

# Comparative demography of black rat snakes (*Elaphe obsoleta*) in Ontario and Maryland

Gabriel Blouin-Demers,<sup>1\*</sup> Kent A. Prior,<sup>1,2</sup> and Patrick J. Weatherhead<sup>1,3</sup>

<sup>1</sup> Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON, K1S 5B6, Canada

<sup>2</sup> Present address: Endangered Species Division, Canadian Wildlife Service, Hull, QC, K1A 0H3, Canada

<sup>3</sup> Present address: Department of Natural Resources and Environmental Sciences, University of Illinois, 1102 South Goodwin Avenue, Urbana, IL 61801, U.S.A.

(Accepted 18 January 2001)

## Abstract

This study investigated how demographic characteristics of black rat snakes *Elaphe obsoleta* are affected by the length of the active season, and also used the resulting demographic data to determine the proximate factors responsible for male-biased sexual size dimorphism (SSD) in the species. Demographic data collected from 1981 to 1998 in Ontario (ON; 583 males and 588 females) and from 1942 to 1976 in Maryland (MD; 180 males and 150 females) were used to develop growth models with the von Bertalanffy growth equation. Instantaneous growth rates declined significantly with increasing snout–vent length (SVL) in males and females of each population. The growth models predicted age using SVL satisfactorily, but the accuracy of the model decreased significantly with increasing SVL. As predicted, based on the brevity of their active season (ON  $\approx$  135 days, MD  $\approx$  190 days), rat snakes of both sexes from Ontario had lower and more variable instantaneous growth rates and matured at a more advanced age (ON  $\approx$  9 years, MD  $\approx$  4 years) than snakes from Maryland. However, the rapid growth and early maturation in Maryland snakes occurred at the expense of longevity (maximum: ON  $\approx$  30 years, MD  $\approx$  20 years). Slower growth and later maturation will make rat snakes in Ontario less capable of recovering from population declines. Within each population, males grew faster than females. Survivorship for Ontario snakes did not vary by sex, but increased significantly with increasing SVL. The demographic consequence of sex differences in growth was a male-biased sex ratio among larger snakes. Because SSD is a function of males growing faster than females, SSD in black rat snakes is probably a product of sexual selection, suggesting that large size confers a mating advantage in males.

**Key words:** demography, growth rates, sexual size dimorphism, snakes, longevity, *Elaphe obsoleta*

## INTRODUCTION

Knowledge of the demography of wild populations is fundamental to understanding a species' ecology (Pielou, 1991; Caughley, 1994). In addition to being essential for management of animal populations, demographic analyses can provide insight into basic aspects of population biology, such as the cost of reproduction and causes of sexual size dimorphism (Dunham, Miles & Reznick, 1988; Madsen & Shine, 1993; Brown & Weatherhead, 1999). Studies that compare populations of the same species in different parts of its range can be of particular value in determining how environmental factors shape life-history attributes (Aldridge & Brown,

1995; Gregory & Larsen, 1996). In his review of the determinants of maturation in animals, Bernardo (1993) indicated there is a need for research on the demography of natural populations that exhibit variation in adult size and/or age at maturity.

Snakes are relatively poorly studied demographically, leaving general patterns of snake demography largely undefined (Parker & Plummer, 1987; Dunham *et al.*, 1988; Seigel, 1993). In turn, this makes it difficult to develop conservation programmes for threatened species (Greene & Campbell, 1992; Mittermeier & Carr, 1994). Here we use data from two long-term population studies of black rat snakes *Elaphe obsoleta* to test predictions about demographic attributes both within and between the populations. In addition to addressing basic ecological questions, we also consider the implications of our results for the conservation of black rat snakes.

For species with broad geographic distributions,

\*All correspondence to present address: Gabriel Blouin-Demers, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Botany and Zoology Building, 1735 Neil Ave, Columbus, OH 43210-1293, U.S.A.  
E-mail: blouin-demers.1@osu.edu

climatic variation across their range is likely to produce differences in demographic characteristics among populations. Homeotherms, for example, often tend to display an increase in body size and a decrease in the ratio of body surface area to body weight with increasing latitude that is believed to reduce heat loss (Bergmann, 1847; Scholander, 1955, 1956). Although the same argument cannot be applied to ectotherms because their body temperatures are affected by temperatures available in their environment, ectotherms in colder environments also tend to be bigger (Larsen & Gregory, 1989; Atkinson & Sibly, 1997). Variation in life history with latitude should be pronounced for ectotherms because their growth is temperature dependent (Forsman, 1993; Sinervo & Adolph, 1994). Black rat snakes have a range that extends from eastern Ontario in Canada to Georgia in the southern United States. In this study we compare aspects of black rat snake demography from a population in Maryland near the centre of the species' distribution with that from a population in Ontario at the northern extreme of the species' range.

The principal factor affecting our two study populations differently seems likely to be the length of the active season. In Ontario, rat snakes spend more time hibernating than being active, with an active season of only 5 months (Weatherhead, 1989). Maryland is  $\approx 600$  km south of the Ontario study area, and although Stickel, Stickel & Schmid (1980) suggested that black rat snakes in Maryland also have a 5-month active period, the annual frost-free period is 40% longer in Maryland. Thus, the snakes' active period in Maryland is almost certainly longer than in Ontario. Extended periods of over-winter dormancy exert direct costs on snakes associated with coping with low temperatures and dehydration (Gregory, 1982; Costanzo, 1989; Prior & Shilton, 1996). As well, a contracted active season must increase the difficulty for individual snakes to accomplish the basic physiological and behavioural activities necessary for survival and reproduction (e.g. shedding, foraging, courtship, embryo development). In general, we expected that the constraints imposed by the more severe environmental conditions in Ontario should promote conservatism in growth and sexual maturation (Roff, 1992). In addition, the environmental stochasticity experienced by rat snakes at the northern extreme of their range should lead to more variable growth rates in Ontario.

Our first objective was to compare growth rates, age at maturity and longevity of snakes in Ontario and Maryland. Negative relationships between the length of the active season and sexual maturation have been found in other snake populations (Larsen & Gregory, 1989). Similar negative relationships have been found for growth rates in lizards (Grant & Dunham, 1990) and suggested for snakes (Macartney, Gregory & Charland, 1990; Luiselli, Capula & Shine, 1997), but we are unaware of any study that has statistically compared growth rates of snake populations having different active seasons. We predicted that the brevity of the

active season in Ontario should result in relatively slow growth and delayed sexual maturity. In addition, for a population to be viable, we predicted that the slower growth and maturation of individual snakes should be compensated for by greater longevity in Ontario (Adolph & Porter, 1996).

In meeting our first objective we developed sex-specific growth models for both rat snake populations. Development of sex-specific growth models provided the opportunity to meet an additional objective associated with investigating differences in sexual size dimorphism (SSD) in the two rat snake populations. Among adult rat snakes, males are larger than females (Ernst & Barbour, 1989). Males may be bigger than females because they grow faster, they live longer, the sexes differ in their age or size at sexual maturity, or some combination of all of these factors. Thus, identifying the relative importance of these factors to SSD can be very revealing about the life history of a population (Brown & Weatherhead, 1999). Similarly, comparing how SSD arises between two populations should also reveal life history differences between them. Once one has identified the extent to which SSD is a consequence of differences in growth between males and females, one can ask questions about its ultimate causes. Male-biased SSD in snakes appears to be a sexually selected trait that evolves through competition among males for females (Shine, 1978, 1994). Thus, differences in SSD between populations should reveal something about how competition for mates differs between the populations. Our goal here was to compare the proximate factors that contribute to SSD in the two rat snake populations. Because many different factors potentially contribute to SSD, we did not have specific predictions for how the populations should differ. Rather, our goal was to use our results to develop hypotheses to direct future investigations of SSD in black rat snakes.

Our final objective was to consider the implications of our demographic analyses for the conservation of black rat snakes. In Canada, black rat snakes have been formally designated as 'threatened' (Prior & Weatherhead, 1998). Determining even basic ecological information such as the age of sexual maturity can be informative for conservation efforts, because the longer it takes individuals to mature, the more slowly a population will be able to recover from declines. Knowing how age of sexual maturity varies latitudinally could allow one to extrapolate from well-studied populations to populations that are targets of conservation efforts, but which have not been adequately studied. We consider these and other implications of our results for black rat snake conservation.

## METHODS

### Study area and data collection

Long-term data were collected between 1981 and 1998 at the Queen's University Biological Station (QUBS),

40 km north of Kingston, Ontario, Canada. Two general approaches were used to capture snakes: opportunistic encounters with snakes found in the field (Prior, Blouin-Demers & Weatherhead, in press); captures made at hibernacula during the spring emergence period (Blouin-Demers, Prior & Weatherhead, 2000). From 1984–98, snakes were captured at 2 hibernacula in the immediate vicinity of QUBS (Curtis and Cow Island) at the time of spring emergence and while the snakes were at large during the remainder of the active season. Moreover, from 1996–98, an additional 4 communal hibernacula within 7 km of QUBS (Two-Island Lake, Dowlsey, Old Rideau Trail, and Bedford) were monitored. All the snakes captured were processed in a similar manner. Each snake was measured to the nearest 1 mm by running a flexible measuring tape along its body, sexed by gently probing the cloaca for the presence of hemipenes using a lubricated cloacal probe, and marked for permanent identification by PIT-tagging. All the procedures and projects we undertook had previously been approved by the Carleton University Animal Care Committee.

To conduct our demographic comparison of populations experiencing different climatic conditions, we obtained raw recapture records from a study of black rat snakes conducted by Stickel *et al.* (1980) at the Patuxent Wildlife Research Center (PWRC), Maryland, U.S.A. (L. Garrett, pers. comm.). PWRC was 1075 ha when the data in Maryland were collected from 1942 to 1976. The Maryland data consisted solely of opportunistic captures of black rat snakes incidental to other fieldwork. The individuals captured were weighed, measured and marked by caudal scale excision. Stickel *et al.* (1980) measured snakes by gently stretching them along a metal measuring tape. It is possible that part of the size difference between populations can be attributed to different measuring techniques. In their original paper, Stickel *et al.* (1980) calculated growth rates using the equation of Brody (1945), determined growth rate-length relationships using parabolic regressions, and derived age-length relationships by calculating the mean growth rate at 10 mm intervals based on the previous equations and then calculating the mean time required to grow each of these 10 mm intervals. Because these analytical methods do not follow established procedures such as using the von Bertalanffy growth equation (Andrews, 1982), Stickel *et al.*'s (1980) analyses could not be compared to any other published study. We therefore used currently recommended methods for growth analysis using their original capture data to generate growth models for their population.

### Growth models

We modelled growth rates with the von Bertalanffy growth model (Fabens, 1965) and used the finite difference approximation form of the differential equation because it allows simple parameter estimation (Andrews, 1982). We used recapture records from the

2 study populations to estimate growth rates as a linear function of body length (Van Devender, 1978). Changes in length ( $\Delta\text{SVL}$ ) and growth interval ( $\Delta\text{T}$ ) for recaptured snakes were used to calculate growth rates (GR) as follows:

$$\text{GR} = \Delta\text{SVL}/\Delta\text{T} \quad (1)$$

In equation 1,  $\Delta\text{SVL}$  equals the SVL growth increment measured in mm and  $\Delta\text{T}$  equals the number of days elapsed between captures, less the days spent in hibernation and emergence periods of each year, under the assumption that snakes did not grow during these periods.

We then generated equations to describe growth rates as a function of the average of initial and final SVL (to avoid biasing growth rates if initial or final SVL were used instead of their average; Van Devender, 1978) using simple linear regression:

$$\text{GR} = a + b*\text{SVL} \quad (2)$$

In equation 2,  $a$  and  $b$  represent the intercept and the slope of the regression line, respectively, and the asymptotic body size is predicted as  $-a/b$ . Because we expected that snakes in our study population might grow slowly, and in order to maximize our ability to detect limited growth, we included only snakes for which the inter-capture interval exceeded 1 growing season. Some snakes were recaptured in more than 2 years. To retain independence of observations, we used only the first and second captures for each individual snake in our analyses.

We had no data on individuals of known age (marked neonates followed through time). Therefore, to estimate age at maturity and longevity, and thus apply these values to our interpretation of demography and life history, it was necessary to generate an equation relating age to SVL. We derived models of age in days relative to SVL by integrating the growth rate equations above as follows:

$$\text{Age} (d) = (1/b) \text{LN}(a + b*\text{SVL}) + c \quad (3)$$

In equation 3,  $a$  and  $b$  are defined as above (both derived from the initial growth rate equations), and  $c$  is a constant of integration (Van Devender, 1978). For both males and females this constant was derived by correcting the equation to ensure that neonates were aged 0 days. We estimated the age of males and females at 10 mm increments over the full range of sizes observed. We obtained age in years by dividing age in days by the number of active days per year. We generated confidence intervals for our growth curves using the standard error estimates of  $a$  and  $b$  derived from the initial growth rate equations. An important assumption of this approach is that black rat snake growth can be described by the same model throughout life. Because we had few captures of juvenile rat snakes, we had to assume that our model developed largely from adult snakes could be extrapolated to juveniles.

We assessed the accuracy with which the growth models predicted a snake's age based on its SVL by

using the model-estimated ages to estimate the elapsed time between 2 successive captures of an individual and then comparing this estimate with the known elapsed time. Actual ages were derived using the model to predict the age of an individual at the time of initial capture ( $t_1$ ) and then adding to this value the number of days elapsed (less days in hibernation) to second capture ( $t_2$ ) (i.e. actual age = predicted age at  $t_1$  + number of active days elapsed to  $t_2$ ). Were our models highly accurate we expected to find little difference between the actual age of an individual at  $t_2$  and that predicted by the model based on SVL at  $t_2$ .

### Data analyses

To quantify demographic structure in the study populations it was useful to organize snakes into size-classes as follows: (1) 250–799 mm SVL; (2) 800–1049 mm SVL; (3) 1050–1299 mm SVL; (4) 1300–1800 mm SVL. Our use of these 4 size classes represents a compromise between the number of categories and the need to retain adequate sample sizes for contingency table analyses. Furthermore, this classification allowed a direct comparison with data available from other studies (Prior *et al.*, in press).

We used ANCOVA (with SVL as the covariate) to compare growth rates for rat snakes from Ontario and Maryland and to compare growth rates between males and females within populations. When there were no significant interactions, we eliminated the interaction term and ran the ANCOVA with the main effects only. We used contingency table analysis to compare the size distribution of individuals among the 2 populations and to look for sex-ratio variation in the different size classes. To determine the effect of sex and size on survival, we used logistic regression where survival was treated as a binary response variable (survive = 1 vs presumed dead = 0). Individual snakes were presumed dead if they were not recaptured within 2 years of initial capture. This time allowance provided a conservative estimate of actual survival because only  $\approx 2\%$  of known survivors eluded recapture for more than 2 years following initial capture. We only used captures made at QUBS hibernacula in this analysis because Prior *et al.* (in press) showed that hibernacula captures are not biased by sex or size, whereas opportunistic captures are biased by size. The size bias in opportunistic captures precluded doing this analysis for the Maryland population.

All the data were screened for violations of assumptions (normality and homogeneity of variance) using box plots. Log transformations were applied when necessary. The homogeneity of variance assumption was violated for the growth rate data and transformations could not solve the problem. However, because the largest variances occurred in the population with the most individuals, the effect was to make our  $F$  tests more conservative (Stevens, 1996). The statistical tests were conducted using JMP version 3.0 software package

for the Macintosh (SAS Institute, 1994). We used  $\alpha = 0.05$  as our significance level, although marginally non-significant results are reported when deemed important. All means are reported  $\pm 1$  standard error.

## RESULTS

The field work conducted at QUBS from 1981 to 1998 resulted in 1141 individuals (583 males and 558 females) being recaptured a total of 1818 times. The number of captures for an individual ranged from one to 21 and spanned from less than 1 y to 14 y. Stickel *et al.* (1980) captured 330 individuals (180 males and 150 females) 704 times over the 35 years of their study at PWRC. The number of individual captures ranged from one to 14.

### Activity season

Weatherhead (1989) established that hibernation in our population lasts from early October to mid-April ( $\approx 190$  days). Blouin-Demers *et al.* (2000) showed that the emergence period is from mid-April to mid-May and lasts on average 40 days in Ontario. We used this information to calculate an active season of 135 days per year for Ontario. Stickel *et al.* (1980) regard the principal active period for rat snakes at PWRC as encompassing the 5 months from 1 May to 30 September (i.e. equivalent to Ontario). However, we consider their estimate of the active season very approximate because the locations of the hibernacula were unknown to these authors. Therefore, dates of entry and exit of hibernacula could not be determined. In addition, the authors mention capturing snakes on warm days even in January, which is not possible in Ontario as the ground is permanently snow-covered from mid-December to late March. PWRC is located approximately 600 km south of QUBS resulting in a 58-day difference in the annual frost-free period (mean frost-free period = 200 days for Baltimore, Maryland vs 142 days for Ottawa, Ontario). We used this difference in the annual frost-free period and the known active season for Ontario to estimate the length of the active season in Maryland. We multiplied the length of the activity season in Ontario (135 days) by 200/142 (the ratio of the number of frost-free days at the two locations) to obtain an estimate of 190 active days per year for Maryland that we used in our growth rate calculations. These calculations assume there are no differences in physiological adaptations to temperature between the two populations.

### Neonate size

We obtained data on neonate size by incubating eggs of 16 gravid females collected in the field. The mean size of 83 female hatchlings was  $284.3 \pm 1.6$  mm and the mean size of 77 male hatchlings was  $285.5 \pm 1.6$  mm. These

**Table 1.** Least square mean growth rates (SE), predicted asymptotic sizes, and simple linear regression equations describing the relationship between growth rate ( $y$ ) and snout-vent length ( $x$ ) for males and females in Ontario and Maryland (all  $P < 0.001$ )

Population	Sex	Growth rate (mm/days)	Equation	$R^2$	$F$ ratio	Asymptote (mm)
Ontario	Males	0.344 (0.030)	$y = -0.0007x + 1.12$	0.14	1,144 d.f., 23.95	1614
	Females	0.266 (0.035)	$y = -0.0008x + 1.13$	0.09	1,104 d.f., 10.60	1515
Maryland	Males	0.333 (0.021)	$y = -0.001x + 1.84$	0.71	1,60 d.f., 146.40	1604
	Females	0.168 (0.027)	$y = -0.001x + 1.70$	0.62	1,36 d.f., 59.39	1482

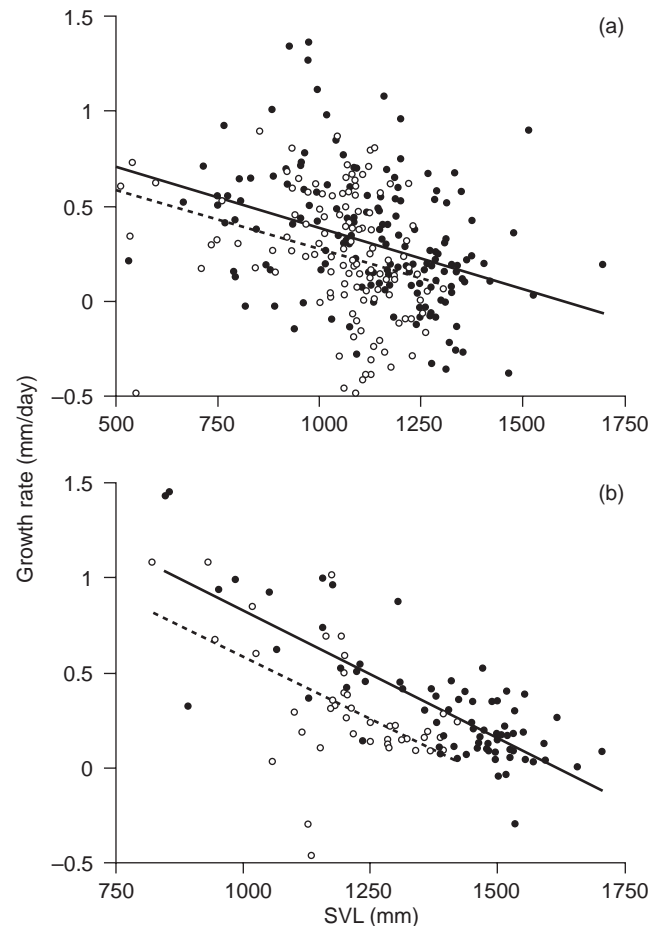
means were not significantly different ( $F_{1,158} = 0.30$ ,  $P = 0.59$ ) and we therefore used an overall mean of 284.9 mm SVL as the mean hatchling size for our population. Stickel *et al.* (1980) reported a mean of  $320 \pm 10.1$  mm and  $330 \pm 5.9$  mm for eight female hatchlings and eight male hatchlings respectively at PWRC, but these data originated from only two clutches and therefore, are unlikely to be representative. For example, within our 16 clutches, the largest mean hatchling size was 332 mm, so chance sampling of a small number of clutches could have produced a much higher estimate of mean hatchling size in our population. Therefore, we assumed that neonate size was the same for both populations.

### Sexual maturity

From 1996 to 1998, we collected 32 gravid females in the field. The smallest gravid female had a SVL of 1050 mm. During the course of an ongoing radio-telemetry study (Blouin-Demers & Weatherhead, in press), we observed 14 mating pairs in the field. The smallest male found in those mating pairs had a SVL of 1060 mm. We therefore estimated the minimum size at maturity for both sexes as 1050 mm SVL in Ontario. Based on 11 egg-laying records, Stickel *et al.* (1980) estimated the size at maturity as 1100 mm for females. The smallest gravid female collected in their study measured 1061 mm. Therefore, the minimum size at maturity seems to be very similar in both populations and we used a value of 1050 mm SVL as our maturity criterion for both sexes in both populations.

### Growth rates

Growth rates declined with increasing SVL for males and females in both Ontario and Maryland (Fig. 1). We expect that the negative growth rates exhibited by some individuals in both populations actually represent instances of measurement error (assuming that they did not shrink between captures). Nevertheless, we elected not to remove these negative errors since we were unable to identify and eliminate the positive errors that should presumably be equally prevalent. Thus, deleting the negative errors alone would have biased our growth rate estimates. To construct our growth rate models, we fitted simple linear regressions to the rela-



**Fig. 1.** (a) Growth rate (mm SVL/day) as a function of snout-vent length (SVL) for Ontario males (filled symbols, solid line) and Ontario females (open symbols, dashed line). (b) Growth rate (mm SVL/day) as a function of SVL for Maryland males (filled symbols, solid line) and Maryland females (open symbols, dashed line).

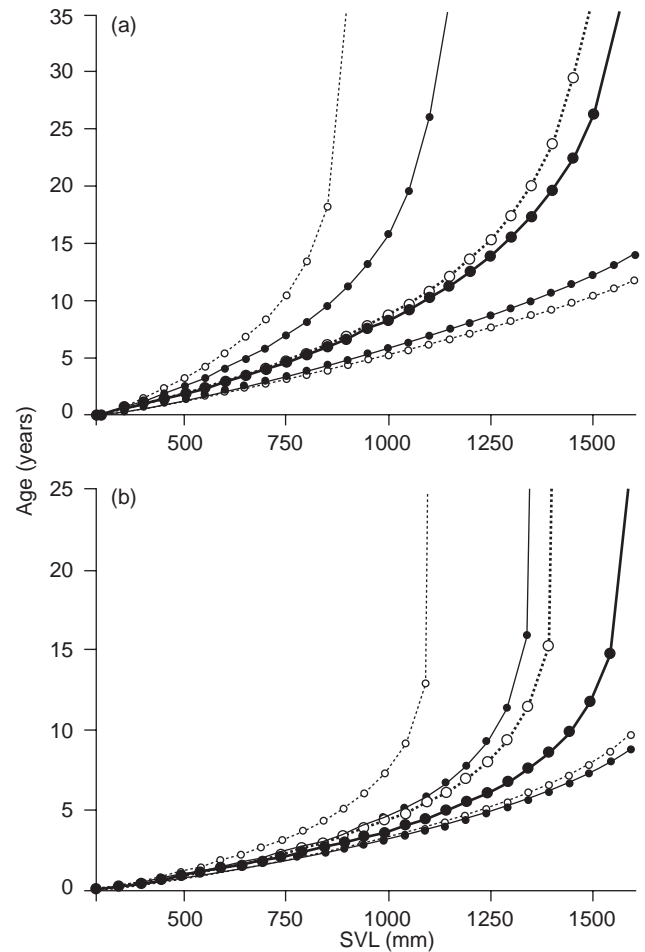
tionships between growth rate and SVL (Table 1). The low  $R^2$  values obtained for the Ontario population reflect the highly variable growth rates observed in this population. We tested whether the variance in growth rates was higher in Ontario by comparing residuals derived from the growth rate versus size regressions for each of the two populations. Levene's tests indicated that variance about the line of best fit was significantly higher in Ontario than in Maryland for both males

( $F_{1,210} = 19.99$ ,  $P < 0.001$ ) and females ( $F_{1,147} = 17.78$ ,  $P < 0.001$ ). Asymptotic sizes were slightly larger in Ontario than in Maryland for both males and females (Table 1).

To determine whether growth rates of rat snakes in Maryland exceeded those from Ontario, we conducted separate ANCOVAs for males and females. The initial ANCOVA for males indicated that the slope of the relationship between growth rate and SVL did not differ significantly between populations ( $F_{1,208} = 0.88$ ,  $P = 0.35$ ). A reduced model showed that, as predicted, males from Maryland grow significantly faster than those from Ontario ( $F_{1,209} = 5.08$ ,  $P = 0.02$ , Fig. 1). For females, the slope of the relationship between growth rate and SVL also did not differ significantly between Maryland and Ontario ( $F_{1,145} = 0.34$ ,  $P = 0.55$ ). A reduced model showed that growth rates for females from Maryland were higher than those from Ontario, but the difference was not significant ( $F_{1,146} = 0.45$ ,  $P = 0.50$ , Fig. 1). However, because both the sample size and sample variance were higher for the Ontario population, our  $F$  tests are conservative (Stevens, 1996). To illustrate the magnitude of the differences in growth rates between the two rat snake populations, one can contrast the amount individuals would grow in a season given their SVL and their number of growing days. These calculations show that on average, individuals in Maryland grow approximately twice as much in a season as individuals in Ontario.

### Growth models

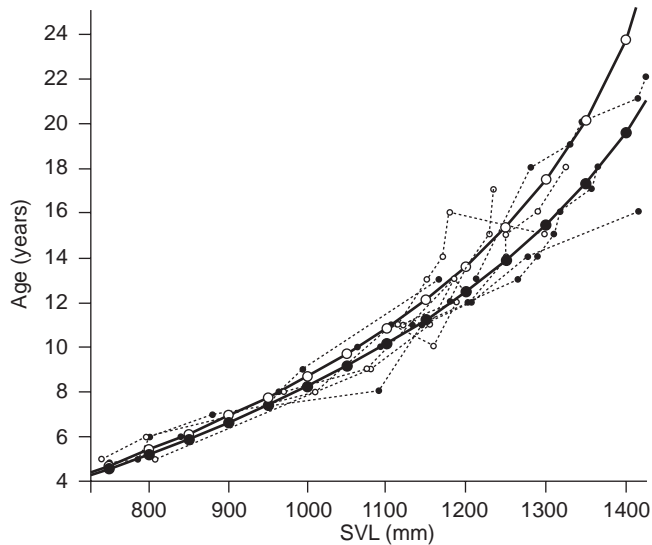
We developed growth models for Ontario snakes separately for each sex (Fig. 2). The resulting models suggest that males in Ontario reach maturity at an average age of 9.1 years, whereas females mature at 9.7 years and that some individuals in this population may be capable of reaching 30+ years. However, differential rates of growth among individuals within each sex mean that there is considerable variation in the age at which snakes in this population reach sexual maturity. To illustrate this, we selected individuals that were captured more than five times and for which the capture history spanned at least 5 years (five males and five females) and superimposed their growth trajectories on the average growth trajectory for their sex. Figure 3 shows that although some individuals exhibit stalled growth for a few years and sudden spurts of growth, there is reasonable agreement between the predicted and observed growth rates. These highly variable growth rates seem likely to be a result of the high environmental stochasticity typical of high latitudes or of high annual variability in foraging success over the relatively short active season. As we predicted, males and females mature much earlier in the Maryland population, 4.0 and 4.8 years respectively, and longevity also seems to be lower, given that we estimate the oldest rat snakes in Maryland to be 20+ years (Fig. 2). However, if we compare the longevity of individuals in the two popu-



**Fig. 2.** (a) Estimated age based on von Bertalanffy growth models as a function of snout–vent length (SVL) for Ontario males (filled symbols, solid line), and females (open symbols, dashed line). Confidence intervals of  $\pm 1$  SE around estimated age are shown as thin lines for each sex. (b) Estimated age based on von Bertalanffy growth models as a function of SVL for Maryland males (filled symbols, solid line), and females (open symbols, dashed lines). Confidence intervals of  $\pm 1$  SE around estimated age are shown as thin lines for each sex.

lations in terms of number of active days, the difference is much less pronounced (Ontario, ON = 135 active days/year \* 30 years = 4050 active days, Maryland, MD = 190 active days/year \* 20 years = 3800 active days).

To examine the accuracy with which our models predict a snake's age based on body size, we contrasted model-estimated ages (predicted ages) and 'actual ages' of individuals at second capture. For males and females in Ontario, we found no difference between the actual and predicted ages (males: mean difference =  $-0.071$  years, paired  $t_{(175)} = -0.55$ ,  $P = 0.59$  and females: mean difference =  $0.016$  years, paired  $t_{(131)} = 0.11$ ,  $P = 0.92$ ). The pattern was the same for males and females in Maryland (males: mean difference =  $-0.25$  years, paired  $t_{(66)} = -1.01$ ,  $P = 0.32$  and females: mean difference =  $-0.32$  years, paired  $t_{(40)} = -1.55$ ,  $P = 0.13$ ). This

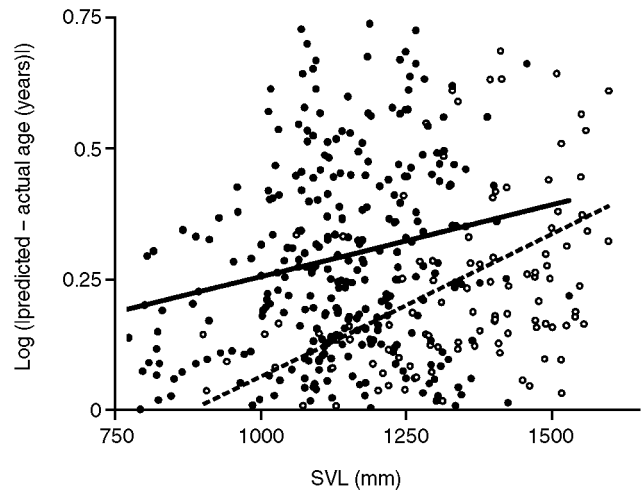


**Fig. 3.** Estimated age based on von Bertalanffy growth models as a function of snout–vent length (SVL) for Ontario males (large filled symbols, solid line) and Ontario females (large open symbols, solid line) with individual growth histories of five individual of each sex superimposed (small symbols, dashed lines).

analysis indicated that there is no bias toward over or under estimating age in our growth models. However, because overestimates and underestimates compensate each other when calculating mean deviations, this analysis does not measure the accuracy of our growth models. Therefore, we also calculated the mean difference between predicted and actual ages at  $t_2$  using absolute values. This analysis showed that actual and predicted ages differed by an average of 1.2 years in Ontario and 1.0 years in Maryland, therefore confirming that our growth models are reasonably accurate. We expected that the accuracy of age determination should decrease for larger snakes because of the wide standard errors of the model for large SVL (Fig. 2). We regressed the absolute values of the difference between predicted and actual ages at  $t_2$  (log transformed to better satisfy the homogeneity of variance assumption) against SVL at  $t_2$ . This analysis showed that growth model accuracy decreased with increasing SVL (Fig. 4) for both Ontario ( $F_{1,305} = 19.64$ ,  $P < 0.001$ ) and Maryland ( $F_{1,108} = 29.56$ ,  $P < 0.001$ ).

### Sexual size dimorphism

To address our second objective and investigate SSD in this species, we compared growth rates between males and females within each population. For Ontario, ANCOVA indicated that the slope of the growth rate versus SVL relationship did not differ between the sexes ( $F_{1,303} = 0.0083$ ,  $P = 0.93$ ). When we considered the reduced model, we found marginally non-significant support for the expectation that males grow faster than females ( $F_{1,304} = 2.88$ ,  $P = 0.09$ , Fig. 1). Similarly, the

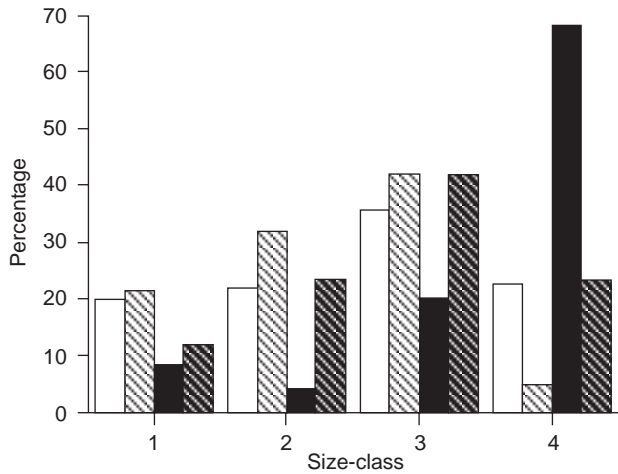


**Fig. 4.** Common logs of the absolute value of the difference between predicted and actual ages as a function of snout–vent length (SVL) at  $t_2$  (see text for details) for Ontario (filled symbols, solid line) and Maryland (open symbols, dashed line) black rat snakes.

slope of the relationship between growth rate and SVL did not differ between the sexes in Maryland ( $F_{1,100} = 0.09$ ,  $P = 0.77$ ). As with the Ontario population, the reduced ANCOVA model demonstrated that males grow faster than females in Maryland, and in this case the difference was significant ( $F_{1,101} = 21.32$ ,  $P < 0.001$ , Fig. 1).

We had sufficient data to test for differences in sex ratios across size-classes within three rat snake hibernacula in Ontario. Our expectation was that males, the faster-growing sex, should predominate in the larger size-classes. Sex ratios did differ significantly among size-classes at all three sites: Curtis ( $n = 136$ ,  $\chi^2_{(3)} = 14.00$ ,  $P = 0.003$ ), Two Island ( $n = 96$ ,  $\chi^2_{(3)} = 9.95$ ,  $P = 0.02$ ), and Dowsley ( $n = 108$ ,  $\chi^2_{(3)} = 11.44$ ,  $P = 0.01$ ), with females being under-represented in the largest size-class (1300–1800 mm SVL). Using the overall population samples (hibernacula and activity season captures pooled for Ontario), sex ratios again differed significantly across size-classes (ON:  $n = 1141$ ,  $\chi^2_{(3)} = 116.33$ ,  $P < 0.001$ ; MD:  $n = 330$ ,  $\chi^2_{(3)} = 56.26$ ,  $P < 0.001$ , Fig. 5). The pattern for both populations was that of proportionately fewer large females. While such unequal sex ratios could arise simply because males grow faster, higher female mortality could also contribute to this disparity.

To assess how survival varies with both sex and body size (SVL), we used logistic regression analysis. The slope of the relationship between survival and SVL did not differ between males and females (Wald  $\chi^2_{(1)} = 1.5136$ ,  $P = 0.22$ ). The reduced logistic regression analysis failed to detect a significant difference in the survival probabilities of males and females (Wald  $\chi^2_{(1)} = 1.1845$ ,  $P = 0.28$ ). However, body size was a significant predictor, with survival increasing with SVL (Wald  $\chi^2_{(1)} = 58.87$ ,  $P < 0.001$ ). Thus, while the sex of an individual *per se* does not influence their survival



**Fig. 5.** Percentage of males (plain) and females (hatched) in each size class (see text for definition of size classes) for Ontario (white background) and Maryland (black background).

probability, because males grow faster than females, and because survival improves with size, males may survive slightly better than females by virtue of their size. Thus, the male-biased sex ratio in the largest size class could be a consequence of both faster growth by males and higher survival of larger snakes.

## DISCUSSION

We found that black rat snakes in Ontario have lower growth rates, mature at a more advanced age but at a similar size, and live longer than rat snakes from Maryland. These results supported our original predictions that a shorter active season should promote conservatism in growth and maturation in Ontario and are in general agreement with those of previous studies indicating that brief and variable active seasons (typical of high latitudes/altitudes) promote relatively slow growth and late sexual maturity in snake populations (Larsen & Gregory, 1989; Brown, 1991; Martin, 1993). The pattern of maturation in the Ontario population (at the same size but older) is one of the five patterns identified by Stearns & Koella (1986) to explain how individuals of a population encountering an unavoidable stress resulting in lower growth rates can maximize their fitness despite the environmental constraints. The greater opportunity to forage and recover reserves spent on reproduction before hibernation allowed by warmer climatic conditions seems sufficient to allow Maryland snakes to grow significantly faster and mature much earlier than Ontario snakes. However, this faster growth and maturation appears to occur at the expense of longevity. These findings corroborate those of other studies that have documented a strong correlation between growth rates of snakes and various environmental and ecological factors (Brown & Parker, 1984; Platt, 1984; Forsman, 1993; Madsen & Shine, 1993).

The influence of environmental conditions on growth rate was further illustrated by population level differences we found between Ontario and Maryland. The highly variable growth rates exhibited by snakes in Ontario suggest that growth rate is influenced more by environmental conditions. Differing energy expenditures (e.g. reproduction) and fluctuation in prey availability may have significant effects on inter-annual growth rates of rat snakes in Ontario. A shorter growing season may mean that chance plays a much greater role in determining growth rates (e.g. number of meals per summer) for snakes in Ontario than it does in Maryland. For example, an early autumn would leave females that have reproduced that year with little time to replenish energy reserves before hibernation. Eggs are laid in mid-July and females weighed a few days after laying have lost more than 20% of their body mass since emergence (Blouin-Demers & Weatherhead, in press). Not only would such a situation preclude any growth that year, it could even jeopardize survival (e.g. Brown & Weatherhead, 1997).

Within each population, males grew faster than females as we had expected based on the male-biased SSD characteristic of the species. Also, males had larger predicted asymptotic sizes than females. Our analyses of survivorship for Ontario snakes showed that the sexes did not differ significantly in survivorship, but that individuals improved their survival prospects with increasing size. However, because males are typically larger than females, it is possible that they have higher survival by virtue of their size. Therefore, SSD in this species is real (as opposed to apparent), because the proximate explanation for SSD is that males grow faster than females. Male-biased SSD in black rat snakes, and observations of male 'combat' in this species (Rigley, 1971; Stickel *et al.*, 1980), suggest that larger males should be more successful in direct competition with other males, and hence should mate with more females and realize higher reproductive success (Shine, 1978, 1994). The sex-specific growth trajectories are responsible for two related demographic attributes. First, differential growth rates result in a disproportionate number of members of the faster growing sex in large size classes, leading to male-biased adult sex ratios. Second, relatively rapid growth by males means that they take less time to reach sexual maturity.

Our results have several implications for the conservation of black rat snakes in Canada. The estimated age of maturity for individuals in Ontario ( $\approx 9$ – $10$  years) is comparable to some populations regarded as noteworthy for exhibiting particularly late maturation. For example, females of temperate-zone populations of timber rattlesnakes delay maturity until they reach 8–10 years (Brown, 1991; Martin, 1993) and female arafura filesnakes do not mature before  $\approx 7$  years (Houston & Shine, 1994). The very late maturation of black rat snakes means that population recovery following a decline would occur extremely slowly. Also, this delayed maturity would make the species especially prone to

declines if anthropogenic factors increased adult mortality. Increasing road densities result in higher mortality rates for black rat snakes. Furthermore, the intentional killing of even a few individual adult snakes by humans each season could have a severe cumulative impact, particularly in isolated populations where the number of reproductive individuals may already be critically low. Finally, the slow growth rates exhibited by rat snakes also mean that even catastrophic reproductive failures, causing the absence of entire year-class cohorts, could easily go unrecognized in populations that are not carefully monitored.

### Acknowledgements

We are grateful to L. Garrett from the Patuxent Wildlife Research Center for providing the recapture records from the study by Stickel, Stickel & Schmid (1980). We thank all the people who helped us catch snakes at the Queen's University Biological Station, particularly G. Brown, K. Kissner, H. McCracken, T. Taylor and C. Verreault, and for funding we thank the Natural Sciences and Engineering Research Council of Canada (research grants to P. J. W. and postgraduate scholarships to G. B.-D.), Parks Canada, the Ontario Graduate Scholarships program (scholarships to K. A. P.), and World Wildlife Fund Canada.

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