studies (Weatherhead and Charland 1985, Durner and Gates 1993) also involved relatively small numbers (7 and 31 snakes, respectively) followed for relatively short periods of time (3 and 5 mo, respectively). In our study we collected data from 52 individuals tracked for periods of up to 41 mo.

Our final goal was to relate our results to the management of black rat snakes. Our study population of black rat snakes occurs as a separate population at the northern extreme of the species' range in eastern Ontario. Recently this population has been classified as threatened in Canada (Prior and Weatherhead 1998). Conservation efforts aimed at improving habitat for this species that rely on the two existing studies of habitat use (Weatherhead and Charland 1985, Durner and Gates 1993) would presumably involve preserving or even creating edge habitats. Such an approach would conflict directly with conservation efforts for many threatened or endangered forest species that are hurt by forest fragmentation. The first step toward resolving this potential conflict is to be certain that a conflict exists. By determining habitat preferences of black rat snakes under natural conditions and the factors that influence habitat use, this study will provide an empirical basis necessary for sound management.

## METHODS

### *Study area*

We conducted this research from 1996 to 1999 in the immediate vicinity of the Queen's University Biological Station near Chaffey's Locks in eastern Ontario (44°34' N, 76°19' W). The study area was ~10 by 3 km and encompassed the Biological Station. The dominant geological feature of the area is the exposed southeastern extension of the Canadian Shield referred to as the Frontenac Axis. This area is characterized by strongly rolling terrain with ridges of granite outcrops alternating with valleys approximately every 500 m and numerous small lakes and wetlands. The study area is mostly second growth forest dominated by deciduous trees (*Acer*, *Quercus*, *Ostrya*, *Populus*, *Fraxinus*, *Carya*, *Ulmus*, *Fagus*, *Tilia*, *Betula*), although some coniferous trees were present in the drier, sandier soils (*Pinus*, *Thuja*, *Juniperus*, *Tsuga*, *Abies*). In addition, the ongoing abandonment of marginal farmland has resulted in old fields and scrub habitats (*Zanthoxylum*, *Juniperus*) being common. Some of the more productive fields are still hayed.

### *Study animals*

To obtain experimental animals, we captured snakes at 13 communal hibernacula in the spring and opportunistically throughout the rest of the active season.

The hibernacula had been located by radio-tracking snakes to their hibernation sites, both as part of previous studies of black rat snakes (Weatherhead and Charland 1985, Weatherhead and Hoysak 1989) and as part of the present study. To capture emerging rat snakes, we constructed 1.5 m high perimeter fences around hibernacula openings. We buried the bottom edge of the plastic fences and installed a funnel trap in one corner of the fence. Traps were installed in early April and we visited sites beginning prior to the start of emergence each spring (Blouin-Demers et al. 2000b) and continuing until the last snake emerged (late May). Upon capture, we determined the sex of snakes by gently probing for the presence of hemipenes, measured their snout-vent length (SVL) to the nearest 1 mm with a metric tape, weighed them to the nearest 1 g with a calibrated spring scale, and marked them by subcutaneous injection of a passive integrated transponder (PIT tag). The experimental animals we selected for this study were captured centrally in the study area. This increased the likelihood that the snakes would remain in the study area during the active season, although we modified the exact boundaries of the study area to accommodate the snakes as necessary.

Our choice of study animals from among the animals we captured was based on sex and size. Snakes had to be large enough to carry a radio transmitter (maximum ratio of transmitter mass:body mass = 0.025:1) and, because females reproduce every second to third year on average (G. Blouin-Demers, unpublished data), we had to track more females than males to obtain an adequate sample of gravid females. The transmitters we used weighed 8.6 g and had a battery life of 20 mo at 20°C (Model SI-2T, Holohil Systems Incorporated, Carp, Ontario). From May 1996 to October 1999, we followed 23 males and 41 females for periods ranging from 16 d to 41 mo. We followed 52 of those snakes (18 males and 34 females) for >3 mo and used only these 52 individuals in our analysis of habitat use.

### *Radiotelemetry*

To implant transmitters we modified the surgical technique described by Reinert and Cundall (1982). This involved using sterile techniques to implant surgically a radio transmitter in the body cavity of the snake, suturing the transmitter to a rib to prevent its migration inside the coelom, and leaving the antennae between the epidermis and the outer body wall. For the surgery we anesthetized snakes using isoflurane gas delivered via a precision vaporizer (Blouin-Demers et al. 2000c). While the snakes were waking up, we injected them with sterile fluids (0.9% lactated Ringer's solution at a dosage of 50 mL/kg) into the coelom to help healing and to avoid damage caused by the antibiotic if the snake was dehydrated. Then we gave the snakes a subcutaneous injection of gentamicin sulfate (reptile dose = 2.5 mg/kg). A single subcutaneous injection maintains therapeutic blood levels of antibiotic

TABLE 1. Structural variables used in the analysis of habitat use by Ontario black rat snakes in 1996 only and from 1996 to 1999 with associated abbreviations and sampling radii.

Variable	Radius (m)	Variable
Variables sampled in 1996–99		
DROCK	30	Distance (m) to nearest rock ( $\geq 20$ cm length)
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)
DEDGE	100	Distance (m) to nearest edge
7.5–15	10	Number of trees $\geq 7.5$ and $< 5$ 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
%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
CANCLO	45†	Canopy closure (%) within cone
Variables sampled only in 1996		
DSNAG	30	Distance (m) to nearest snag
DBHSNAG	30	Dbh (cm) of nearest snag ( $\geq 30$ cm dbh)
DECSNAG	30	Decay state (scale from 1 to 7) of nearest snag
DBHOVER	30	Dbh (cm) of nearest overstory tree
LROCK	30	Length (cm) of nearest rock ( $\geq 20$ cm)
LLOG	30	Length (m) of nearest log ( $\geq 7.5$ cm diameter)
DLOG	30	Mean diameter (cm) of nearest log ( $\geq 7.5$ cm)
NUNDER	5	Number of understory trees ( $< 7.5$ cm dbh, $> 2$ m height)
%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

Note: Dbh = diameter at breast height.

† Measured in degrees.

for 72 h. Because we gave a second injection before release (72 h postsurgery), gentamicin sulfate gave a total of 144 h of antibiotic coverage. The snakes were kept in captivity, provided warmth, and monitored for 3 d following surgery. Water was not provided because if the snakes soaked themselves, premature melting of the stitches could occur.

After releasing each snake at its capture location, we located the snakes on average every 48 h from their emergence in late April until they re-entered their hibernacula in early October. Upon locating a snake, we recorded its location, position, and behavior (concealed, resting/basking, or traveling). All locations of snakes were flagged and later mapped using a global positioning system (GPS) unit with submeter accuracy in the field (MC-V Asset Surveyor Version 3.16 in a GPS Pathfinder with a Probeacon, Trimble Navigation Limited, Sunnyvale, California). The Universal Transverse Mercator coordinates (North American Datum of 1983) of each location were used to calculate the distance moved between relocations.

#### Habitat characterization

We did not conduct habitat characterization at locations where snakes were found actively traveling to avoid including instances where snakes may have been

disturbed by our approach, and to make our study comparable to other studies of snake habitat use (Reinert 1984, 1992). This accounted for only 285 of 3847 (~7%) locations. We also excluded instances where snakes were found in buildings because these sites could not be characterized adequately with our habitat sampling scheme (see below). Snakes were in buildings in 270 of 3847 (~7%) relocations. When snakes were perched  $\geq 3$  m in trees (1126 of 3847 or 29% of relocations), we did not measure the habitat variables at ground level (Table 1) because ground characteristics are unlikely to affect an individual in this situation, but instead substituted individual means for those variables (Stevens 1996) to be able to use these locations in our analyses (see below). For each snake, we only quantified the habitat at every second relocation to keep the habitat sampling manageable. We quantified the habitat at a given position on average 7 d after the individual had moved to another location to prevent disturbance and at the same time minimize phenological changes between occupancy and sampling. Locations at which a snake was observed more than once were only included once in the analysis of habitat use. To quantify the available habitat, which is necessary to determine whether the snakes were using habitat nonrandomly, we repeated the same habitat analysis and character-

ization at sites selected by walking a randomly determined distance (10 to 200 paces, determined by a die with 20 faces and multiplying by 10) in a randomly selected direction ( $1^\circ$  to  $360^\circ$ , determined by spinning the bearing dial disc on a compass) from snake locations. While we concede that our random points are not a true random sample of the available habitat because they are in the vicinity of snake locations, our random points were representative of the habitats among which the snakes could choose (Keller and Hesse 2000) because snakes regularly moved  $>200$  paces between relocations. To keep the sample size manageable and approximately the same for random locations and each snake reproductive group, we only determined random habitat points for every fourth snake location.

To characterize the habitat at snake and random locations, we measured 28 structural variables within circular plots of different radii, depending on the variable of interest, all centered at the snake or random location (Table 1). We measured distance variables to the nearest centimeter with a 50-m measuring tape. To evaluate percent ground cover and canopy closure, we used a sighting tube (a  $50 \times 2.5$  cm piece of piping) with a cross wire at one end. This was a modified version of Winkworth and Goodall's (1962) apparatus. We aimed the tube randomly 50 times in a 2 m radius plot and recorded the type of ground cover "hit" in the cross wire. We then multiplied the number of "hits" for each cover type by two and recorded this as the percent ground cover. The same procedure was used 20 times at an angle  $>45^\circ$  from horizontal to determine the percent canopy closure. We defined an edge as the boundary between an "open" or two-dimensional habitat (e.g., hay fields, rock outcrops, marshes) and a "closed" or three-dimensional habitat (e.g., deciduous forest, coniferous forest). These are the types of edges that are associated with a higher density of breeding birds (Gates and Gysel 1978), and that also provide a forest snake with thermoregulatory opportunities because they offer simultaneous access to shady and sunny microhabitats. An additional benefit of this definition was that all edges (or habitat boundaries) were obvious features of the landscape and it made measuring distances from edges an objective process.

After the 1996 field season, we ran a preliminary multivariate analysis of variance (MANOVA) and associated discriminant function analysis (DFA) to identify which variables were contributing to the multivariate group differences between random sites and sites used by snakes (see below). From 1997 to 1999, we discontinued sampling the 13 discriminant variables that had pooled within-group correlations with the discriminant functions  $\leq 0.10$  (Table 1). This was a conservative approach because variables with loadings  $\leq 0.40$  are usually deemed unimportant to discrimination in DFA (Stevens 1996, Clark and Shutler 1999). We used a conservative approach to ensure that all potentially meaningful variables were retained for fur-

ther sampling. From 1997 to 1999, we only measured the 15 structural variables retained after the preliminary analysis (Table 1).

At each snake or random location we also recorded the general habitat type as forest, field, marsh, natural edge, or artificial edge. We defined an artificial edge as having been created by humans (e.g., edge between field and forest), whereas natural edges were not the result of human activity (e.g., edge between marsh and forest). We considered a snake to be in an edge when it was within 15 m of the boundary between any open habitat (marsh, open water, rock outcrop, field, road) and forest. We identified shedding sites of our study animals by monitoring their skin condition and, in many instances, by finding their shed skin. The skin of black rat snakes becomes dull and bluish (this is most noticeable when the eyes become clouded) in the days before shedding, whereas the skin appears dark and very shiny immediately following shedding. Identifying shedding sites was made easier by the fact that black rat snakes spend several days inactive at their shedding site prior to shedding.

#### *Small mammal trapping*

To quantify mammalian prey densities in different habitats, we captured small mammals live from June to August of 1997 to 1999 using 45 mouse live traps (model 101, Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) baited with peanut butter and provided with cotton for use as bedding. We trapped small mammals in edges between forests and fields (artificial edges) and in edges between forests and rock outcrops (natural edges) because these are the two most common types of edges in the study area. We placed the traps 10 m apart in lines of 15 traps (thus each trap line covered 150 m). We placed one trap line in the forest 30 m from the edge, one trap line at the edge, and one trap line in the open habitat 30 m from the edge. We left the traps in a given location for a period of 2 wk and then moved them to another location. The traps were checked every morning and because we needed food items for another experiment, we used removal trapping to derive an index of prey density. Species that are prey of rat snakes (e.g., *Peromyscus*, *Blarina*, *Tamias*, *Microtus*) were euthanized in the field using cervical dislocation following capture. Live-trapping followed by euthanasia (as opposed to lethal capture using snap traps) allowed us to release nonprey species (e.g., *Rana*, *Bufo*) inadvertently captured. To index the abundance of small mammals, we calculated the average number of captures per number of trap-days in each habitat for each trapping day (where one trap-day is equal to one working trap set for one day).

#### *Analyses*

We divided the snakes into three groups based on their reproductive status: males, nongravid females, and gravid females. The reproductive state of females

was assessed in June by externally palpating the oviducts for the presence of eggs and confirmed in July by nesting activity. Because female black rat snakes do not reproduce every year, some individuals changed groups from one year to the next. Because female black rat snakes very seldom moved while gravid, fewer locations were obtained for this group. We used MANOVA to determine if there was a significant difference in habitat centroids of each group and DFA to examine along which axes the groups differed and which variables contributed most to separation among groups. To facilitate the interpretation of discriminant functions, we limited our interpretation to the five variables with the highest correlations (in absolute values) with each function.

An assumption common to all analysis of variance (ANOVA) models is that observations are sampled at random. While truly random samples of organisms are extremely hard to obtain in nature, this assumption is particularly dubious when radiotelemetry is used because many observations are derived from relatively few individuals. In such a case, an aberrant individual sampled repeatedly can severely bias the conclusions one would reach when treating each observation as an independent sample. In our study, the individual snake sampled the most only accounted for 7.2% of the total number of snake locations, so no individual had the opportunity to unduly bias the group means. Another potential solution to this problem would have been to use mean habitat vectors for each individual as the basis for analyses. However, using this approach usually does not change the conclusions of the analyses (Reinert 1984) while not making use of all the information available, such as the variation found within individuals.

One assumption specific to MANOVA is the homogeneity of covariance matrices, usually tested using Box's test. This assumption is rarely met with habitat use data because it would require that each segment of the population responds similarly to the different habitat variables (Reinert 1984). If this assumption is violated and the sample sizes for each group differ substantially, biased tests of significance can result (Stevens 1996). Because female black rat snakes are not gravid each year and because they are very stationary while gravid, the number of locations for this group was approximately half that of the other groups. To ensure that this difference in sample sizes did not unduly bias our tests of significance, we also conducted our analyses using a computer-generated, randomly selected subset of our data designed to achieve equal sample sizes in each group. Because the results for all analyses remained qualitatively unchanged (all significant relationships remained significant, no new significant relationship appeared, and the variables contributing the most to group differences were the same), we only present the results of the analyses using the complete data set.

To determine if the use of edges by black rat snakes

was consistent with the hypothesis that rat snakes prefer edges for foraging, we examined if the preference for edges was constant over the duration of the active season. We divided the snake locations into edge and non-edge habitat and determined the proportion of snake locations that were in edges for each month of the main active season (May to August). Observations from earlier and later in the season were not included in this analysis because there were too few to analyze. To contrast the distances moved between relocations for the three snake groups during the period prior to egg laying (1 June to 15 July), we divided the distances moved between relocations into four classes (0 m, 1 to 10 m, 11 to 100 m, and 101 to 1000 m). We also divided the behavior of all snakes located prior to the time females started egg laying as either traveling, resting/basking, or concealed. When comparing the distances moved and behavior of all snakes in edges and forests, we used the same categories but included relocations from the whole active season.

The analyses were conducted on JMP Version 3.2 (SAS Institute 1997) and SPSS Version 6.1 (SPSS 1995) on a Macintosh desktop computer. We inspected box plots to determine if the assumptions of normality and homogeneity of variance were upheld. The continuous habitat structure variables were log-transformed to improve their adherence to the assumption of normality. Significance of statistical tests was accepted at  $\alpha = 0.05$ , but marginally nonsignificant results are reported when deemed important. All means are reported  $\pm$  one standard error.

## RESULTS

From 1996 to 1999, we sampled habitat characteristics at 165 random locations, 195 locations of males, 190 locations of nongravid females, and 81 locations of gravid females. Snakes often remained in the same location for many days, and often returned to previously used locations. In addition, we only sampled every second relocation for each individual. Thus, the number of locations we sampled (466) was much less than the total number of times we located snakes (3847). Snakes clearly used their habitat nonrandomly ( $\chi^2 = 61.2$ ,  $df = 15$ ,  $P < 0.001$ ), preferring edge habitats and avoiding water bodies (Table 2).

Before we used MANOVA, we tested the assumption of homogeneity of covariance matrices. As expected with biological data, the Box's test indicated that the covariance matrices were heterogeneous (Box's  $M = 798.36$ ,  $F = 2.11$ ,  $df = 360$ ,  $351883.2$ ,  $P < 0.001$ ). However, many authors have defended the heuristic value of multivariate methods despite the common violation of this assumption with ecological data (Pimentel 1979, Stevens 1996). The mean scores on each variable for the random locations and the locations of the three snake groups are presented in Table 3. We included all shedding sites (except sites located in buildings) in the calculations because these sites also

TABLE 2. Habitat types where the random points were located and where male, nongravid female, and gravid female black rat snakes followed by radiotelemetry in Ontario from 1996 to 1999 were located.

Habitat type	Random	Males	Nongravid females	Gravid females
Artificial edge	19 (11.5)	31 (15.9)	30 (15.8)	22 (27.2)
Natural edge	51 (30.9)	86 (44.1)	83 (43.7)	32 (39.5)
Field	5 (3.0)	2 (1.0)	2 (1.0)	2 (2.4)
Forest	69 (41.8)	74 (37.9)	69 (36.3)	24 (29.6)
Wetland	7 (4.2)	2 (1.0)	6 (3.2)	1 (1.2)
Water body	14 (8.5)	0 (0.0)	0 (0.0)	0 (0.0)
Total	165	195	190	81

Note: The percentages of the total for each column are given in parentheses.

were used by snakes when they were not shedding. The overall MANOVA indicated that the habitat characteristics of the three groups of snakes and the randomly sampled points were significantly different (Wilk's  $\Lambda = 0.630$ ,  $F = 6.80$ ,  $df = 45$ ,  $1821.9$ ,  $P < 0.001$ ). Distances between group centroids in the discriminant space showed that males, nongravid females, and gravid females all used habitat nonrandomly (Table 4). Among the three classes of snakes, males and nongravid females did not differ significantly from one another, whereas gravid females were significantly different from both other groups (Table 4). In addition, gravid females used habitat that was the least available in the study area (largest distance in the discriminant space from the random group), followed by males, and then by nongravid females.

The DFA derived three discriminant functions that summarized multivariate differences among our four types of locations. Only the first discriminant function ( $\chi^2 = 283.3$ ,  $df = 45$ ,  $P < 0.001$ ) and the second discriminant function ( $\chi^2 = 59.0$ ,  $df = 28$ ,  $P < 0.001$ ) accounted for a significant amount of the total variation, with the first discriminant function explaining 81.7% of the total variation (Table 5). The pooled with-

in-group correlations of habitat variables indicated that DOVER, DUNDER, DLOG, and DEDGE contributed strongly and positively, whereas %LOG contributed strongly but negatively, to the first function (Table 5). This function can be interpreted as a gradient from sites far from trees, logs, and edges with low ground cover of logs to sites close to trees, edges, and logs with high ground cover of logs (Fig. 1). For the second function, >45 and DROCK contributed strongly and positively, whereas 15–30, %ROCK, and 7.5–15 contributed strongly but negatively (Table 5). The second function indicated a gradient from sites close to rocks with many small and medium trees, few large trees, and high ground cover of rocks toward sites far from rocks with few small and medium trees, many large trees, and low ground cover of rocks (Fig. 1).

Separation of the random group from the three snake groups along the first discriminant function (Fig. 1) reflects that the available habitat was mostly far from trees and edges with low ground cover of logs, whereas snakes tended to be found close to trees and edges with extensive ground cover of logs. Gravid females had the strongest preference for sites close to edges and trees with high ground cover of logs as indicated by their

TABLE 3. Means of variables used in the analysis of habitat use for the random locations and locations of male, nongravid female, and gravid female black rat snakes followed by radiotelemetry in Ontario from 1996 to 1999.

Variable	Random ( $n = 165$ )	Males ( $n = 195$ )	Nongravid females ( $n = 190$ )	Gravid females ( $n = 81$ )
DROCK	5.43 (0.64)	2.45 (0.29)	2.85 (0.28)	2.60 (0.35)
DLOG	5.64 (0.58)	3.22 (0.31)	3.04 (0.35)	2.23 (0.29)
DOVER	4.84 (0.54)	2.26 (0.19)	2.70 (0.24)	1.56 (0.26)
DUNDER	3.93 (0.55)	1.83 (0.24)	1.84 (0.21)	1.23 (0.15)
DEDEGE	25.84 (4.37)	17.42 (3.41)	17.46 (3.12)	18.68 (3.39)
7.5–15	12.47 (0.82)	10.81 (0.64)	10.24 (0.66)	7.91 (0.87)
15–30	5.61 (0.42)	4.71 (0.27)	4.62 (0.31)	3.22 (0.37)
30–45	1.35 (0.12)	1.42 (0.11)	1.36 (0.12)	1.49 (0.17)
>45	0.36 (0.07)	0.32 (0.05)	0.40 (0.05)	0.78 (0.10)
%ROCK	8.33 (1.14)	16.63 (1.51)	17.81 (1.44)	11.99 (1.62)
%LEAF	27.67 (1.85)	20.61 (1.43)	23.21 (1.57)	24.22 (2.30)
%LOG	7.02 (0.97)	11.32 (0.81)	11.94 (0.89)	14.31 (1.61)
%GRASS	22.70 (1.90)	16.64 (1.29)	16.09 (1.36)	15.01 (1.98)
%SHRUB	16.62 (1.45)	20.34 (1.46)	22.26 (1.63)	26.25 (2.26)
CANCLO	55.59 (2.96)	53.53 (2.22)	49.53 (2.40)	56.67 (3.12)

Note: The standard errors are given in parentheses. For definitions of variables, see Table 1.

TABLE 4. Distances between the four group centroids in the discriminant space and their statistical significance for the analysis of habitat use in Ontario black rat snakes followed by radiotelemetry from 1996 to 1999.

Group	Group					
	Random		Males		Non-gravid females	
	Distance ( <i>F</i> )	<i>P</i>	Distance ( <i>F</i> )	<i>P</i>	Distance ( <i>F</i> )	<i>P</i>
Males	1.40 (11.47)	<0.001				
Nongravid females	1.25 (8.97)	<0.001	0.44 (1.22)	0.25		
Gravid females	2.06 (15.08)	<0.001	1.10 (4.54)	<0.001	1.09 (4.39)	<0.001

Note: The *F* statistic with 15 and 613 degrees of freedom is given in parentheses.

position on the first discriminant axis. The second discriminant function provided further separation between gravid females and the other two snake groups. Gravid females were associated more with larger trees, less with small and medium trees, and less with rocks than males and nongravid females.

The habitat use of males and nongravid females did not differ significantly, suggesting that the differences we observed in habitat use among the three groups are not a function of the sex of the individual per se, but rather, a consequence of the reproductive state of females. To examine more formally if the difference in habitat use we observed between gravid females and the other two snake groups was due to the reproductive condition of the females, we contrasted the habitat use of snakes followed in multiple years. We had sufficient data ( $\geq 10$  characterized locations in each year) to test for multivariate differences in habitat use among years for three males and one female. The three males were followed in 1996 and in 1997 and, in each case, there were no significant differences between their habitat use in each year (Wilk's  $\Lambda = 0.011$ ,  $F = 11.74$ ,  $df = 2, 15$ ,  $P = 0.08$ ; Wilk's  $\Lambda = 0.278$ ,  $F = 0.69$ ,  $df = 4,$

15,  $P = 0.73$ ; Wilk's  $\Lambda = 0.445$ ,  $F = 0.91$ ,  $df = 11, 15$ ,  $P = 0.57$ ). The single female was followed in 1997 (nongravid) and in 1998 (gravid) and there was a significant difference in her habitat use between years (Wilk's  $\Lambda = 0.132$ ,  $F = 5.25$ ,  $df = 12, 15$ ,  $P = 0.003$ ), with a stronger preference for sites close to large trees and edges when gravid than when nongravid.

When we examined if habitat use by black rat snakes varied seasonally, we found that although snakes were found in edges more often than in all other habitat types combined throughout the active season, their use of edges increased significantly over the active season ( $N = 447$ ,  $\chi^2 = 8.90$ ,  $df = 3$ ,  $P = 0.03$ , Table 6). We also compared the mass of 11 gravid females at emergence from hibernation in early May to their mass following parturition in July. All gravid females lost mass following emergence (mean loss = 108.8 g or 21.3% of postpartum mass, paired  $t = 8.56$ ,  $df = 11$ ,  $P < 0.001$ ). During the same period, 17 nongravid females gained mass (mean gain = 63.8 g, paired  $t = 3.23$ ,  $df = 16$ ,  $P = 0.005$ ) and 16 males maintained the same mass (mean gain = 9.4 g, paired  $t = 0.75$ ,  $df = 15$ ,  $P =$

TABLE 5. Summary statistics for the three discriminant functions and their pooled within-groups correlations (*r*) with the discriminating variables used in the analysis of habitat use by Ontario black rat snakes followed by radiotelemetry from 1996 to 1999.

Statistic	Function 1	Function 2	Function 3
Eigenvalue	0.4423	0.0754	0.0227
$\chi^2$ test	$\chi^2 = 283.3$ ( $df = 45, P < 0.001$ )	$\chi^2 = 59.0$ ( $df = 28, P < 0.001$ )	$\chi^2 = 13.9$ ( $df = 13, P = 0.38$ )
Percentage of variance explained	81.7	13.9	4.2
<i>r</i> , DROCK	0.28	0.37	-0.01
<i>r</i> , DLOG	0.33	0.04	0.53
<i>r</i> , DOVER	0.47	0.02	-0.15
<i>r</i> , DUNDER	0.38	0.03	-0.01
<i>r</i> , DEDGE	0.30	-0.26	-0.08
<i>r</i> , 7.5-15	0.15	-0.28	0.07
<i>r</i> , 15-30	0.13	-0.35	0.06
<i>r</i> , 30-45	-0.04	0.07	0.13
<i>r</i> , > 45	-0.18	0.59	-0.07
<i>r</i> , %ROCK	-0.21	-0.29	-0.08
<i>r</i> , %LEAF	0.04	0.19	-0.13
<i>r</i> , %LOG	-0.34	-0.15	-0.14
<i>r</i> , %GRASS	0.10	0.05	0.32
<i>r</i> , %SHRUB	-0.30	0.24	-0.19
<i>r</i> , CANCLO	-0.15	0.11	0.29



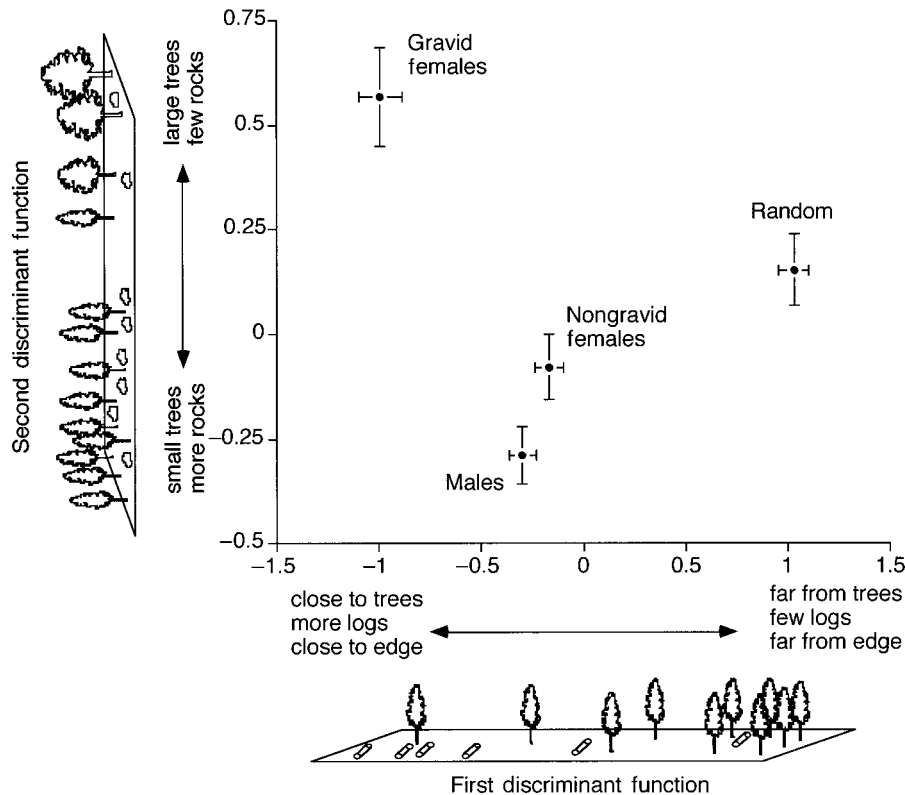


FIG. 1. Positions and standard errors of the group centroids of random locations and locations of gravid female, nongravid female, and male black rat snakes on the two significant discriminant axes with pictorial interpretation of associated habitat gradients in the analysis of habitat use by radio-implanted black rat snakes in Ontario from 1996 to 1999.

0.46). This suggests that females reduced their feeding when they were gravid.

Groups also differed significantly in the distance moved between successive relocations during the time that females were carrying their eggs ( $N = 1271$ ,  $\chi^2 = 72.38$ ,  $df = 6$ ,  $P < 0.001$ ). A posteriori tests of independence revealed that this relationship was a consequence of gravid females moving significantly less between relocations than nongravid females or males, with the latter two groups not differing significantly. Gravid females had not moved for 64% of the relocations and had moved 10 m or less in 75% of the relocations (Fig. 2). By contrast, nongravid females had moved 10 m or less in 53% of the relocations and males in 47% of the relocations (Fig. 2). Also, during the

active season black rat snakes were likely to move shorter distances between relocations when in edges than when in the forest ( $N = 3375$ ,  $\chi^2 = 46.54$ ,  $df = 3$ ,  $P < 0.001$ , Fig. 3). The only movement category that was more prevalent in forests than in edges was 101–1000 m (Fig. 3).

We monitored 55 shedding events from 37 of our radio-tracked snakes. The 37 individuals used 36 different shedding sites (10 individuals used more than one site and 15 sites were used by two to four radio-tracked snakes). Shedding sites were regularly shared by gravid females, nongravid females, and males. In addition, we found the shed skins of unmarked black rat snakes at 17 of the 36 shedding sites, so the sites used by the snakes we tracked were also used by other

TABLE 6. Number of black rat snake locations followed by radiotelemetry from 1996 to 1999 in edge habitats and other habitat types for the four months of the primary active season in Ontario.

Habitat	Month				Total
	May	June	July	August	
Edge	59 (51.8)	84 (59.6)	68 (66.0)	63 (70.8)	274 (61.3)
Other	55 (48.2)	57 (40.4)	35 (34.0)	26 (29.2)	173 (38.7)
Total	114	141	103	89	447

Note: The percentages of the total for each column are given in parentheses.

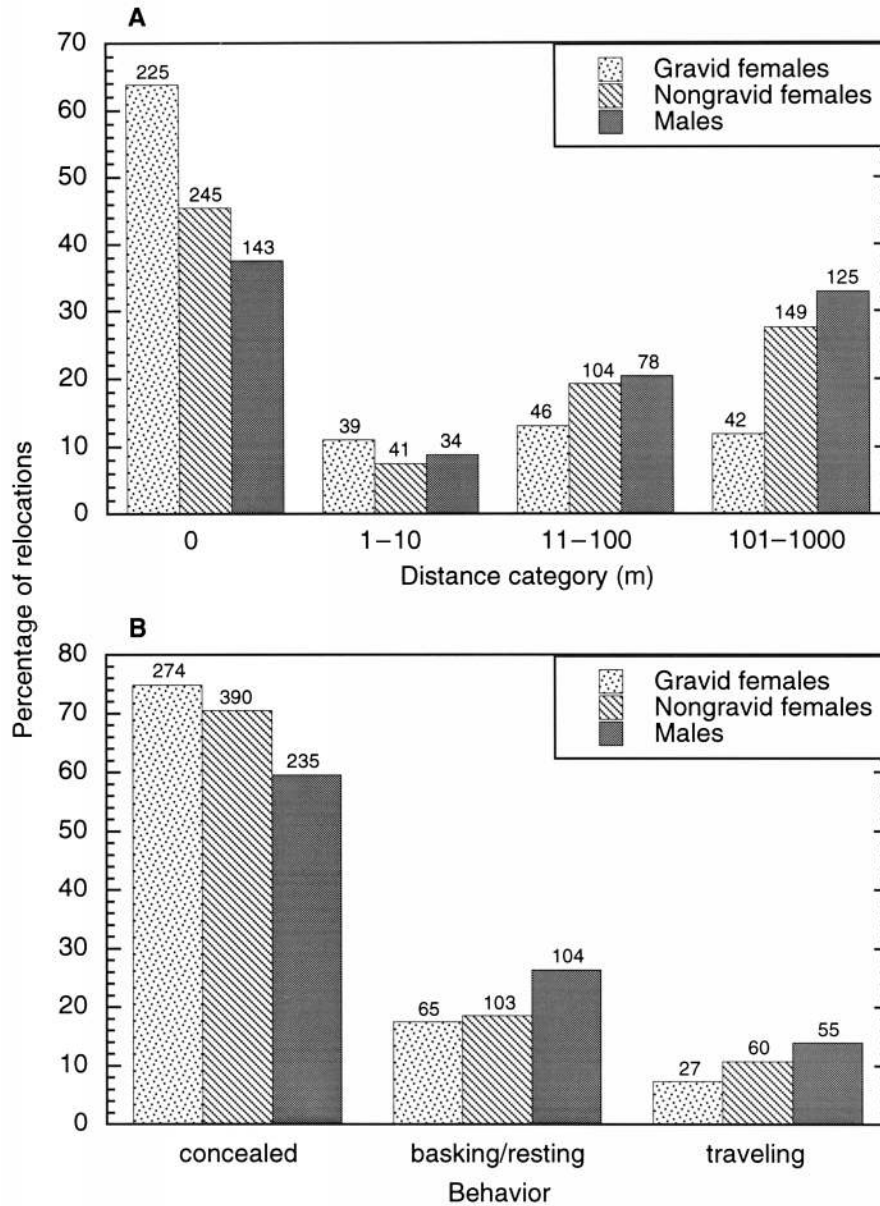


FIG. 2. (A) Distance categories moved between successive relocations and (B) behavior exhibited at relocation for radio-implanted gravid female, nongravid female, and male black rat snakes in Ontario from 1996 to 1999. Only relocations from the time period when females carry their eggs were included; sample sizes are shown above each bar.

snakes in the population. We divided the shedding sites into seven habitat categories and determined how many sites were situated in edges (Table 7). Based on the availability of artificial and natural edges in the study area, shedding sites were significantly more likely to be in edges than in other habitat types ( $N = 201$ ,  $\chi^2 = 12.64$ ,  $df = 2$ ,  $P = 0.002$ ).

Greater preference for edge by gravid females could also be a function of edges providing safer sites. DFA indicated that gravid females preferred sites with higher ground cover of logs and were found near trees more often than the other snake groups. In fact, 59% of lo-

cations of gravid female were in trees (DOVER or DUNDER = 0) whereas nongravid females and males were in trees 31% and 33% of the time, respectively. However, rocks often provide retreats for black rat snakes (snakes were under rocks in 15.7% of the relocations) and rocks were more abundant at sites where males and nongravid females were located (mean  $\approx 17\%$  rock cover, Table 3) than at sites where gravid females were located (mean  $\approx 12\%$  rock cover, Table 3). The three groups of snakes also differed in their frequency of traveling, resting/basking, or being concealed during the time that females were carrying their

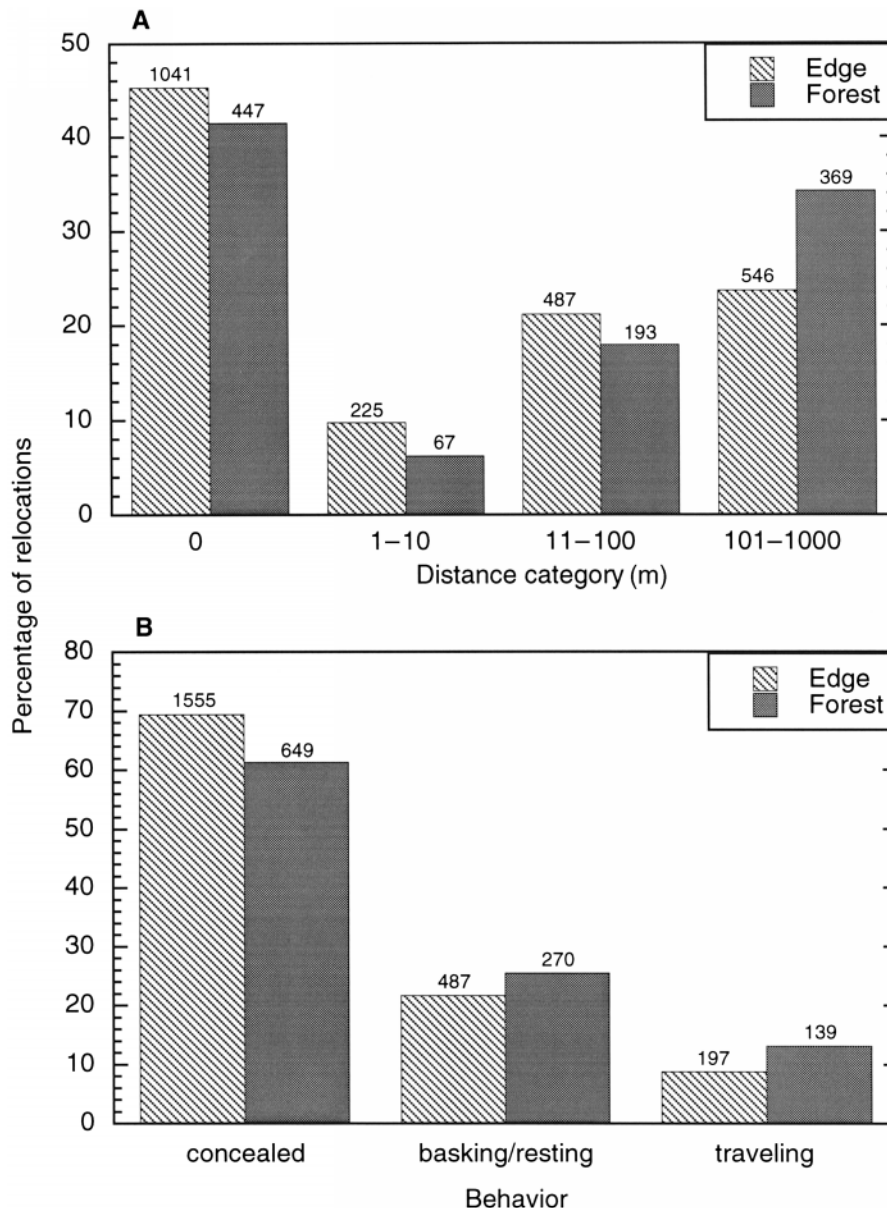


FIG. 3. (A) Distance categories moved between successive relocations and (B) behavior exhibited at relocation in edges and forest for radio-implanted black rat snakes in Ontario from 1996 to 1999. Relocations from the whole active season were included; sample sizes are shown above each bar.

eggs ( $N = 1313$ ,  $\chi^2 = 23.46$ ,  $df = 4$ ,  $P < 0.001$ ). However, a posteriori tests of independence revealed that this relationship was a result of males being concealed less than gravid females or nongravid females, while the latter two groups did not differ significantly (Fig. 2). During the active season, black rat snakes were concealed more often and visible (basking/resting or traveling) less often when relocated in edges than in the forest ( $N = 3297$ ,  $\chi^2 = 24.26$ ,  $df = 2$ ,  $P < 0.001$ , Fig. 3).

MANOVA of random habitat samples indicated that natural and artificial edges differed structurally (Wilk's

$\Lambda = 0.716$ ,  $F = 1.92$ ,  $df = 13, 63$ ,  $P = 0.044$ ). DFA indicated that the only difference was higher ground cover of rocks in natural edges (these sites were often at the edge of rock outcrops) and more ground cover of grass in artificial edges (these sites were often at the edge of hayfields). Although natural edges were  $\sim 2.5$  times more abundant than artificial edges in the study area, snakes were no more likely to be found in natural edges than in artificial edges, based on the availability of both types of edges ( $N = 354$ ,  $\chi^2 = 0.12$ ,  $df = 1$ ,  $P = 0.73$ , Table 2). This was also true when we considered gravid females alone ( $N = 123$ ,  $\chi^2 = 0.67$ ,  $df$

TABLE 7. Numbers of each type of shedding site, numbers of radio-implanted Ontario black rat snakes that used each type of site from 1996 to 1999, and numbers of shedding sites that were in artificial and natural edge habitats.

Shedding sites	Sites (N)	Individuals (N)	Artificial edge		Natural edge	
			(N)	(N)	(N)	(N)
Old barns	3 (8.3)	5 (9.8)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Old mining machinery	1 (2.8)	2 (3.9)	0 (0.0)	0 (0.0)	1 (5.3)	1 (5.3)
Cracks in house foundations	4 (11.1)	5 (9.8)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Old hay piles	3 (8.3)	5 (9.8)	3 (37.5)	0 (0.0)	0 (0.0)	0 (0.0)
Large hollow logs	3 (8.3)	4 (7.8)	0 (0.0)	0 (0.0)	3 (15.8)	3 (15.8)
Crevice in rock outcrops	9 (25.0)	8 (15.7)	3 (37.5)	3 (37.5)	6 (31.6)	6 (31.6)
Standing hollow snags	13 (36.1)	22 (43.1)	2 (25.0)	2 (25.0)	9 (47.4)	9 (47.4)
Total	36	51	8	8	19	19

Note: The percentages of the total for each column are given in parentheses.

= 1,  $P = 0.41$ ). Shedding sites also were not more likely to be in artificial edges than in natural edges given the availability of the two edge types ( $N = 97$ ,  $\chi^2 = 0.06$ ,  $df = 1$ ,  $P = 0.81$ ).

We trapped small mammals on 215 d, for a total of 5039 trap-days, and captured 187 individuals of species on which rat snakes prey (126 *Peromyscus*, 28 *Blarina*, 22 *Tamias*, and 11 *Microtus*). Before pooling the data for natural and artificial edges, we ensured that our index of small mammal abundance did not differ between edge types ( $t = 0.684$ ,  $df = 86$ ,  $P = 0.49$ ). A two-way ANOVA on the pooled data indicated that there was a significant month by habitat interaction ( $F = 3.19$ ,  $df = 2, 206$ ,  $P = 0.03$ ). Separate one-way ANOVAs for each month showed that capture success varied significantly between habitats only in August ( $F = 8.25$ ,  $df = 2, 64$ ,  $P < 0.001$ ). Tukey-Kramer hsd tests on the August data showed that capture success was higher in forests and edges than in the open habitats (Fig. 4). If we consider the data for edges only, ANOVA revealed that there were no monthly differences in the index of small mammal abundance ( $F = 2.69$ ,  $df = 2, 85$ ,  $P = 0.07$ ).

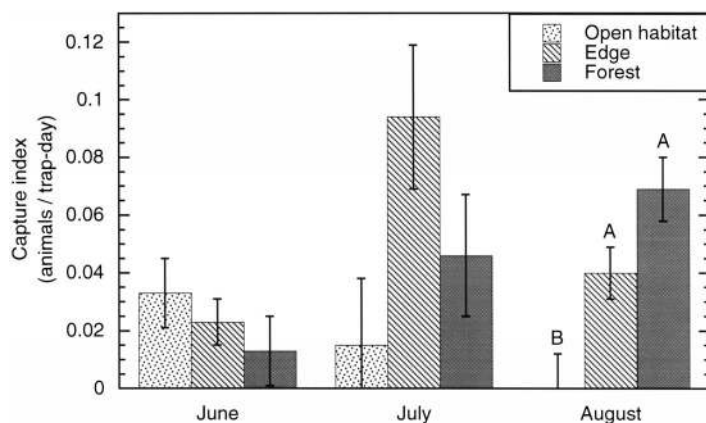
#### DISCUSSION

Our study confirms that black rat snakes prefer edge habitat (Weatherhead and Charland 1985, Durner and

Gates 1993). Furthermore, our results indicate that the preference for edges is equally strong in human-disturbed landscapes and in more pristine landscapes where the edges occur naturally. Finally, as we summarize below, of the hypotheses we tested, the best explanation for why black rat snakes prefer edges is that edges facilitate behavioral thermoregulation.

Weatherhead and Charland (1985) proposed that black rat snakes might prefer edges because breeding birds make edges more profitable habitats in which to forage. They based that hypothesis on their observation that the preference for edges by black rat snakes in their study was most pronounced early in the season. Studying the same population of black rat snakes, we found exactly the opposite pattern; although edges were preferred in all months, the use of edge habitat increased from May to August. The most obvious reason for this discrepancy is that Weatherhead and Charland (1985) only tracked seven snakes for one year resulting in only 118 locations of snakes. In fact, the decline in the use of edges occurred in only one of the two habitats analyzed, and this result was based on only 13 locations. With much more extensive data, we found that black rat snakes used edges more later in the season, after the period of avian reproduction is over. This is not consistent with the hypothesis that snakes are attracted to edges principally to forage for avian eggs

FIG. 4. Mean index of small mammal capture success in open habitats, edges, and forest for June, July, and August in Ontario from 1997 to 1999. Error bars indicate one standard error. Within a month, means with the same letters are deemed not significantly different based on Tukey-Kramer hsd tests; when there are no letters, there were no significant differences for the month. A "trap-day" is defined as one working trap set for one day.



and nestlings. Also, mammalian prey densities did not vary seasonally and were not higher in edges than in the forest. Therefore, if black rat snakes were selecting habitat principally for foraging on small mammals, then the snakes should have been found in forests as often as in edges throughout the active season, a pattern clearly different from what we observed. This evidence suggests that edges are not selected primarily for foraging, although this does not mean that edges are not good foraging habitats or that the snakes do not forage in edges.

Also inconsistent with the foraging hypothesis was the loss of mass we documented for gravid females. Gravid females used edges more extensively than males and nongravid females. If gravid females used edges to forage, they should have at least maintained their mass from emergence to postegg laying. However, the mean loss of >21% of body mass suggests that females forage very little when gravid. This result, combined with the general inactivity we documented for gravid females, suggests that gravid females were not using edges to forage. It does not necessarily follow that males and nongravid females used habitat on the same basis as gravid females. In fact, *Elaphe obsoleta* actively search for prey (Jackson 1970, 1978) and, although they were concealed more often in edges than in forest, short localized movements most likely to be associated with foraging (11–100 m) were more frequent in edges than in the forest. However, our data for gravid females, combined with the seasonal patterns of habitat use by all snakes, point to some reason other than foraging explaining the general preference for edges.

We also rejected the hypothesis that edges were preferred by gravid females because they provided superior protection from predators. The behavioral analysis suggested that gravid females were not actively avoiding predators more than nongravid females and, although we did not quantify retreat sites per se, our impression was that features such as snags and rock crevices were abundant throughout our study area, and did not occur primarily in edge habitat. We did find that some natural edges appeared to offer better retreat sites than artificial edges for snakes because of their rocky ground cover. Because the snakes did not differentiate between natural and artificial edges, however, we conclude that it was a general structural feature of edges that attracted them and that edges were not used primarily to avoid predation.

Weatherhead and Charland (1985) also proposed that black rat snakes might prefer edges because increased solar radiation allows snakes to bask to increase body temperatures. Presumably, edges also facilitate thermoregulation because they provide simultaneous access to open sunny habitats to increase body temperatures and shaded forests to decrease body temperatures. Our observations are generally consistent with this hypothesis. First, the clear preference for edge hab-

itat by gravid females is consistent with their need to maintain higher body temperatures. Among viviparous snakes, effective thermoregulation is important for gravid females because the phenotype and fitness of their offspring are dependent upon the body temperatures they experience during development (Alberts et al. 1997, Shine et al. 1997, Blouin-Demers et al. 2000a). Black rat snakes are oviparous, so the importance of maintaining body temperature for them must be associated with general metabolic function being more efficient at optimal body temperatures. Mobilizing the nutrients for eggs seems likely to be facilitated by the female maintaining her body temperature. At the northern extreme of the species' distribution where we studied black rat snakes, the short active season must place a premium on developing and laying the eggs quickly so they have adequate time to incubate.

The trade-off between behavioral thermoregulation and other activities may favor careful thermoregulation more in gravid females, but nongravid females and males should also benefit from some thermoregulation. Ecdysis is something that all snakes do, and snakes increase their body temperatures during ecdysis (Gibson et al. 1989, Peterson et al. 1993). Thus, the fact that shedding sites were located disproportionately in edge habitat is also consistent with edges being used for increasing body temperatures. Although our observations are consistent with the thermoregulation hypothesis, all our tests are indirect. To confirm that patterns of habitat use by black rat snakes and the divergence in habitat use between reproductive females and the other groups is linked to thermoregulation, we will need to determine if snakes thermoregulate differently in edges than in other habitat types. Our expectation is that edges should be ideal habitats to maintain optimal body temperatures because they allow simultaneous access to shaded microhabitats to decrease body temperatures and sunny microhabitats to increase body temperatures.

Our results have several implications for conservation. Weatherhead and Charland (1985) had hypothesized that the ideal habitat for black rat snakes is a mosaic of field and forest where the scale of fragmentation is sufficiently small that each individual snake can include both forest and edges within its home range. The results we presented here support this hypothesis and extend its implications to more pristine landscapes. The ideal pristine habitat for black rat snakes would also be a mosaic of forest and open habitats, but the open habitats would be natural (e.g., marshes, rock outcrops) instead of man-made (e.g., fields). In both agricultural and pristine habitat, the scale of forest fragmentation is important. An area with several large fields and several large forest patches would provide much less edge for the snakes than the same area divided into many smaller patches of field and forest. As such, we would expect the former situation to support fewer black rat snakes than the latter

situation. Of course from the snakes' perspective, either situation is superior to even larger scale deforestation, a phenomenon hypothesized to be the cause of the almost complete disappearance of black rat snakes from southwestern Ontario (Prior and Weatherhead 1998).

Our results indicated that black rat snakes do not discriminate between artificial and natural edges. Thus, if conservation of black rat snakes is the goal, it should be possible simply to create more edge. However, increasing edge habitat through forest fragmentation is detrimental to many species of forest birds because rates of nest predation are higher near some edges (Gates and Gysel 1978, Andrén and Angelstam 1988). Where black rat snakes occur, they may be responsible for some of the increased nest predation, even though their foraging in edges seems likely to be coincidental to their preference for that habitat. Thus, conservation efforts intended to protect black rat snakes by preserving or creating their preferred edge habitats seem likely to contribute to declines of forest-interior species of birds.

Several research directions are suggested by our results. First, the thermoregulation hypothesis should be tested directly by determining how strongly habitat use and thermoregulation are linked in black rat snakes. Second, because snakes have been identified as important nest predators in fragmented forest habitat (Robinson et al. 1995), it would be informative to know whether all snakes respond to edges in the same way and for the same reasons. This will improve the ability to predict the consequences for either future fragmentation or attempts to remedy current fragmentation. Interesting in this regard is evidence that tropical snakes may benefit from forest fragmentation (Henderson and Winstel 1995). It seems unlikely that edge habitat is important for thermoregulation in tropical snakes. If different snake species respond to habitat fragmentation for different reasons, the challenge that will arise will be to develop a general theory that accounts for that variation.

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