Habitat use and movement patterns of juvenile black ratsnakes (*Elaphe obsoleta*) and their conservation implications

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ABSTRACT

For species of conservation concern, it is essential to have an understanding of the behaviour, spatial ecology, and habitat use at all life stages so that we may develop appropriate conservation strategies. The central goal of this study was to describe the habitat use and movement patterns of juvenile black ratsnakes and contrast them to those of adults to identify any ontogenetic changes that should be included in the management plan of the species.

In Chapter One, I compared habitat use data for 153 juvenile snake locations that I collected in 2003-2004 to habitat use data for 384 locations of adult males and non-gravid females previously analysed by Blouin-Demers and Weatherhead (2001) and collected between 1996-2000. All snakes were located using radio-telemetry. Habitat use was determined by measuring structural habitat variables.

There was an ontogenetic shift in the habitat use of black ratsnakes in a relatively pristine habitat at both a macrohabitat and microhabitat scale. Juveniles used forest and edge macrohabitats more, but used microhabitats in proportion to their availability. Blouin-Demers and Weatherhead (2001) showed that adult black ratsnakes select at both scales: they use edges and sites with open canopy and many rocks and logs.

My results support previous findings that edge habitat is important to black ratsnakes. Although juveniles use edges less often than do adults, they are still found in edges 50% of the time. Juveniles use mature forest interior more than do adults. Forest management planning within the range of this species should include maintaining mature forest stands with many large trees.

In Chapter Two, I examined how movement patterns and spatial ecology change with size. I used movement data from 42 adults (16 males and 26 non-gravid females) previously published by Blouin-Demers and Weatherhead (2002) collected from 1996-2002 and juvenile data (n = 34) collected by Blouin-Demers and Weatherhead from 2000-2002 and that I collected in 2003-2004.

My results indicated a clear ontogenetic shift in the movement patterns and spatial ecology of black ratsnakes. I found that daily and seasonal movements, home range size and fidelity, behaviour, and fidelity to over-wintering sites all vary with size.

The results suggested that juvenile black ratsnakes, especially males, may be in a dispersal stage. If juveniles are playing a significant role in maintaining gene flow through dispersal, then adequate protection requires sufficient protected habitat to allow juvenile dispersal. I also showed that juveniles rarely attend communal hibernacula and often switch between hibernacula. Therefore, habitat to be protected cannot simply be defined as a fixed radius around a communal hibernaculum because many juveniles do not attend these communal hibernacula. This study reinforces the importance of understanding ontogenetic changes in the ecology of species of conservation concern. Insight into an ontogenetic shift in habitat use would be essential for sound management of any species where juveniles have more specific structural needs than adults, due to intense predation risk, specific prey requirements etc. Ontogenetic shifts in movement patterns and spatial ecology have to be considered in management decisions.

RÉSUMÉ

Pour les espèces en péril, il est essentiel d'avoir une compréhension du comportement, de l'écologie spatiale et de l'utilisation de l'habitat à toutes les étapes de la vie de sorte que nous puissions développer des stratégies de conservation appropriées. Le but central de cette étude était de décrire les préférences d'habitat et les patrons de déplacement des couleuvres obscures juvéniles et de les comparer à ceux des adultes afin d`identifier des changements ontogénétiques qui devraient être inclus dans le plan de gestion de l'espèces.

Au premier chapître, j'ai comparé des données de préférence d'habitat des serpents juvéniles pour 153 localisations caractérisés en 2003-2004 aux données de préférence d'habitat des mâles adultes et des femelles adultes non-gravides pour 384 localisations précédemment analysées par Blouin-Demers et Weatherhead (2001) et charactérisées entre 1996-2000. Tous les serpents ont été localisés en utilisant la radio-télémétrie. Les préférences d'habitat ont été déterminées en mesurant des variables structurales d'habitat.

Une variation ontogénétique était évidente dans les préférences d'habitat des couleuvres obscures dans un habitat relativement naturel à l`échelle du macrohabitat et du microhabitat. Les juvéniles choisissent davantage les macrohabitats de forêt et de bordure, mais utilisent les microhabitats proportionnellement à leur disponibilité. Blouin-Demers et Weatherhead (2001) ont prouvé que les couleuvres obscures adultes choisissent aux deux échelles : elles préfèrent les bordures et utilisent des emplacements avec une canopée ouverte et beaucoup de roches et de bûches.

Mes résultats soutiennent les résultats précédents qui tendent à démontrer que les bordures sont importantes pour les couleuvres obscures. Bien que les juvéniles utilsient les bordures moins souvent que des adultes, ils y sont tout de même trouvés 50% du temps. Les

juvéniles emploient l'intérieur des forêts matures davantage que des adultes. La planification de la gestion de la forêt dans l'aire de répartition de cette espèce devrait inclure le maintien de peuplements de forêt mature avec beaucoup de grands arbres.

Au deuxième chapître, j'ai examiné comment les patrons de déplacement et l'écologie spatiale changent avec la taille. J'ai employé des données de mouvement de 42 adultes (16 mâles et 26 femelles non-gravides) précédemment publiées par Blouin-Demers et Weatherhead (2002) amassées de 1996-2002 ainsi que des données sur les juvéniles (n = 34) amassées par Blouin-Demers et Weatherhead en 2000-2002 et par moi-même en 2003-2004.

Mes résultats ont indiqué une variation ontogénétique évidente dans les patrons de déplacement et l'écologie spatiale des couleuvres obscures. J'ai trouvé que les mouvements quotidiens et saisonniers, la fidélité au domaine vital ainsi que sa taille, le comportement, et la fidélité aux sites d'hivernage changent tous avec la taille.

Les résultats ont suggéré que les couleuvres obscures juvéniles - particulièrement les mâles - sont peut-être dans une étape de dispersion. Si les juvéniles jouent un rôle significatif dans le maintien du flux génétique par la dispersion, la protection de l'espèce exige l'établissement d'habitat protégé suffisant pour permettre la dispersion juvénile. J'ai également démontré que les juvéniles utilisent rarement les hibernacles communaux et changent souvent d'hibernacle. Par conséquent, l'habitat à protéger ne peut pas être défini simplement comme un rayon fixe autour d'un hibernacle communal parce que beaucoup de juvéniles n'y sont pas présents. Cette étude renforce l'importance de comprendre les changements ontogénétiques dans l'écologie des espèces en péril. La connaissance de la variation ontogénétique dans l'utilisation de l'habitat est essentielle pour la gestion saine de toutes les espèces où les juvéniles ont des besoins d'habitat structuraux plus spécifiques que les adultes, dû aux risques élevés de prédation, aux besoins de proies spécifiques, etc. Des

variations ontogénétiques dans les patrons de déplacement et dans l'écologie spatiale doivent

aussi être considérées dans les décisions de gestion.

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General Introduction

Federal governments are increasingly regulating the process of recovery planning for species of conservation concern. In both Canada and the US, legally defining the critical habitat of a species is an integral part of this process. The definition of critical habitat determines the extent to which the species will be protected. For many species, rarity, and the resulting difficulty of rigorous scientific study, will make this a challenging task.

An understanding of the behaviour, movements, and habitat use at all life stages is important for developing conservation strategies for species of conservation concern. For most species at risk, however, efforts have focused exclusively on the spatial and resource requirements of adults (Wong et al 2003, Russo et al 2002). Thus, we run the risk of mismanaging those species if the ecology of other life stages differs from that of adults. The bias towards the study of adults results from logistical difficulties associated with studying other life stages. In snakes, for example, the smaller size and more cryptic behaviour and appearance of juveniles make them more difficult to study (Shine et al. 2002). We cannot assume that adult ecology reflects that of juveniles, because different age classes differ in spatial, habitat, or prey requirements (Reinert 1993). These differences could impact the legal definition of critical habitat, and thus, the design of conservation efforts for the species. Declining species that are managed for human exploitation, such as Pacific salmon, are a notable exception to the bias of studying adults only. For these species, researchers have long recognized the importance of including all life stages in management plans (Cisceros-Mata et al 1995, Gerber and Heppell 2004, Rogers-Bennett and Pearse 2001). Similar breadth of research is required for non-

exploited species of conservation concern (e.g. Blanchard and Knight 1991, Myers and Vaughan 2003).

Animal populations where individuals vary widely in size often exhibit intraspecific variation in niche occupation (Werner and Gilliam 1984). For many organisms, body size is functionally related both to the exploitation of resources and to predation risk, and thus, strongly influences an individual's spatial behaviour, habitat use, and position in a community (Werner and Gilliam 1984). Organisms such as reptiles that can increase in body mass by more than two orders of magnitude from birth or hatching to adulthood, are most likely to exhibit ontogenetic niche shifts as a result of changing needs and vulnerabilities (Polis 1984).

Terrestrial snakes present an interesting model for examining ontogenetic niche shifts. Large differences in body size between conspecifics suggest that snakes are likely to experience ontogenetic changes in their resource use and vulnerability to predation. Body size can also affect the thermoregulatory requirements, behaviour, and physiological performance of snakes (Shine et al 2002), thus potentially affecting their movement patterns and habitat use.

My general goal in this thesis is to describe the habitat use and movement patterns of juvenile black ratsnakes and to contrast them to those of adults. This will allow me to identify ontogenetic changes that should be included in the design of recovery efforts and conservation management of the species.

The black ratsnake (*Elaphe obsoleta*) is an example of a species of conservation concern in Canada where spatial behaviour and habitat use of adults have been well documented (Weatherhead and Charland 1985, Weatherhead and Hoysak 1989, Blouin-Demers and Weatherhead 2001, Blouin-Demers and Weatherhead 2002, Prior and Weatherhead 1998, Prior et al. 2001), but we know very little about juveniles.

Black ratsnakes can increase 100 fold in mass from hatching to adulthood (Blouin-Demers et al 2002). They have a prolonged adolescence (Blouin-Demers et al 2002, Blouin-Demers et al 2005), and juveniles rarely attend communal hibernacula used by adults (Prior et al. 2001). The differences in reproductive state, size, and hibernation strategy suggest a strong potential for alternative spatial behaviour and habitat use among neonates, juveniles, and adults that could be important to the understanding and conservation of the species.

CHAPTER ONE

Habitat use by juvenile black ratsnakes (*Elaphe obsoleta*)

Introduction

Habitat loss, fragmentation, and degradation are common forces behind the decline of many species. It is essential to the persistence of these species that their habitat use be well understood, so that the necessary landscape, environmental, and structural features can be preserved. In both Canada and the US, legally defining the critical habitat of a species is an integral part of the protection process. To develop a sound definition of a species' critical habitat, a detailed understanding of habitat use, and how age, sex, reproductive state, and season affect that use, is necessary. For most species of conservation concern, limited funding, small population size, and the absence of long-term monitoring will make defining the critical habitat very challenging.

Despite its obvious importance, in-depth research on juveniles of non-resource species of conservation concern is scant. Conservation research on juveniles has largely been limited to amassing demographic data on survival and predator vulnerability for use in population viability analyses (Johnson and Braun 1999, Lamberson et al 1992, Price and Kelly 1994, Holmes and York 2003). It is risky to disregard the importance of understanding juvenile ecology and habitat use for conservation. It is especially risky for species that vary greatly in size, and are thus likely to exhibit ontogenetic niche shifts, where habitat use could change dramatically as a function of size.

Populations where animals vary greatly in size often exhibit intraspecific variation in niche occupation (Werner and Gilliam 1984). For many organisms, body size is functionally related to both the exploitation of resources and predation risk, and thus can strongly influence an individual's behaviour and habitat use (Werner and Gilliam 1984). Organisms such as

reptiles that increase by 2 or more orders of magnitude in size from birth or hatching to adulthood are most likely to exhibit ontogenetic niche shifts as a result of changing needs and vulnerabilities (Polis 1984).

The black ratsnake (*Elaphe obsoleta*) is an example of a species of conservation concern in Canada where spatial behaviour and habitat use of adults have been well documented (Weatherhead and Charland 1985, Weatherhead and Hoysak 1989, Blouin-Demers and Weatherhead 2001, Blouin-Demers and Weatherhead 2002, Prior and Weatherhead 1998, Prior et al. 2001). Black ratsnakes are listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The status report and the recovery plan are based solely on research on adults. My goal in this chapter is to describe the habitat use of juveniles black ratsnakes and to identify ontogenetic changes in habitat use by comparing my data to data already published on adults. This study will serve as an example of how information on multiple age classes of a species can affect strategies for conservation.

The black ratsnake is a good model to examine differences in habitat use due to size. Black ratsnakes can increase 100 fold in mass from hatching to adulthood (Blouin-Demers et al 2002). The black ratsnake has a prolonged adolescence. Based on field-observations, the age of maturation for black ratsnakes was originally estimated at nine or ten years in Canada (Blouin-Demers et al 2002). Recently, genetic work has shown that some individuals mature as early as approximately 5 years of age (Blouin-Demers et al 2005). Juveniles rarely attend the communal hibernacula used by adults (Prior et al. 2001). Because juvenile and adult ratsnakes are particularly different, I expected their patterns of habitat use to differ also.

Habitat use analyses of adult black ratsnakes have examined differences between males, non-reproductive females, and reproductive females. All adult black ratsnakes used edge

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habitats often (Weatherhead and Charland 1985, Durner and Gates 1993, and Blouin-Demers and Weatherhead 2001). Non-reproductive adult females and adult males did not differ significantly in their habitat use. Both used areas that were in close proximity to small trees, rocks, and had extensive ground cover of shrubs and logs (Blouin-Demers and Weatherhead 2001). Reproductive females differed in that they showed an increased use of edges and areas with larger trees and fewer rocks (Blouin-Demers and Weatherhead 2001).

Blouin-Demers and Weatherhead (2002a, b and 2001) showed that habitat use in adult black ratsnakes is driven by thermoregulation. Thermoregulatory requirements for ectothermic animals are influenced by size because smaller individuals warm and cool more quickly than larger ones (Stevenson 1985, Carrascal et al 1992). This difference could result in alternative habitat use by juvenile snakes.

The diet of black ratsnakes was examined in both adults and juveniles: both feed primarily on mammals, but also prey on birds. There was an ontogenetic shift noted where the diet of adult black ratsnakes changed to include eastern chipmunks (*Tamias striatus*) with a corresponding decrease in the abundance of small prey. The use of avian prey remained the same in both groups (Weatherhead et al. 2003). An ontogenetic shift in prey species use could lead also to a shift in the microhabitat used by black ratsnakes while hunting.

Survivorship increases with body size in black ratsnakes (Weatherhead et al 2002), suggesting a potentially increased predation risk for juveniles. If smaller black ratsnakes experience a higher predation rate than adults, then I predicted that they should use habitats with more retreat sites than adults (e.g., rocks, logs, medium and large trees) and should be found less often in the open where they would be more vulnerable to predators.

Materials and Methods

This study was based on habitat use data that I collected during the snake active seasons of 2003-2004, and on data collected between 1996-2000 that was published by Blouin-Demers and Weatherhead (2001). All fieldwork was conducted at the Queen's University Biological Station (QUBS), approximately 150 km south of Ottawa, Ontario.

Study individuals were captured using two methods. Some study animals were caught in funnel traps at fenced communal hibernacula during spring emergence (Blouin-Demers et al. 2000). The remaining individuals were caught opportunistically. Many juvenile black ratsnakes do not attend communal hibernacula (Prior et al.2001).

In the laboratory, snakes were measured, weighed, and sexed. Any previously unknown snake was marked with a passive integrated transponder tag (Anitech Identification Systems Inc., Markham, Ontario). I selected 17 individuals between 140 g and 250 g for transmitter implantation, ensuring that the transmitter represented at most 4% of the mass of the individual. The maximum mass was to ensure that the individuals were juveniles and not adults; maturity occurs around 105 cm snout-vent length and 300 g in this population (Blouin-Demers et al. 2002). The size that was used in this study to mark the age of maturity was originally estimated based on field observations (Blouin-Demers et al. 2002). Recently, however, genetic work has shown that some individuals as small as 88.5 cm snout-to-vent length were fathering young (Blouin-Demers et al. 2005). The radio-transmitters (Model SB-2T, Holohil Systems Inc, Carp, Ontario, 5.5g, 12 months battery life at 20°C Celsius) were implanted using a modification of the procedure described by Reinert and Cundall (1982), see Weatherhead and Blouin-Demers (2004)

for details. Details on the anaesthesia are described in Blouin-Demers et al. (2000). The snakes were kept overnight in the laboratory and then released at their point of capture.

After release, the snakes were located on average every 2-3 days from spring emergence, or from time of first capture, until they entered their over-wintering site in late September to early October. They were located using a telemetry receiver (TRX-2000s, Wildlife Materials Inc, Carbondale, Illinois) and a directional three-element yagi antenna (F173-3FB, Wildlife Materials Inc., Carbondale Illinois). Their daily positions were flagged and recorded using a GPS76 unit (Garmin International Inc., Olathe, Kansas) in the Universal Transverse Mercator (datum NAD83) co-ordinates system.

A habitat characterization was performed at each snake location. To minimize disturbance to the snakes, I performed habitat analyses only after the snake had moved to a new location. To make the juvenile and adult data comparable, I measured the 15 variables used by Blouin-Demers and Weatherhead (2001) (Table 1-1). I also measured 8 new variables to ensure that all potential habitat associations were explored (Table 1-2). Locations that were used more than once are only included once in the habitat analysis. I also quantified available habitat to determine if snakes were using the habitat non-randomly. I repeated the habitat analyses at paired random locations selected by walking a randomly determined distance (10-200 paces, determined using a 20-face die multiplied by 10) in a randomly selected direction (1-360 degrees, determined by spinning the bearing dial disc on a compass).

Statistical Analyses

The snakes were divided into two groups: juveniles and adults based on their size (> or < 105 cm SVL). Only data for males and non-gravid females from the Blouin-Demers and

Weatherhead (2001) study were used in the adult group to ensure that results would reflect differences due to size and age, not to reproductive status. Blouin-Demers and Weatherhead (2001) showed that the habitat use of males and non-reproductive females does not differ significantly, while gravid female black ratsnakes have alternative habitat use due to their reproductive condition.

Contingency table analysis was used to test if groups used macrohabitat types non-randomly. Macrohabitat use was divided into 3 categories: forest, edge, and open. Edge is defined as any area that is 15 m or less from where 3-dimensional habitat (forest) meets 2-dimensional open habitat (e.g., field, rocky outcrop, marsh).

Two discriminant function analyses (DFA) were performed. The first was used to examine which of the 15 shared variables most contributed to the separation between juvenile and adult snake locations and random locations. The second DFA was used to examine which of 23 variables measured most contributed to the separation between juvenile locations and random locations.

The statistical analyses performed for this study assume that the snake locations sampled were random and independent. The assumption of independence is contentious since the data were derived from multiple observations per individual, so some pseudo-replication occurred. The interpretations resulting from the analyses could prove problematic if specimens show high individual heterogeneity and if the number of individuals is small and unequal between the groups. In this study, 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. For these data, performing the analysis using substituted group means for each individual does not alter the

results. This method, however, reduces the sample size and ignores the variation found within individuals (Blouin-Demers and Weatherhead 2001).

The analyses were conducted on Splus version 6.1 for Windows (Insightful Corp., 1988, 2002) and Systat version 11 (Systat Software Inc., 2004). Data were transformed, when necessary, to improve their adherence to the assumption of normality. Significance of statistical test was accepted at $\alpha = 0.05$.

Results

From 2003-2004, I followed 17 juvenile ratsnakes for periods ranging from 58 to 268 days (mean 133.4 ± 81 days). I sampled habitat characteristics at 153 juvenile locations. I used habitat characterizations from 384 adult locations collected for a study by Blouin-Demers and Weatherhead (2001) sampled from 1996-1999. Adult locations were those of adult males and non-gravid females only. I also used 317 random locations from both studies (165 adult random locations and 153 juvenile random locations).

Contingency table analysis showed a significant overall difference among groups in their use of edge, forest, and open habitats ($\chi^2 = 33.11$, d.f. = 4, p < 0.0001). A post-hoc analysis of subsets of the groups showed significant differences between the use of macrohabitats for all groups: Juvenile vs. Random ($\chi^2 = 15.05$, d.f. = 2, p = 0.0005), and Juvenile vs. Adult ($\chi^2 = 16.7$, d.f. = 2, p = 0.0002). Edges constituted 43% of the study area, but were used more frequently by adults (58%), and to a lesser extent by juveniles (48%) (Fig. 1-1). Juveniles used forests (50%) more than they were randomly available (44%), where adults used forests less often (33%).

Neither group used open habitats as often as they were available (14%), but adults (9%) used these areas more than juveniles (2%).

A MANOVA using 15 shared habitat variables showed that there was a significant overall difference between the group centroids of the adult and juvenile snake locations and the juvenile and adult random locations (Wilk's $\lambda = 0.595$, $F_{1,15}=22.21$, p<0.001), and justified continuing with the discriminant function analysis.

A DFA was used to test which of the 15 shared variables most contributed to the separation between the group centroids. The model produced one significant discriminant function (Wilk's $\lambda = 0.664$, $F_{15,373} = 12.582$, p <0.001). The pooled within-group correlations of habitat variables indicated that DROCK, SHRUB, and MEDIUM trees contributed strongly and positively, while LARGE and LOGSTICK contributed negatively. This function can be interpreted as a gradient from juveniles using areas with large trees, high log and stick ground cover, and closer to rocks, to adults using areas with medium trees and high shrub cover as shown by the group means (Table 1-3).

A MANOVA using 23 habitat variables showed no significant difference between the centroids for juvenile and random locations (Wilk's $\lambda = 0.945$, $F_{23,268} = 0.709$, p = 0.830) (For group means see Table 1-4). If juveniles are in a dispersal stage, then they could potentially be less selective, meaning more random in their habitat use, at locations where they were found only once. To test this, I performed a MANOVA using the 23 variables to compare between juvenile locations that were used only once versus those that were used more than once and found no significant difference between the group centroids (Wilk's $\lambda = 0.998$, $F_{23,153}= 0.879$, p = 0.760) showing that there was no significant difference between sites used once, and sites used more than once by juveniles.

To ensure that any differences found were not due to differences in sample size between the juvenile and adult groups, I determined the effect size for the analyses between juvenile and random locations and between adult and random locations. For the juvenile versus random location analysis, 8% of the multivariate variation of the dependent variables is explained by the group factor (multivariate $\eta^2 = 0.079$). For the adult versus random analysis, 27% of the total multivariate variation of the dependent variables is explained by the group factor (multivariate $\eta^2 = 0.271$).

Discussion

My results clearly indicate an ontogenetic shift in the habitat use of black ratsnakes. Juvenile habitat use is significantly different from adult use at both a macrohabitat and a microhabitat scale. Juveniles appear to select at a macrohabitat scale because they use edges and forest more than they are randomly available, but use the microhabitat randomly, whereas adults have been shown to be selective, or use habitat non-randomly, at both macrohabitat and microhabitat scales (Blouin-Demers and Weatherhead 2001). This difference was not due to a smaller sample size of juveniles leading to a non-significant result, the effect size was much smaller for juveniles than for adults.

In previous studies, edge habitat has been shown to be very important for adult black ratsnakes (Weatherhead and Charland 1985, Blouin-Demers and Weatherhead 2001). I showed that, as predicted, I showed that juveniles are less dependent on edges than are adults, although they still use edges more than they are randomly available. Although neither group uses open

habitats as often as they are randomly available, juveniles were found in open habitats only 1/4 as often as adults.

Adult black ratsnakes use edges extensively for their thermoregulatory benefits (Blouin-Demers and Weatherhead 2001). In edge habitats, individuals are able to move readily from shade to sun. Juveniles are equally dependent on behavioural thermoregulation as adult males and non-gravid females. Smaller individuals, however, require less time to heat and cool and, as such, need to be exposed less often to high temperatures to achieve the same thermoregulatory benefits as larger individuals (Stevenson 1985, Carrascal et al 1992). This advantage should allow juveniles to devote more time to activities other than thermoregulation (Carrascal et al 1992), and could explain why they are found less often in edges than adults, and are found so rarely in open habitats.

The reduced use of edges and open habitats by juveniles translated into an increased use of forests. The macrohabitat analysis showed that juveniles use forests more than they are randomly available. Adults use forests significantly less than they are available. Juvenile black ratsnakes are not only using forests, but the trees themselves. A post hoc analysis showed that juveniles were found in trees in 51% of locations compared to only 37% for adults. They were most often found above 3 metres and in large trees. In 80% of all juvenile locations no visual contact was possible, compared to no visuals in 68% of adult locations. This evidence suggests that juveniles are using large trees as retreat sites and supports my prediction that juveniles may be responding to an increased risk of predation due to their smaller size. It is also likely that this increased predation risk contributes to juveniles avoiding the exposure of open habitats, and to the decrease shown in the use of edge habitat.

Despite the clear habitat selection by juveniles at a macrohabitat scale, there was no significant difference between the use of microhabitat by juvenile black ratsnakes from what is available to them. In the relatively pristine habitat of the study area, juvenile black ratsnakes do not select for specific structural habitat variables. During the prolonged adolescence of black ratsnakes, juveniles appear to be in a dispersal stage (see Chapter 2) when careful microhabitat selection may be secondary to searching for a home range in which to settle. Previous studies have shown that adult black ratsnakes have high site fidelity to hibernacula, nests, and annual home ranges (Prior et al. 2001, Weatherhead and Hoysak 1989, Blouin-Demers and Weatherhead 2002). Little is known, however, about juvenile black ratsnake movement patterns and home range. If juvenile ratsnakes were dispersing, I would expect them to have larger home ranges, and show less overlap in home ranges over consecutive years than adults. I would also predict that juveniles should show less fidelity to their over-wintering locations. These predictions will be tested in Chapter 2.

Smaller individuals are more vulnerable and are thus susceptible to a wider breadth of predators (Werner and Gilliam 1984). In black ratsnakes, a positive correlation has been shown between body size and survivorship (Weatherhead et al 2002). If the increase in predation risk for juvenile black ratsnakes is significant, it is possible that juvenile black ratsnakes are unable to be as choosy as adults in their habitat use. Further investigation into juvenile predation risk and their response to this risk may lead to a better understanding of the link between predation risk and habitat use.

Conservation Implications

My results have implications for the conservation of black ratsnakes and, more broadly, for conservation planning in general. Black ratsnakes are long-lived and have a prolonged adolescence. Sound management of these species requires that the needs and vulnerabilities of juveniles be included in conservation planning. This study has provided a more complete understanding of the habitat use of the species and highlights potential risks associated with ignoring ontogenetic shifts in the habitat use of species of conservation concern.

This study supports the findings of both Weatherhead and Charland (1985) and Blouin-Demers and Weatherhead (2001) on the importance of edge habitat to black ratsnakes. Although juvenile black ratsnakes have a decreased dependence on edge habitat compared to adults, they are still found in edges 50% of the time. Therefore, juvenile habitat use is accounted for in previous conservation recommendations that the legal definition of critical habitat for a black ratsnakes should include a mosaic that allows for both forest and edges (Blouin-Demers and Weatherhead 2001). However, juveniles differ from adults in that they have a higher use of mature forest interiors. Forest management planning in the areas inhabited by black ratsnakes should, therefore, include maintaining mature forest stands with many large trees.

My results show that juvenile black ratsnakes use the available microhabitat randomly compared to adults. It is important to specify that this study was conducted in a relatively pristine area. These results do not suggest that any habitat is adequate for juveniles, but that they make full use of the historically available habitat. Therefore, for this species, most habitat considerations in conservation planning that protect the adults will also allow for the persistence of juveniles, providing that sufficient areas of natural habitat are protected. In a broader conservation context, however, the importance of my findings of an ontogenetic shift in habitat use should not be overlooked.

Insight into an ontogenetic shift in habitat use would be essential for sound management of any species where juveniles have more specific structural needs than adults, due to intense predation risk, specific prey requirements etc. This consideration is especially important for species that are long-lived with delayed maturity, and / or for species where adult survivorship is high and coupled with low recruitment. For all species of conservation concern, it is vital that juveniles be included in management plans to protect the next generation of reproductive adults.

Table 1-1. Structural variables measured for the analysis of microhabitat use of adult and juvenile black ratsnakes followed by radio-telemetry in eastern Ontario between 1996 and 2004.

Variable	Description
Drock	Distance to closest rock (>20cm in length) within 30m (m)
Dlog	Distance to closest log (>7.5cm diameter) within 30m (m)
Canclo	Percentage canopy cover
Dedge	Distance to edge within 100m (m)
Rock	Percentage cover of rock (within 1m radius)
Leaf	Percentage cover of leaf litter (within 1m radius)
Grass	Percentage cover of grass (within 1m radius)
Shrub	Percentage cover of shrubs (height <2m) (within 1m radius)
Logstick	Percentage cover of logs and sticks (within 1m radius)
Dover	Distance to closest overstory tree (>7.5m DBH, height >2m) (m)
Small	Number of overstory trees of DBH 7.5-15cm (within 10m radius)
Medium	Number of overstory trees of DBH 15-30cm (within 10m radius)
Large	Number of overstory trees of DBH 30-45cm (within 10m radius)
Xlarge	Number of overstory trees of DBH >45cm (within 10m radius)
Dunder	Distance to closest understory tree (< 7.5cm DBH and height >2m) (m)

Table 1-2. 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 (>20cm in length) within 30m (m)
Lrock	Length to closest rock (>20cm in length) within 30m (m)
Nrock	Number of rocks within 20m (>20cm in length)
Dlog	Distance to closest log (>7.5cm diameter) within 30m (m)
Llog	Length of closest log (>7.5cm diameter) within 30m (m)
Dmlog	Diametre of closest log (>7.5cm diameter) within 30m (m)
Nlog	Number of logs within 20m (>7.5cm diameter)
Canclo	Percentage canopy cover
Dedge	Distance to edge within 100m (m)
Rock	Percentage cover of rock (within 1m radius)
Leaf	Percentage cover of leaf litter (within 1m radius)
Grass	Percentage cover of grass (within 1m radius)
Shrub	Percentage cover of shrubs (height <2m) (within 1m radius)
Herb	Percentage cover of herbs (within 1m radius)
Sticks	Percentage cover of sticks or logs (height <2m) (within 1m radius)
Dover	Distance to closest overstory tree (>7.5m DBH, height >2m) (m)
Decay	Decay state of nearest overstory tree (most decayed (1) – least decayed (7))

Table 1-2. Continued.

Small	Number of overstory trees of DBH 7.5-15cm (within 10m radius)
Medium	Number of overstory trees of DBH 15-30cm (within 10m radius)
Large	Number of overstory trees of DBH 30-45cm (within 10m radius)
Xlarge	Number of overstory trees of DBH >45cm (within 10m radius)
Dunder	Distance to closest understory tree (< 7.5cm DBH and height >2m) (m)
Nunder	Number of understory trees of DBH <7.5cm and >2m in height

Table 1-3. Group means (and standard errors) for 15 microhabitat variables (defined in Table 1-1) shared between adults and juveniles.

Variable	Adult (> 105cm SVL)			Juvenile (< 105cm SVL)		
	Mean (± 1SE)	Min.	Max.	Mean (± 1SE)	Min.	Max.
Drock	2.65 (±0.20)	0.0	30.0	1.15 (±0.41)	0.0	20.0
Dlog	3.13 (±0.23)	0.0	30.0	2.45 (±0.36)	0.0	10.4
Llog	4.76 (±0.17)	0.5	20.5	2.01 (±0.28)	0.11	11.8
Rock	15.73 (±1.04)	0.0	95.0	21.17 (±3.80)	0.0	100.0
Leaf	21.89 (±1.06)	0.0	80.0	22.08 (±2.19)	0.0	66.0
Log	21.29 (±1.09)	0.0	100.0	8.43 (±2.15)	0.0	80.0
Grass	11.63 (±0.60)	0.0	70.0	19.17 (±2.66)	0.0	75.0
Shrub	16.37 (±0.93)	0.0	100.0	7.83 (±1.56)	0.0	50.0
Dover	2.48 (±0.15)	0.0	16.7	1.53 (±0.24)	0.0	8.0
Small	10.52 (±0.46)	0.0	54.0	10.0 (±0.91)	0.0	25.0
Medium	4.66 (±0.21)	0.0	22.0	3.83 (±0.39)	0.0	14.0
Large	1.39 (±0.08)	0.0	10.0	3.07 (0.38)	0.0	12.0
Xlarge	0.36 (0.04)	0.0	3.0	0.34 (±0.08)	0.0	2.0
Dunder	1.83 (0.16)	0.0	30.0	1.83 (0.44)	0.13	20.0
Canclo	51.55 (1.63)	0.0	100.0	63.75 (±2.80)	10.0	96.0
Dedge	17.44 (3.00)	-40.0	100.0	26.13 (±5.00)	-30.0	100.0

Table 1-4. Group means (and standard errors) for 23 habitat variables (defined in Table 1-2) shared between juvenile and random locations.

	Juvenile Locations			Random Locations		
	Mean (±1SE)	Min.	Max.	Mean (±1SE)	Min.	Max.
Drock	1.84 (±0.35)	0.0	20.0	2.5 (±0.38)	0.0	26.0
Lrock	0.48 (±0.02)	0.15	2.35	1.0 (±0.43)	0.20	62.0
Nrock	36.74 (±0.28)	0.0	100.0	33.9 (±2.8)	0.0	103.0
Dlog	2.77 (±0.25)	0.0	20.0	3.9 (±0.39)	0.0	20.0
Llog	2.15 (±0.17)	0.11	12.3	2.41 (±0.2)	0.26	13.0
Dmlog	0.18 (±0.01)	0.08	1.12	0.18 (±0.02)	0.08	2.5
Nlog	3.84 (±0.37)	0.0	30.0	3.24 (±0.26)	0.0	17.0
Canclo	65.81 (±1.8)	0.0	96.0	65.8 (±2.0)	0.0	96.0
Dedge	25.62 (±2.8)	-30.0	100.0	27.8 (±3.28)	-80.0	100.0
Rock	16.1 (±1.8)	0.0	100.0	11.5 (±0.1.5)	0.0	100.0
Leaf	23.97 (±0.1.5)	0.0	80.0	27.2 (±1.8)	0.0	94.0
Grass	21.48 (±1.93)	0.0	100.0	25.8 (±2.3)	0.0	100.0
Shrub	9.8 (±1.25)	0.0	100.0	8.9 (±1.3)	0.0	114.0
Herb	9.9 (±0.89)	0.0	60.0	10.7 (±1.3)	0.0	100.0
Sticks	12.94 (±0.97)	0.0	50.0	10.1 (±0.92)	0.0	72.0
Dover	1.58 (±0.19)	0.0	15.0	2.3 (±0.34)	0.0	20.0
Decay	5.5 (±0.15)	0.0	7.0	6.0 (±0.13)	0.0	7.0
Small	9.5 (±0.55)	0.0	14.0	10.1 (±0.61)	0.0	36.0

Table 1-4. Continued.

Medium	3.53 (±0.24)	0.0	14.0	3.47 (±0.22)	0.0	13.0
Large	3.2 (±0.22)	0.0	12.0	3.24 (±0.24)	0.0	13.0
Xlarge	0.51 (±0.07)	0.0	5.0	0.43 (±0.07)	0.0	4.0
Dunder	1.5 (±0.18)	0.0	20.0	2.1 (±0.27)	0.0	20.0
Nunder	23.8 (±1.4)	0.0	100.0	24.4 (±1.6)	0.0	100.0
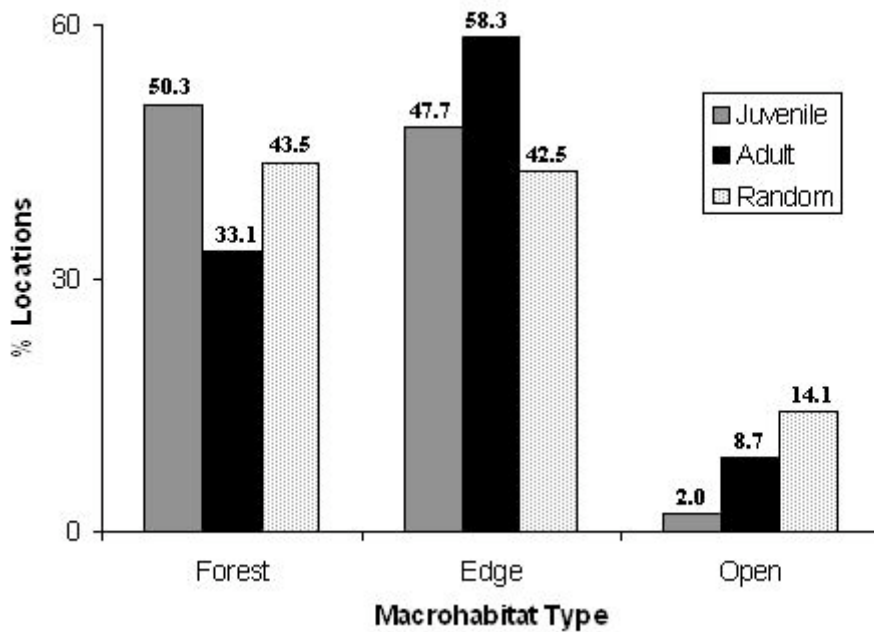
Fig. 1-1. Percentage use of macrohabitat types by juvenile and adult black ratsnakes located using radio-telemetry in eastern Ontario between 1996-2004.

CHAPTER TWO

Movement patterns of juvenile black ratsnakes (*Elaphe obsoleta*)

Introduction

Knowledge of spatial ecology and movement patterns is essential to our understanding of any species. How an individual travels through the space it inhabits relates directly to its needs and to the structural and functional resources of the habitat. This understanding is especially important for the management and protection of species of conservation concern (Weatherhead and Prior 1992). Data on movement, home range size, and site fidelity are necessary to inform the appropriate size and location of reserves and to determine the vulnerability to landscape fragmentation (Webb and Shine 1997, Wielgus 2002).

The importance of movement patterns to conservation is equal across all life stages of a species. Juveniles are likely to exhibit alternative behaviours and preferences compared to adults and, thus, should be included in ecological and behavioural research to ensure informed management. Due to their smaller size, juveniles have different selection pressures, dietary preferences, vagility, and predation risk than adults (Reinert 1993, Werner and Gilliam 1984). Juveniles, by definition, do not reproduce, have different physiological requirements than adults, and have a propensity to disperse, all of which predict that species may exhibit ontogenetic shifts in movement patterns and spatial ecology (Reinert 1993, Roe et al 2004, Greenwood 1980, Johnson and Gaines 1990).

Much of the conservation research to date has focused largely on adults, ignoring the needs of juveniles (Wong et al 2003, Russo et al 2002). This is especially true for terrestrial species. If reported, data on juveniles are incidental, often due to indiscriminate sampling, and are rarely the focus of any discussion (Palomares et al 2000, Blanchard and Knight 1991). Research on commercially harvested species is a notable exception, as considerable resources and effort are expended towards the investigation of the juvenile life stages. For these species,

researchers have long recognized the importance of protecting juveniles to maintain stable populations (Cisceros-Mata et al 1995, Gerber and Heppell 2004, Rogers-Bennett and Pearse 2001).

The black ratsnake (*Elaphe obsoleta*) is an example of a species of conservation concern in Canada where our knowledge of spatial behaviour and habitat use, and the resulting recovery plans, have been based solely on research on adults. The general goal of this chapter is to identify any ontogenetic differences in the spatial ecology and movement patterns of black rat snakes that could influence the management and conservation of the species.

Little is known about the ecology of juvenile black ratsnakes, but the potential for differences in movement and spatial behaviour in this species is high. Black ratsnakes can increase 100 fold in mass from hatching to adulthood (Blouin-Demers et al 2002). The black ratsnake has a prolonged adolescence. Based on field-observations, the age of maturation for black ratsnakes was originally estimated at nine or ten years in Canada (Blouin-Demers et al 2002). Recently, genetic work has shown that some individuals mature as early as approximately 5 years of age (Blouin-Demers et al. 2005). Juveniles rarely attend the communal hibernacula used by adults (Prior et al. 2001), and have alternative dietary preferences due to their size (Weatherhead et al 2000). Due to these aspects of the black ratsnake's ecology, and the propensity of juveniles of any species to disperse, there is strong potential for ontogenetic changes in their movement patterns and spatial behaviour.

The movement patterns and spatial behaviour of adult black ratsnakes have been well documented (Weatherhead and Charland 1985, Weatherhead and Hoysak 1989, Blouin-Demers and Weatherhead 2001, Blouin-Demers and Weatherhead 2002). Radio-telemetry studies have demonstrated that adult black ratsnakes are faithful to home ranges, nesting sites, and communal

over-wintering locations (Prior et al. 2001, Weatherhead and Hoysak 1989, Blouin-Demers and Weatherhead 2002). Although some individuals over-winter within their home range, individuals have been found as far away as 4 km from their hibernacula during the active season (Blouin-Demers and Weatherhead 2002). Reproductive females travel each year to preferred nesting sites that are, on average, 490 m from their hibernacula (Blouin-Demers and Weatherhead 2002). The mean home range size for adult black ratsnakes is 18.5 ha (Blouin-Demers and Weatherhead 2002).

Dispersal is most likely to occur before sexual maturity (Greenwood 1980, Johnson and Gaines 1990). Movement data can be used to test this assumption for black ratsnakes. Adult black ratsnakes show a strong fidelity to home range and over-wintering hibernacula (Prior et al. 2001, Weatherhead and Hoysak 1989, Blouin-Demers and Weatherhead 2002). If juvenile black ratsnakes are in a dispersal stage, I predicted that they should move more often, over longer distances, and travel further from the hibernacula than adults. They should show less overlap in home ranges over consecutive years than adults and have larger home ranges than those of adults. I also predicted that juveniles should be less faithful to their over-wintering locations.

Body size is positively correlated with survivorship in black ratsnakes (Weatherhead et al 2002). Since smaller individuals are more vulnerable and susceptible to a greater breadth of predators (Werner and Gilliam 1984), decreased survivorship may indicate increased predation risk. If smaller black ratsnakes experience a higher predation rate than adults, then I predicted that they should be visible less often than adults when located using radio-telemetry.

Materials and Methods

Blouin-Demers and Weatherhead provided movement data that were collected from 1996-2000 (Blouin-Demers and Weatherhead 2002) and 2001-2002 (Blouin-Demers and Weatherhead unpublished) on 59 individuals. I collected additional movement data in 2003-2004 on 17 individuals. All work was done in the vicinity of the Queen's University Biological Station (QUBS), approximately 150 km south of Ottawa, Ontario. The landscape and vegetation of the study area have been described elsewhere (Blouin-Demers and Weatherhead, 2001).

Snakes were captured in funnel traps at fenced communal hibernacula during spring emergence, or opportunistically during the active season. Many juvenile black ratsnakes do not attend communal hibernacula (Prior et al.2001). I used a sample of juveniles that hibernate individually as well as individuals that hibernate communally to ensure that any ontogenetic differences are not confounded by the over-wintering strategy of the individual.

In the laboratory, snakes were measured, weighed, and sexed. Any previously unknown snake was injected with a subcutaneous passive integrated transponder tag (Anithech Identification Systems Inc., Markham, Ontario).

Individuals were selected for transmitter implantation based on size and sex. I used a subset of 42 sexually mature individuals (greater than 105 cm in snout to vent length) from the study of Blouin-Demers and Weatherhead (2002) that were implanted with radio-transmitters (Model SI-2T, Holohil Systems Inc, Carp, Ontario, 8.6g, 20 months battery life at 20°C). Only adult males (n = 16) and adult non-gravid females (n = 26) were used in the comparison with juveniles to ensure that results would reflect differences due to size and age, not to reproductive status. Data on 34 juveniles (44.3 cm to 102.8 cm and 140 to 250 g) from Blouin-Demers and

Weatherhead (unpublished) and my study were collected using a smaller radio-transmitter (Model SB-2T, Holohil Systems Inc, Carp, Ontario, 5.5 g, 12 months battery life at 20°C) The transmitter represented at most 4% of the mass of the individual. The maximum size was to ensure that the individuals were juveniles and not adults; maturity occurs around 105 cm snout-vent length and 300 g in this population (Blouin-Demers et al. 2002). The size that was used in this study to mark the age of maturity was originally estimated based on field observations (Blouin-Demers et al. 2002). Recently, however, genetic work has shown that some individuals were fathering young as small as 88.5 cm snout-to-vent length (Blouin-Demers et al. 2005). Thus, I used SVL as a predictor variable in my analyses instead of juvenile and adult. The surgical implantations of the radio-transmitters were performed using a modification of the procedure described by Reinert and Cundall (1982), see Weatherhead and Blouin-Demers (2004) for details. Details on the anaesthesia and surgical procedure are described in Blouin-Demers et al. (2000). The snakes were kept overnight in the laboratory and then released at their point of capture.

After release, the snakes were located on average every 2-3 days from spring emergence, or from time of first capture, until they entered their over-wintering site in late September to early October. They were located using a telemetry receiver (TRX-2000s, Wildlife Materials Inc, Carbondale, Illinois) and a directional three-element antenna (F173-3FB, Wildlife Materials Inc., Carbondale Illinois). Upon locating an individual, I recorded its location, position, and behaviour (no visual, basking / resting, or travelling,). Their daily positions were flagged and recorded using a GPS76 unit (Garmin International Inc., Olathe, Kansas) in the Universal Transverse Mercator (datum NAD83) co-ordinates system.

From 1996-2004, 76 black ratsnakes (39 non-reproductive females, 37 males) were relocated a total of 3316 times. Individuals were followed for periods ranging from 6 to 173 days (mean = 43.6 ± 3.27 days).

I calculated movement statistics for 76 individual snakes (39 females, 37 males) for a total of 3316 locations. I calculated the effect of SVL on the mean distance an individual was from its hibernaculum during the active season, the total distance an individual travelled during the active season, the mean distance travelled between relocations, the mean distance travelled between locations when relocations were >2m apart, the behaviour when located (not visible, basking/resting, travelling), and on the frequency the individual travelled distances within the intervals of 0-10, 11-100, and 101-1000m. For each of these calculations, data were first averaged across individuals.

Home range estimates were calculated using 100 and 95% minimum convex polygons (MCP). The 100% MCP is the area of a convex polygon that incorporates all points where an individual has been located. The 95% MCP uses 95% of the points that are closest to the harmonic mean centre of the range. This method excludes any outliers, and possibly atypical locations, that unduly enlarge the home range size. I excluded the commute between the individual's hibernaculum and its home range. Although black ratsnakes are terrestrial (Blouin-Demers and Weatherhead, 2001), they cross bodies of water readily and, therefore, open water was sometimes present in MCP's. I removed water areas from the area of each MCP so that each MCP represents the dry land area only. I only calculated home ranges for individuals in a given year that were tracked for at least June, July, and August which is when ratsnakes are most active in Ontario. Based on this criterion, I calculated home ranges for 63 individuals (38 females, 25 males) for a total of 83 snake years (47 female years, 36 male years). The area of the

100 and 95% MCP home ranges and the distance between their hibernaculum and the nearest point of its 100 and 95% MCP were calculated for each individual.

I also calculated the percentage fidelity to hibernacula based on all individuals followed during at least 2 winters (n = 43) 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 (n = 19).

Statistical Analyses

Analyses were conducted using Splus version 6.1 for Windows (Insightful Corp., 1988, 2002), Systat version 11 (Systat Software Inc., 2004), JMP version 3.2 (SAS Institute Inc. 1997), and ArcView Geographical Information System version 3.0 (Environmental Systems Research Institute 1996) equipped with the Animal Movement Extension version 1.1 (Hodge and Eichenlaub 1997). I inspected box plots and used Kolmogorov-Smirnov tests to determine if the assumptions of normality and homogeneity of variance were upheld. Transformations were performed on some variables to meet these assumptions. Significance of statistical tests was accepted at alpha = 0.05. All means are reported $\pm$ 1SE.

Results

I used an ANCOVA to examine the relationship between the total distance travelled by an individual over the course of the active season and SVL, while controlling for sex. There was no significant interaction between SVL and sex (R^2 = <0.001, $F_{1, 94}$ = 0.0726, p =0.788), nor was there a significant relationship with sex (R^2 =0.015, $F_{1, 94}$ = 1.543, p = 0.217). A significant relationship with SVL (R^2 =0.093, $F_{1, 94}$ = 9.600, p = 0.003) showed that larger snakes travelled further over the course of the active season (Fig. 2-1).

I used an ANCOVA to look at how SVL influences the mean distance an individual travels between relocations (log transformed) while controlling for sex. I found no significant interaction between SVL and sex (R^2 = <0.001, $F_{1,94}$ = 0.067, p = 0.797). There was no significant relationship with SVL (R^2 = 0.014, $F_{1,94}$ = 1.319, p = 0.254) or sex (R^2 = 0.001, $F_{1,94}$ = 0.130, p = 0.719) and the mean distance travelled. Individuals are often repeatedly located in the same location. Thus, I also considered only instances where the snakes moved >2m (log transformed). Again, this analysis showed no interaction between SVL and sex (R^2 = 0.004, $F_{1,94}$ = 0.373, p = 0.543), and no significant relationship with SVL (R^2 = 0.005, $F_{1,94}$ = 0.430, p = 0.514) or sex (R^2 = 0.015, $F_{1,94}$ = 1.364, p = 0.246).

I divided the distance travelled between locations into three intervals 0-10 m, 11-100 m, and 101-1000 m and found a significant relationship with SVL (Wald's χ^2_2 = 22.024, p <0.001) and sex (Wald's χ^2_2 = 27.285, p <0.001). Figure 2-2 shows that juvenile black ratsnakes more often move short distances (0-10m), and move long distances (11-100m, 101-1000m) less often than adults.

To determine if smaller snakes move more often, I used an ANCOVA to examine the relationship between SVL and the percentage of times that a snake had moved when relocated, while controlling for sex. No significant interaction was found ($R^2 = <0.001$, $F_{1,94} = 0.020$, $p = 0.888$). A significant relationship with sex ($R^2 = 0.203$, $F_{1,94} = 24.287$, $p = <0.001$) showed that males move significantly more often than females (64.3 % and 53.1 % of time, respectively). I also found that smaller snakes appear to move more often than larger snakes, but results were not significant ($R^2 = 0.025$, $F_{1,94} = 2.985$, $p = 0.087$).

I used an ANCOVA to determine if the mean distance an individual travelled away from its hibernaculum during the active season was related to SVL and sex. No significant interaction was found between SVL and sex ($R^2 = 0.011$, $F_{1,86} = 0.919$, $p = 0.341$). I found no significant relationship with SVL ($R^2 = 0.015$, $F_{1,86} = 1.257$, $p = 0.265$) or sex ($R^2 = 0.012$, $F_{1,86} = 1.008$, $p = 0.318$).

Home range size varied greatly across individuals. Averaged across all individuals, the mean 100% MCP home range was 14.34 ± 1.92 ha and the mean 95% MCP home range was 12.18 ± 1.67 ha. I used ANCOVA to determine if there was a relationship between SVL or sex and the size of an individual's 100 and 95% MCP home range. I found a significant interaction between the response variables (100% MCP: $R^2 = 0.044$, $F_{1,80} = 6.00$, $p = 0.017$, 95% MCP: $R^2 = 0.036$, $F_{1,80} = 4.69$, $p = 0.033$), so I ran separate linear regressions for each sex and found that both home range estimates (log transformed) increased as SVL increased (MCP 100%: males $R^2 = 0.429$, $F_{1,33} = 24.79$, $p < 0.001$, females $R^2 = 0.392$, $F_{1,44} = 28.35$, $p < 0.001$; MCP 95%: males $R^2 = 0.417$, $F_{1,33} = 23.61$, $p < 0.001$, females $R^2 = 0.328$, $F_{1,44} = 21.48$, $p < 0.001$), but home range size increased more rapidly with SVL in males than in females (Fig. 2-3).

The mean distance between the closest point of the 100 and 95% home ranges and the hibernaculum (Dhib) was 328.38 ± 53.0 m and $339.29 + 53.1$ m respectively. I used ANCOVA to test if the distance (log transformed) to the 100 and 95% home ranges varied with SVL and sex. I found a significant interaction between SVL and sex (MCP 100%: $R^2 = 0.077$, $F_{1,79} = 6.485$, p = 0.0129, MCP 95%: $R^2 = 0.077$, $F_{1,79} = 6.484$, p = 0.0129), so I ran separate linear regression for each sex and found that, in females, Dhib increased as SVL increased (MCP 100%: $R^2 = 0.167$, $F_{1,44} = 8.596$, p = 0.0054; MCP 95%: $R^2 = 0.00181$, $F_{1,44} = 0.060$, p = 0.809). However, there was no significant relationship found with males (MCP 100%: $R^2 = 0.00181$, $F_{1,34} = 0.060$, p = 0.809, MCP 95%: $R^2 = 0.00181$, $F_{1,43} = 0.060$, p = 0.809) (Fig. 2-4).

I calculated the percentage overlap of 100% MCP home ranges over consecutive years. I used ANCOVA to examine the relationship between the percentage overlap and SVL and sex. I found no significant interaction between the response variables ($R^2 = 0.016$, $F_{1,20} = 0.318$, p = 0.500). I found a significant relationship between SVL and percentage overlap of home range ($R^2 = 0.300$, $F_{1,20} = 5.965$, p = 0.0296) that showed that the larger snakes are more faithful to their home range. I found no difference in home range fidelity between the sexes ($R^2 = 0.037$, $F_{1,20} = 0.717$, p = 0.413).

Using a paired t-test, I compared 100% MCP home range size estimates (log transformed) between years for 12 snakes where home range estimates were available for multiple years. The test showed a significant difference between years (t = -4.924., df = 11, p = 0.0045). On average, the home range estimate from the larger year was 42% larger than the smaller year's home range estimate. This difference, however, is not as great as the difference in home range estimates between individuals. Using the predictive equations of the regressions of home range size on SVL, I examined the difference between individuals and found that the

largest snake in the study has a home range estimate that is 97% larger than the smallest snake in the study. I can, therefore, still be confident that the differences found are more due to difference between individuals.

I calculated the percentage fidelity to hibernacula for radio-tracked juveniles and adults and found that adults are significantly more faithful to their over-wintering sites (Wald's $\chi^2{}_{1,43}$ = 4.21, p = 0.0401, R^2 = 0.178).

I used logistic regression to examine the relationship between SVL, controlling for sex, and the behaviour of the snake (not visible, basking/resting, travelling), identified as it was located using radio-telemetry. I found a significant interaction between sex and SVL (F_2 = 6.15, p = 0.046), so I examined each sex separately. There was a significant difference for both males ($\chi^2{}_2$ = 49.66, p < 0.001) and females ($\chi^2{}_2$ = 13.814, p = 0.001). For both sexes, as SVL increases, the snakes are more likely to be seen when located. Males are seen basking and/or resting more often, and are seen travelling less often as they increase in SVL. As SVL increases, females bask and/or rest more often and are seen travelling more often.

Discussion

My results indicate a clear ontogenetic shift in the movement patterns and spatial ecology of black ratsnakes, provide some evidence that juvenile male black ratsnakes may be in a dispersal stage, and provide further evidence for a higher predation risk for smaller individuals. These findings have important conservation implications for how we manage species at risk.

Larger black ratsnakes move longer total distances over the active season, move longer distances between relocations, and they may move less often than smaller individuals. Larger

black ratsnakes have bigger home ranges, are more faithful to their home range, and are more faithful to their over-wintering sites than smaller snakes.

My results show that juvenile black ratsnakes, and especially juvenile males, exhibit some behaviour that may indicate that they are in a dispersal stage. As predicted, smaller snakes may move more often than larger snakes, although results were not significant. Results from an examination of the frequency of movement between the four status groups (juvenile male, juvenile female, non-gravid female, and adult male), however, show that juvenile males move significantly more often than juvenile females and adult non-gravid females. They do not, however, move significantly more often than adult males, but the pattern of movement between the two groups is very different.

Adult males have large increases in frequency of movements and distances moved during the mating season to increase their reproductive success by increasing the chance of encountering females (Blouin-Demers and Weatherhead 2002). This contrasts with the movement pattern of juveniles that travel consistently and move more often, over small daily distances. Results in Figure 2-5A show a small increase in the distance travelled per day by juvenile males during mating season. This increase is likely due to the influence of males that are beginning to reproduce at a young age. For this study, I classified individuals that were below 105 cm snout-to-vent length (SVL) as juveniles, which corresponded with an estimation of size of maturity in black ratsnakes by Blouin-Demers and Weatherhead (2002). This estimation, however, was based only on observed matings and, since then, Blouin-Demers et al (2005) have shown using genetic parentage analyses that some males as small as 88.5 cm SVL were fathering young, which could explain the movements of juvenile males during the mating season.

I predicted that smaller snakes would move further distances between relocations than larger snakes, but results show no relationship with the size or the sex of the snake. Although not significant, juvenile snakes tend to move more often over short distances (0-10m) than adults.

I also predicted that smaller snakes would travel further distances away from their hibernacula than larger snakes. Results show, however, that males of all sizes travel, on average, equal distances from their hibernacula and that larger non-gravid adult females actually travel further than juvenile females. Again, for males, this result may be due to differences in the pattern of movement between smaller and larger snakes, as maximum movements by juvenile males are higher than for adult males.

Also contrary to my predictions, smaller snakes have smaller home ranges than larger individuals. For males, this result may be explained by the movement patterns of juvenile male black ratsnakes. Juvenile males travel in a seemingly continuous, directional movement away from the hibernacula during the first half of the active season, and return via a similar behaviour during the remainder of the season (Figure 2-5B). In comparison, adult males and non-gravid adult females both travel more quickly and reach their near maximum distance away from the hibernacula much earlier in the season. They then remain there well after juvenile males have begun their return, and make their return journeys to the hibernacula later in the season.

These differences in movement patterns result in juvenile males having differently shaped home ranges than adult males. Since juvenile males travel at least as far from the hibernacula as adult males and non-gravid females, yet still occupy smaller home ranges, the shape of their home range is necessarily elongated in a direction away from the hibernacula.

Thus, the result that home range size increases with snake size does not rule out juvenile male dispersal.

Unlike juvenile males, juvenile females show a movement pattern similar to those of adult males and non-gravid females, yet they do not travel as far from the hibernacula. It is, therefore, not surprising that they have smaller home ranges than the adult snakes.

As I predicted, radio-tracked juveniles are less faithful to over-wintering sites than adults, returning only 71% of the time to the previous year's hibernacula. This contrasts strongly with 97% hibernacula fidelity in radio-tracked adults. Home range fidelity over consecutive years is also significantly lower for smaller individuals.

Juvenile female black ratsnakes do not exhibit the exploratory patterns or dispersal behaviour in their movements as juvenile males. It is only as they increase in size that they travel further from their hibernacula or are seen travelling more often. It is difficult, however, to completely rule out juvenile female dispersal since sample sizes of individuals radio-tracked over consecutive years were too small to statistically examine the home range and hibernacula fidelity differences between the sexes.

Dispersal behaviour is often sex-biased, where one sex disperses more frequently, sooner, or to a greater extent than the other sex (Lowe 2000). This bias has often been explained as inbreeding avoidance, but it has also been related to competition for mates (Williams et al 2005). Greenwood (1980) suggested that polygyny and male competition for access to mates is often associated with male dispersal, which allows for greater access to females. Male-biased sexual size dimorphism in black ratsnakes has been related to males actively competing for access to females (Shine 1978, Blouin-Demers et al. 2002, Blouin-Demers and Weatherhead 2002,). This ultimately results in an increased reproductive success for larger males (Blouin-Demers et al.

2005). The mating system of black ratsnakes, including male competition, corresponds with Greenwood's (1980) prediction for, and supports my findings of potential male-biased dispersal in black ratsnakes.

A positive correlation between survivorship and snake size has been documented for black ratsnakes (Weatherhead et al 2002). The ontogenetic shift observed in the movement data also supports the prediction that higher predation risk for juveniles contributes to this correlation. Overall visibility of the snake and noted basking and resting behaviour located using radio-telemetry increases, as predicted, with snake size. In addition, when juveniles were located, they were often high in the tree canopy. This behaviour suggests predator avoidance as it decreased with an increase in snake size.

An alternative hypothesis, as discussed in Chapter 1, is that juveniles are visible less often, and are seen basking or resting less often because smaller snakes need to be exposed less often to high temperatures to achieve the same thermoregulatory benefits as larger individuals (Stevenson 1985, Carrascal et al 1992).

The data used in this study were collected during two separate study periods. In order to ensure that the effects observed along SVL were not due to a temporal influence, I compared the juveniles sampled during the first study period (1996-2000) versus those sampled during the 2003-2004 field seasons. No significant difference was found between the data sets.

Conservation Implications

This study has several conservation considerations for the black ratsnake and, more generally, for how we manage species at risk.

The principal factor responsible for the decline of black ratsnakes in Canada is habitat loss and fragmentation (Prior and Weatherhead 1998). Blouin-Demers and Weatherhead (2002) state that the genetic integrity of black ratsnakes is susceptible to landscape fragmentation because of the high gene flow present between hibernacula. They further state that sufficient habitat buffers need to be maintained around these areas to allow for members of different hibernacula to come into contact during the mating season. My results suggest that juvenile dispersal may play a significant role in gene flow. Adequate protection for the genetic integrity of the populations requires, therefore, sufficient habitat that will not only allow for inter-hibernacula mating, but for juvenile dispersal. Since juveniles only rarely attend communal hibernacula and often switch between hibernacula, protected habitat needs to include more than a radius around communal hibernacula because this radius may not encompass the habitat used by juveniles.

Understanding neonatal dispersal will help to clarify the means of dispersal in black ratsnakes. A current long-term neonate mark and recapture study is underway. To date over 1800 neonates have hatched in the lab and have been marked with a passive integrated transponder tag before being returned to the location where the eggs were collected (Blouin-Demers and Weatherhead unpublished data). The eventual appearance of these individuals at monitored communal hibernacula as juveniles or adults will elucidate much about the spatial use and the contribution of dispersal to the genetic diversity of black ratsnakes.

This study reinforces the importance of understanding the ecology of species of conservation concern at all life stages. Ontogenetic shifts in movement patterns and spatial ecology should be considered in management decisions.

Table 2-1. Summary statistics for the 100 and 95% minimum convex polygon (MCP) home ranges of juvenile and adult black rat snakes radio-tracked between 1996 to 2004 in eastern Ontario.

| Home-range variable	Adult Males (> 105cm SVL)			Adult Non-gravid Females (>105cm SVL)			Juvenile Males (< 105cm SVL)			Juvenile Females (< 105cm SVL)		
	Mean ±1SE	Max.	Min.	Mean ± 1SE	Max.	Min.	Mean ± 1SE	Max.	Min.	Mean ± 1SE	Max.	Min.
No. of days tracked	145.7 ± 7.44	206	10	135.78 ± 3.8	181	87	119.6 ± 8.8	227	58	150.9 ± 13.6	268	73
No. of times located	58.53 ± 4.0	94	38	48.91 ± 1.87	74	26	26.5 ± 3.4	58	7	30 ± 3.9	58	10
No. of unique locations	27.5	50	18	21.47 ± 1.1	39	10	16.6 ± 1.9	34	5	14.5 ± 2.2	37	4
Area of 100% MCP (ha)	31.78 ± 5.6	72.2	4.11	12.33 ± 2.43	60.4	1.21	6.59 ± 1.2	21.9	1.15	7.71 ± 3.5	49.7	0.065
Area of 95% MCP (ha)	26.57 ± 4.7	58.7	4.11	9.94 ± 2.21	60.4	0.83	6.33 ± 1.2	21.9	1.15	7.37 ± 3.5	49.7	0.065
Distance from hibernaculum to 100% MCP (m)	272.2 ± 55.3	748	0	369.3 ± 122.8	3810	13.0	397.9 ± 75.5	1170	0	216.7 ± 65.2	730	0
Distance from hibernaculum to 95% MCP (m)	272.2 ± 55.3	748	0	392.6 ± 122.8	3810	13	397.4 ± 75.6	1170	0	217.0 ± 65.2	730	0
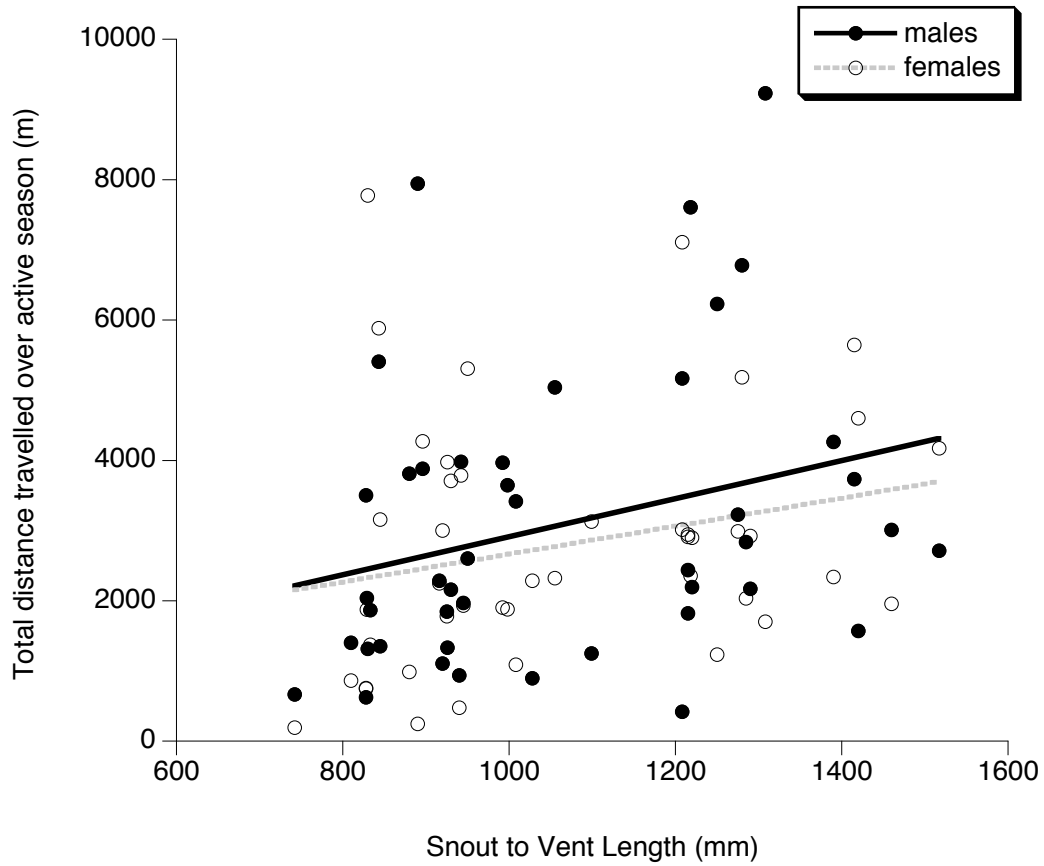
Fig. 2-1. Total distance travelled (m) during the active season months May to September versus snout-to-vent length (mm) by black ratsnakes in eastern Ontario. Snakes were located using radio-telemetry between 1996-2004.
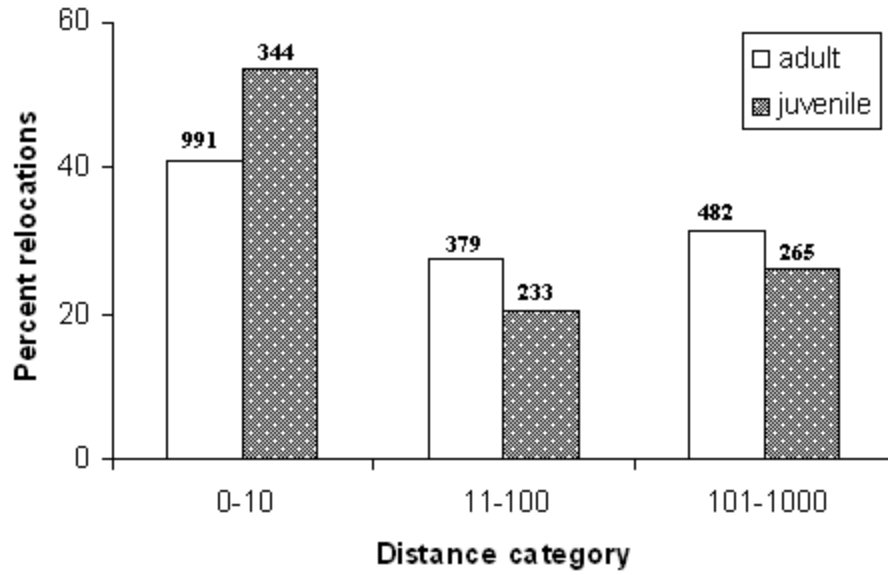
Fig. 2-2. Distance categories travelled between relocations during the active season by juveniles and adult black ratsnakes in eastern Ontario. Snakes were located using radio-telemetry between 1996-2004. Values above bars equal number of snake locations.
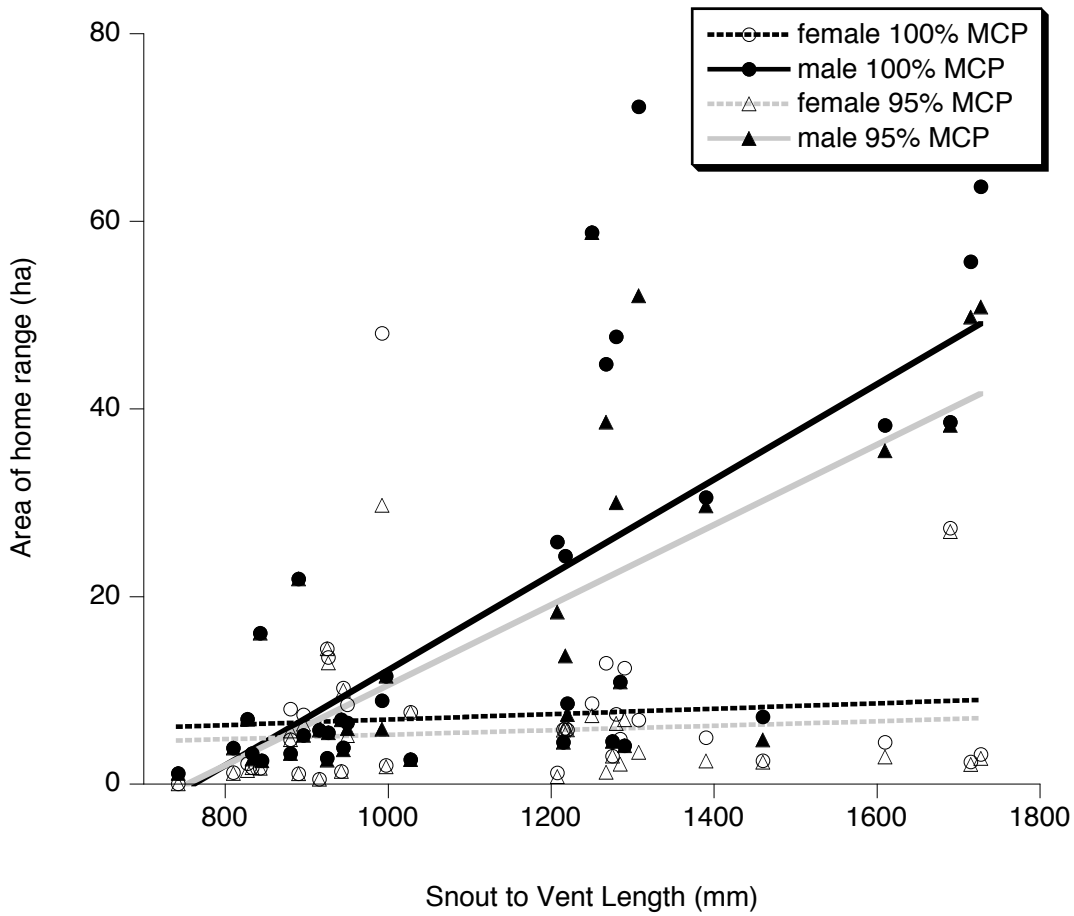
Fig. 2-3. 100% MCP and 95% MCP home range size (ha) versus snout-to-vent length (mm) for male and female black ratsnakes in eastern Ontario. Snakes were located using radio-telemetry between 1996-2004.
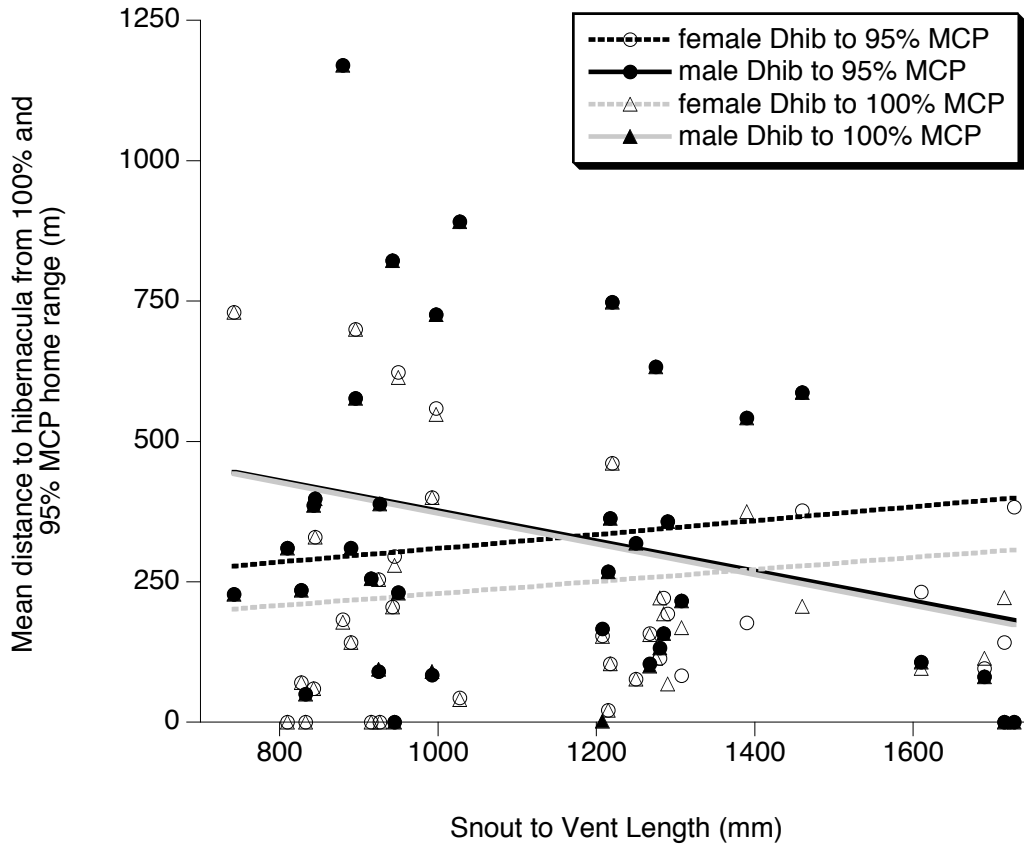
Fig. 2-4. Mean distance to 100% MCP and 95% MCP home range from hibernacula (m) versus snout-to-vent length male and female black ratsnakes radio-tracked in eastern Ontario between 1996-2004.
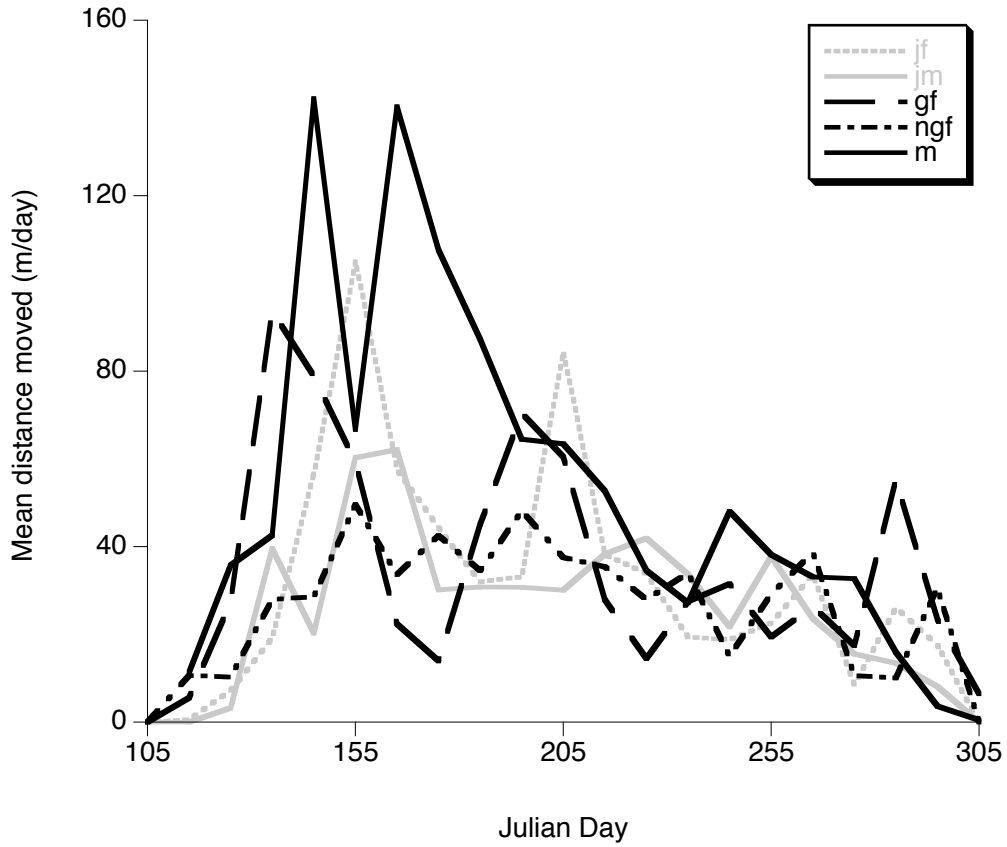
Fig. 2-5. Mean distance moved per day at 10-day intervals for juvenile female (jf), juvenile male (jm), adult gravid female (gf), adult non-gravid female (ngf), and adult male (m) black ratsnakes radio-tracked between 1996-2004.
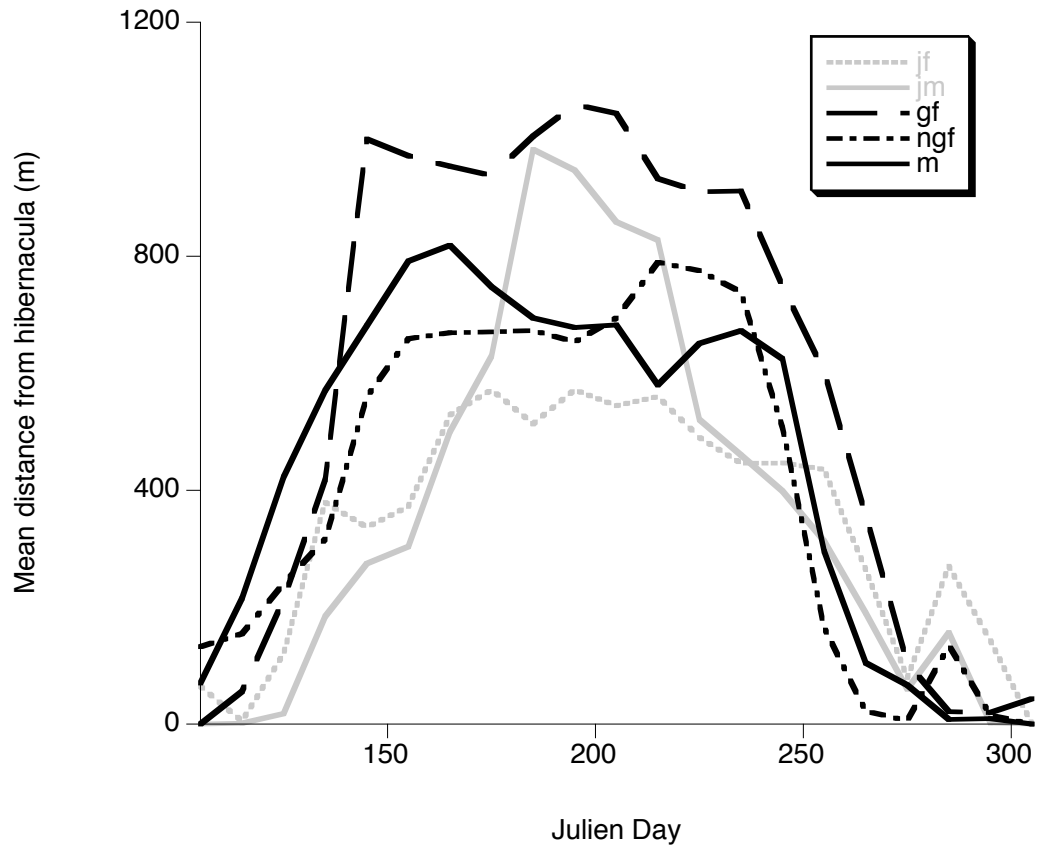
Fig. 2-6. Mean distance from an individual's hibernaculum at 10-day intervals for juvenile female (jf), juvenile male (jm), adult gravid female (gf), adult non-gravid female (ngf), and adult male black ratsnakes radio-tracked between 1996-2004.

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