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PATTERNS OF VARIATION IN SPRING EMERGENCE BY BLACK RAT SNAKES (*ELAPHE OBSOLETA OBSOLETA*)

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ABSTRACT: Substantial individual variation in timing of emergence from hibernation has been reported among reptiles, although few studies have addressed the causes of that variation. Here we report patterns of spring emergence by black rat snakes (*Elaphe obsoleta obsoleta*) observed at 13 communal hibernacula in eastern Ontario from 1992–1997. Because our study area is at the northern extreme of the species' range, we expected synchronous emergence given the very short active season (about 5 months). Despite these apparent time constraints, however, the emergence period lasted an average of 40 days. Although we found significant variation in timing of emergence among years and among hibernacula, we found no evidence of a simple latitudinal gradient in mean emergence dates. Within hibernacula, significantly more snakes emerged on days with high maximum air temperatures, but maximum air temperature explained only a small amount of the variation among years in emergence dates. Larger individuals emerged earlier than smaller individuals, as predicted if early spring predation risk is higher for smaller snakes. Females tended to emerge slightly earlier than males. Condition was not a significant factor determining timing of emergence in our population. Individuals demonstrated significant repeatability between years in their time of emergence relative to other snakes in the same hibernaculum.

Key words: Hibernation; Communal hibernacula; Spring emergence; Predation-risk hypothesis; Black rat snake; *Elaphe obsoleta*

PROLONGED overwinter hibernation is an important life-history characteristic for many temperate-zone reptiles. In the most northern species of snakes, this annual period of inactivity may last as long as 7 mo,

collectively accounting for more than half the life of an individual (Aleksiuk and Gregory, 1974; Gregory, 1974; Weatherhead, 1989). Thus, hibernation has received substantial attention (e.g., Charland, 1989; Drda, 1968; Hirth, 1966; Owens, 1949). Most notably, several studies have focused on the physiological adaptations associated with hibernation (Aleksiuk, 1970, 1976; Congdon et al., 1979; Costanzo, 1989; Crews et al., 1987; Graham and Graham, 1992; Ultsch, 1989),

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environmental correlates of hibernation periodicity (Crawford, 1991; Grobman, 1990; Macartney et al., 1989; Sexton and Hunt, 1980; Sexton and Marion, 1981), wintering environment and body temperature profiles (Brown et al., 1974; Jacob and Painter, 1980; Taylor and Nol, 1989; Weatherhead, 1989), and simple descriptions of population structure and spring emergence (Parker, 1976; Parker and Brown, 1973). Although substantial individual variation in dates of spring emergence has been reported among reptiles (Costanzo, 1986; Graves and Duvall, 1990; Prestt, 1971; Viitanen, 1967), few studies have addressed the factors that influence these intraspecific patterns of emergence and almost no studies have investigated aspects of among-population variation in emergence behavior across either spatial or temporal scales (but see Viitanen, 1967). From the perspective of evolutionary ecology, identifying the factors that influence spring emergence should allow some insight into why individuals make different trade offs between the apparent risks associated with early emergence (e.g., exposure to lethal environmental conditions) and the potential advantages of a longer active season (e.g., more time available for foraging). From an applied perspective, understanding how key variables influence the timing of spring emergence may enable natural resource agencies to predict seasonal activity patterns more accurately and thus develop more efficient management programs (e.g., schedules for population monitoring). Here we report the results of a 6-yr study of spring emergence patterns of communally hibernating populations of black rat snakes (*Elaphe obsoleta obsoleta*) at the northern extreme of the species' range in eastern Ontario.

We consider variation in emergence time at two levels. First, at the population level, we consider variation in mean emergence times among different hibernacula in the same year, and for the same hibernacula among years. The short active season in Ontario (about 5 mo) severely limits the annual opportunity to accomplish basic physiological maintenance, foraging, growth, and reproductive activities. Thus, we ex-

pected that all individuals in the population should initiate their active season as early as possible every year, resulting in synchronous emergence. We assume that snakes generally should time their emergence to coincide with the availability of appropriate environmental conditions, particularly temperature (Crawford, 1991). If snakes respond directly to changes in temperature within their hibernaculum (Sexton and Hunt, 1980), then hibernaculum-specific factors (e.g., microclimate, topography, internal features of the hibernaculum) should determine when snakes emerge. Thus, we would not expect a simple relationship between latitude and emergence time over the relatively short latitudinal range that we consider here. Also, within hibernacula, emergence times should vary among years, with snakes emerging earlier in warmer springs. Conversely, if snakes emerge on a fixed schedule (Weatherhead, 1989), then we would expect a simple latitudinal pattern of emergence and relatively little variation among years within hibernacula.

We also consider variation in emergence timing among individuals within hibernacula. A species' mating system may have a primary influence on temporal patterns of spring emergence in snakes (Duvall et al., 1993; Gregory, 1974, 1982, 1984). For example, in species that mate immediately upon emergence from hibernation, males should emerge earlier than females to maximize their chances of encountering receptive females. An alternative hypothesis to explain later emergence by females is that more males are infertile early in the season, so by emerging later, females decrease the risk of mating with an infertile male (Olsson and Madsen, 1996). Both hypotheses apply only to species that mate upon emergence from hibernation. By contrast, in species for which courtship and mating occur after dispersal from the hibernacula, males and females are expected to emerge at the same time (Gregory, 1984). We tested the prediction that male and female black rat snakes should not differ in their timing of spring emergence because they mate in late spring following dispersal from hibernacula (Durner and Gates, 1993; Weatherhead and Hoysak, 1989).

Gregory (1984) proposed that smaller individuals should emerge earlier than larger individuals because of their superior thermoregulatory ability. The lower thermal inertia of smaller snakes allows them to increase their body temperature faster than larger individuals (Stevenson, 1985). Thus, small snakes can achieve the preferred body temperature across a broader range of microclimatic conditions than can larger snakes, thus extending their active period. If so, then smaller black rat snakes should emerge earlier than larger individuals. An alternative hypothesis is that larger (i.e., reproductive) individuals should emerge earlier than smaller (i.e., nonreproductive) individuals because they need to prepare their gonads for reproduction. Adults of all temperate zone snakes complete all or part of secondary vitellogenesis or spermatogenesis in the spring (Aldridge, 1979*a,b*). Thus, this hypothesis predicts that sexually mature individuals should emerge first. If eggs are more expensive to produce than sperm, then females might require more time than males to prepare for reproduction. If so, then among sexually mature snakes, females should emerge before males. Also, because females in our population reproduce every second or third year (G. Blouin-Demers, unpublished data), we expected currently reproductive females to emerge earlier than nonreproductive females. Furthermore, if gravid females are under selective pressure to emerge early, yet they reproduce biennially or triennially, then we expected females to exhibit lower year to year repeatability in their timing of emergence relative to males.

Another alternative hypothesis related to the size of individual snakes is that emergence time varies with predation risk. Under the cool climatic conditions prevailing in the spring, snakes may be at a greater risk because their locomotory performance is reduced. Risk of predation should be higher for smaller snakes because they are susceptible to a broader range of predators. Thus, we expected that larger snakes should emerge earlier than smaller snakes, but that controlling for size, males and females should emerge at the same time.

An individual's body condition (e.g., per-

cent fat reserves) has also been proposed as contributing to individual variation in the timing of spring emergence (e.g., Duvall and Graves, 1990). However, it remains uncertain whether individuals in poor condition should emerge earlier or later than those in good condition. It is conceivable that those in poor condition should emerge sooner because they have more urgent energy requirements. By contrast, individuals in relatively poor condition may be less able to cope with marginal climatic conditions prevalent during early spring, obliging them to delay emergence. Here we simply test the prediction that emergence time should vary with individual condition.

Finally, it is also possible that some individuals are predisposed to emerge either relatively early or late in the emergence period, regardless of any particular physical trait. Our final goal was to examine the consistency of individual emergence timing among years, to assess the possibility that some intrinsic individual factor underlies variation in timing of emergence, independent of phenotypic factors.

MATERIALS AND METHODS

Study Sites and Data Collection

We obtained data on spring emergence patterns between 1992 and 1997 from 13 hibernacula in three study regions of the Frontenac Axis: the St. Lawrence region (three hibernacula), the Queen's Station region (eight hibernacula), and the Murphy's Point region (two hibernacula) (Fig. 1, Table 1). Sampled hibernacula fell within a 1 km radius in the St. Lawrence region, a 4-km radius in the Queen's Station region, and a 1.5-km radius in the Murphy's Point region. All hibernacula had been located previously as part of radio-telemetry studies (e.g., Weatherhead and Charland, 1985; Weatherhead and Hoysak, 1989). Habitat features of the study area and of many of the hibernacula that we studied have been described by Prior and Weatherhead (1996).

Because of certain habitat characteristics (e.g., extreme topographic relief) and due to shifts in the primary focus of our field studies, hibernacula sampling methods dif-

TABLE 1.—Total captures of black rat snakes at hibernacula between 1992 and 1997. Not all hibernacula were sampled each year. Sampling protocols differed among some sites and are detailed below.

Region	Hibernacula*	1992	1993	1994	1995	1996	1997
Murphy's Point	Hydroline	30	44	61	—	—	—
	Mine	15	11	16	—	—	—
Queen's Station	Curtis	27	23	31	20	20	19
	Cow Island	12	7	9	—	—	—
	Two Island	—	—	—	—	33	33
	Dowsley	—	—	—	—	48	34
	Beaver	—	—	—	—	6	—
	Old Rideau	—	—	—	—	—	23
	Bedford	—	—	—	—	—	15
	Garter Lake	—	—	—	—	—	20
St. Lawrence	La Rue Mills	13	26	28	—	—	—
	Hill Upper	7	13	4	7	7	4
	Hill Lower	19	21	18	24	26	27
Annual totals		123	145	167	51	140	175

* Hibernacula within the Queen's Station region were always sampled each day and perimeter fences were installed at all sites except Cow Island. In 1992, hibernacula within the St. Lawrence and Murphy's Point regions were sampled every second day and all the sites were checked each day thereafter. La Rue Mills and Hill Upper were equipped with drift fences, Hill Lower and Hydroline were equipped with perimeter fences, and the Mine site was never fenced.

ferred somewhat among sites and through time (see Table 1 for details). In general, we employed two different techniques to sample emerging rat snakes: drift-fences (1.5-m high barriers of plastic sheeting fixed to a wood frame of posts and rails, bottom edge of plastic buried, funnel traps at both ends of fence) established in the vicinity of hibernacula or perimeter-traps (circular drift-fences, as above, that surrounded hibernacula openings). In addition, careful searches of the ground and trees were conducted at all hibernacula.

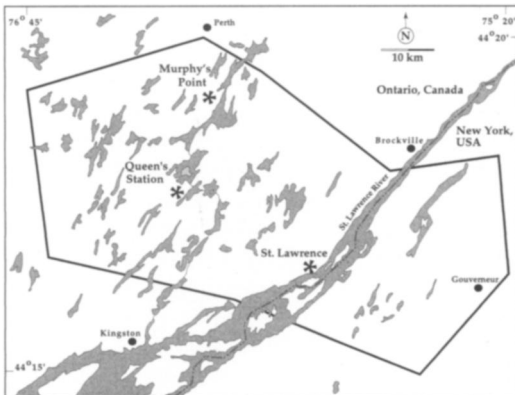


FIG. 1.—Extent of the disjunct Frontenac axis population of black rat snakes. The three study regions were St. Lawrence (three hibernacula), Queen's University Biological Station (eight hibernacula), and Murphy's Point (two hibernacula).

Traps were installed and/or site visits begun prior to the start of emergence each spring (i.e., mid-April) and continued until well after the last snake emerged (i.e., usually 1 June). All snakes trapped or encountered during daily visits to each site were assumed to have emerged from hibernation on the date of capture (recorded as Julian date). Snakes captured at all sites were processed in a similar manner. Upon capture, snakes were sexed by gently probing for the presence of hemipenes, measured for snout-vent length (SVL) to the nearest 1 mm with a metric tape, weighed to the nearest 1 g with a calibrated spring-scale (except at Hill Island after 1994), marked by heat-branding the caudal scutes in a unique numeric pattern or by PIT-tagging (except at Murphy's Point and Hill Island where PIT-tagging was not begun until 1994), and released (usually minutes after, and always within 24 h) at the point of capture. Snakes were handled in accordance with the principles and guidelines of the Canadian Council of Animal Care.

Climatic data for this study were obtained from the Queen's University Biological Station's meteorological station. This station is centrally positioned in the Queen's Station region, within 50 km of all hibernacula that we studied (Fig. 1). While data from this station do not provide infor-

mation on the specific microclimatic conditions prevailing at each hibernacula, they do provide approximate values of conditions throughout the study area generally.

Data Analysis

We used General Linear Models (GLM), Analysis of Covariance (ANCOVA), Analysis of Variance (ANOVA), and multiple linear regression to investigate the significance of different predictor variables on our main response variable: Julian date of emergence. All possible interaction terms were included in our initial models. However, because no interactions were significant, we present only results of the reduced models with interactions excluded. In all cases, we verified that the assumptions for ANOVA were met in our analyses. When required, we used Tukey-Kramer HSD tests for post-hoc comparisons of means with $\alpha = 0.05$ for all analyses. To investigate individual patterns, we conducted analyses separately for each year to avoid the problems associated with pseudoreplication, because some individuals were captured in more than one year. All statistical analyses were conducted using JMP® software for Macintosh (SAS Institute Inc., 1994).

RESULTS

We accumulated data on 551 individual black rat snakes from a total of 801 captures from 1992–1997. Our yearly captures ranged from 51 (1995) to 175 (1997). Contrary to our expectation of synchronous emergence, the emergence season lasted an average of 40 days and started as early as 10 April (1994) and ended as late as 2 June (1997), with the yearly mean emergence dates ranging from 2 May (1993 and 1995) to 9 May (1996 and 1997). Our maximum number of captures per hibernaculum was 61 (Hydroline in 1994) and the minimum was four (Hill Upper in 1994 and 1997). The mean emergence date for individual hibernacula ranged from 28 April (Mine) to 11 May (Dowsley). These summary statistics illustrate the substantial variation that we observed in timing of emergence.

Population Patterns

To investigate variability in mean emergence date among each of the six study years, the three study regions across the Frontenac Axis, and the 13 hibernacula, we used ANOVA with year, region, and hibernaculum (nested within region) as predictor variables and Julian date of emergence as the response variable. This model was significant ($F_{17,790} = 10.27$, $P = 0.00001$) and indicated that year ($F_{5,790} = 9.71$, $P = 0.00001$), region ($F_{2,790} = 9.82$, $P = 0.0001$), and hibernaculum ($F_{10,790} = 8.13$, $P = 0.00001$) all had a significant effect on mean emergence date.

These results required us to standardize emergence dates in order to conduct analyses on pooled data. To assess patterns among years, we had to standardize for hibernacula, and to assess patterns among hibernacula, we had to standardize for years. We generated emergence dates standardized for hibernacula using the residuals from an ANOVA with hibernacula as the predictor variable and emergence date as the response variable. Likewise, we calculated emergence dates standardized for year using the residuals from an ANOVA with year as the predictor variable and emergence date as the response variable.

Employing these standardized data, we performed Tukey-Kramer HSD tests to determine among which years, regions, and hibernacula (nested within region) significant differences in emergence date occurred. HSD tests on yearly mean emergence dates standardized for hibernacula indicated that most years were significantly different from most others. For example, rat snakes emerged significantly earlier in 1995, on average 3.54 days earlier than in other study years. HSD tests on regional mean emergence dates standardized for years indicated that rat snakes in the St. Lawrence region tended to emerge significantly later than those in the other two regions, despite the fact that this region is the most southerly. Differences between the standardized means for each region indicated that emergence occurred on average 1.59 and 2.32 days later in the St. Lawrence region than in the Murphy's Point and

Queen's Station regions, respectively. HSD tests on hibernacula mean emergence dates standardized for year also indicated that most hibernacula differed significantly from each other. For example, snakes occupying the Mine hibernaculum emerged 6.62 days earlier on average than snakes using other sites. The substantial annual and hibernacula variation that we observed and lack of a simple latitudinal gradient in mean emergence dates are consistent with the hypothesis that black rat snakes emerge in response to the microclimatic conditions prevailing at their hibernaculum, and inconsistent with the hypothesis that black rat snakes emerge on a fixed schedule.

We used a GLM to investigate the relationship between annual variation in emergence date and climatic conditions prevailing in each year. We used the Julian date of emergence (weighted for the number of snakes emerging on that day) as the response variable and year, daily maximum radiation (kW/m^2), daily maximum air temperature ($^{\circ}\text{C}$) and daily rainfall (mm) as predictor variables. We included the data for every day of the emergence period of each year in the model. The model was significant ($F_{8,151} = 4.38$, $P = 0.0001$), with only year ($F_{5,151} = 4.11$, $P = 0.002$) and maximum air temperature ($F_{1,151} = 17.07$, $P = 0.0001$) as significant individual effects. This indicates that snakes emerged earlier in warmer years, but also that some annual variation was unexplained by variation in weather. To investigate more closely the relationship between climate and emergence behavior, we used multiple linear regression analysis. We used the number of snakes emerging each day as the response variable and the three climatic variables as predictor variables. Because the snake population in a hibernaculum is finite and very few snakes are left inside the hibernaculum on the very warm days at the end of the emergence season, there was a potential for spurious relationships if we included data for the whole emergence season. Thus, we excluded from this analysis the last 25% of the snakes to emerge in each year. The model was significant ($F_{3,138} = 32.76$, $P = 0.00001$) and maximum air temperature ($F_{1,138} = 78.89$, $P = 0.00001$) was the only

significant individual effect. More snakes emerged on warmer days (Fig. 2).

Individual Patterns

We calculated an index of relative body condition (i.e., proportion of body fat) for individual snakes by using the residuals of a regression of the log of body mass on the log of SVL divided by the log of mass. The data were log transformed because growth trajectories in snakes, as in most other animals, are not linear. Inspection of the plot of the log transformed data and the regression line indicated that there was no size bias in our condition estimate (i.e., log transformation correctly linearized the relationship). ANOVA indicated that our condition index was not sex-biased ($F_{1,699} = 0.0034$, $P = 0.9534$). However, we recognize that our index of condition is not independent of the variables used to generate it (because fat is a component of body mass) and that estimates calculated in this fashion will be confounded whenever fat varies nonrandomly with length (Weatherhead and Brown, 1996). One way to reduce the effect of this problem is to calculate the condition index for individuals spanning a narrow size range, because then, even if fat reserves vary nonrandomly with length, the effect on the calculated index should be minimal. Thus, we selected a narrow size range around the most abundant size class [we chose 100–125 cm SVL (44% of the snakes sampled), as opposed to 39–163 cm SVL (whole sample)] and recalculated the condition index for these individuals only. We conducted separate analyses using the “whole sample index” and the “restricted sample index” to confirm that the effect (or lack of effect) of condition in the models was not due to a bias in our “whole sample index” of condition.

To test the predictions of the effects of sex, SVL, and condition on the timing of spring emergence, we used a GLM with sex, SVL, and the “whole sample index” of condition as predictor variables and date of emergence (standardized for hibernacula) as the response variable. The models were significant in all years, except in 1995 where we had the smallest sample size (Table 2). Sex and condition were not significant in

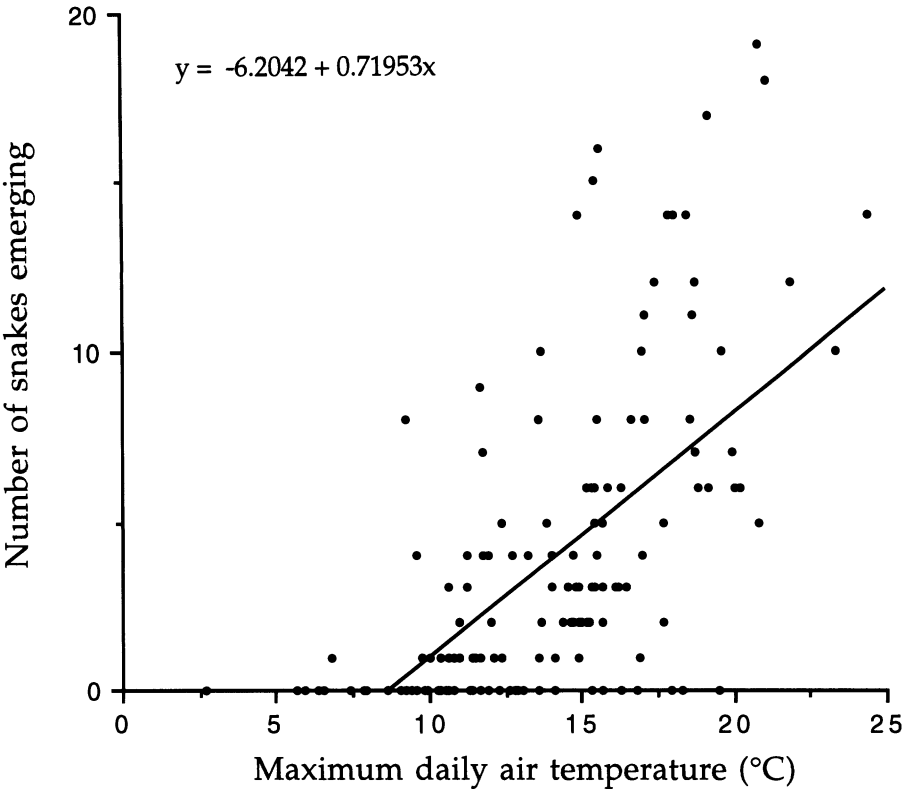


FIG. 2.—Relationship between the maximum daily air temperature (°C) recorded at the Queen’s University Biological Station and the number of snakes emerging from the 13 hibernacula in the study area on that day ($F_{1,138} = 78.89$, $P = 0.00001$, $R^2 = 0.42$). The last 25% of snakes to emerge in each year were excluded (see text).

TABLE 2.—Results of GLM for each year with sex, SVL, and “whole sample index” of condition as the predictor variables and Julian date of emergence (standardized for hibernacula) as the response variable.

Year	Predictor	Estimate	<i>F</i> ratio	<i>P</i>
1992 model ($F_{3,119} = 5.64$, $P = 0.001$)	Sex	−0.14	$F_{1,119} = 0.08$	0.78
	SVL	−0.09	$F_{1,119} = 16.21$	0.0001
	Condition	−25.94	$F_{1,119} = 1.68$	0.20
1993 model ($F_{3,137} = 4.81$, $P = 0.003$)	Sex	−0.92	$F_{1,137} = 3.62$	0.06
	SVL	−0.08	$F_{1,137} = 11.90$	0.0007
	Condition	6.30	$F_{1,137} = 0.14$	0.70
1994 model ($F_{3,162} = 15.06$, $P = 0.00001$)	Sex	−1.13	$F_{1,162} = 2.25$	0.14
	SVL	−0.21	$F_{1,162} = 43.65$	0.00001
	Condition	20.24	$F_{1,162} = 0.42$	0.52
1995 model ($F_{3,17} = 0.80$, $P = 0.51$)	Sex	−0.62	$F_{1,17} = 0.08$	0.78
	SVL	−0.09	$F_{1,17} = 0.57$	0.46
	Condition	−65.82	$F_{1,17} = 0.67$	0.42
1996 model ($F_{3,106} = 9.67$, $P = 0.00001$)	Sex	−0.46	$F_{1,106} = 0.57$	0.45
	SVL	−0.12	$F_{1,106} = 23.70$	0.00001
	Condition	−34.81	$F_{1,106} = 3.44$	0.07
1997 model ($F_{1,139} = 19.03$, $P = 0.0001$)	Sex	−0.69	$F_{1,139} = 1.75$	0.22
	SVL	−0.20	$F_{1,139} = 56.82$	0.00001
	Condition	−17.28	$F_{1,139} = 0.85$	0.36

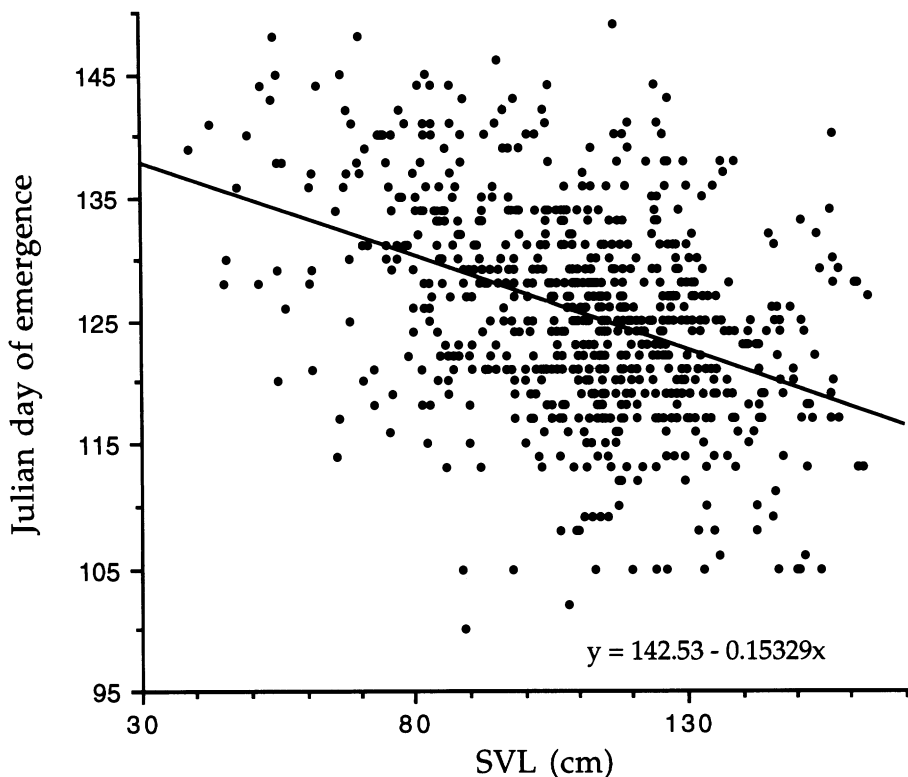


FIG. 3.—Relationship between SVL (cm) and Julian date of emergence ($F_{1,800} = 204.43$, $P = 0.00001$, $R^2 = 0.20$). This relationship was highly significant in five out of six years (Table 2).

any year (Table 2). SVL had a strong effect in all years except in 1995, with larger individuals emerging earlier than smaller individuals (Fig. 3). To confirm that mature individuals emerged earlier than immature individuals, we repeated the analysis, replacing the continuous variable SVL by the class variable mature/immature. We defined a mature snake as being >105 cm SVL, which is the size of the smallest snakes in our population known to reproduce (G. Blouin-Demers, unpublished data). This reanalysis provided qualitatively similar results. Mature snakes emerged earlier than immature snakes. This result is opposite to that predicted by the thermal-inertia hypothesis, but is consistent with both the hypothesis that sexually mature snakes emerge earlier to prepare for reproduction and the hypothesis that larger snakes emerge earlier because the risk of predation in early spring is lower for larger snakes.

Although sex and condition did not have a significant effect in any given year, we looked at the direction of deviation for each year and used the proportions of the binomial distribution to test for significance of the trend (Zar, 1984). For sex, the direction of deviation was the same in all 6 yr, with the females emerging earlier ($P = 0.016$). On average, females emerged on 5 May and the males on 6 May. We had predicted no sex bias based on the mating system of black rat snakes and on the predation-risk hypothesis. However, earlier emergence by females may be consistent with the preparation-for-reproduction hypothesis. As a further test of the preparation-for-reproduction hypothesis, we compared emergence dates for four gravid and eight non-gravid females monitored by radio-telemetry during the 1996 and 1997 field seasons as part of an ongoing telemetry study. We used a Kruskal-Wallis test with the class variable gravid/non-gravid as

the predictor variable and emergence date standardized for years and hibernacula as the response variable. Although the difference was not significant ($n = 13$, $\chi^2 = 0.38$, $P = 0.54$), gravid females actually tended to emerge later (mean date of emergence = 7 May) than non-gravid females (mean date of emergence = 5 May), a trend contrary to the preparation-for-reproduction hypothesis.

For the analysis of the effect of condition using the "whole sample index", the individuals in better condition emerged earlier in four of the six years. This trend was obviously not significant based on the binomial distribution ($P = 0.34$) and thus failed to support the prediction of early emergence by snakes in good condition. Repeating the GLM analysis using the "restricted sample index" produced results that were qualitatively similar to the results of the initial GLM, confirming that condition is not an important factor affecting emergence in our black rat snake population.

We selected the individuals for which we had more than one capture ($n = 126$) to investigate the consistency with which individual snakes emerged from hibernation relative to other snakes in their hibernaculum. To avoid the problems associated with pseudoreplication and because few individuals had more than two captures ($n = 9$), we limited our analysis to the first two captures for each individual. Because we demonstrated significant effects of hibernaculum and SVL on emergence date, we standardized emergence date for those variables by using the residuals from an ANCOVA with hibernaculum and SVL as predictor variables and date of emergence as the response variable. We then used simple linear regression analysis to investigate the relationship between the standardized date of first capture and the standardized date of second capture. If individual snakes are consistent in their time of emergence, we expected a positive relationship between the standardized dates of first and second capture. We first performed this analysis for all snakes to investigate the possibility that some intrinsic individual factor underlies emergence behavior and then repeated the

analysis just for mature individuals to test the prediction of the preparation-for-reproduction hypothesis, that males should be more consistent than females. While the analysis (Fig. 4) for all snakes demonstrated statistically significant repeatability in emergence date ($F_{1,125} = 11.93$, $P = 0.0008$), the R^2 indicated that this repeatability was relatively low ($R^2 = 0.09$), suggesting that individuals are not highly consistent in their timing of emergence among years and that intrinsic factors probably play a moderate role in emergence behavior. However, the analysis for mature individuals only indicated stronger repeatability ($F_{1,83} = 20.29$, $P = 0.00001$, $R^2 = 0.20$), suggesting that as snakes mature they become more consistent in their emergence behavior. Finally, we repeated the analysis separately by sex (Fig. 4) using mature individuals only (males: $F_{1,39} = 5.33$, $P = 0.03$, $R^2 = 0.12$; females: $F_{1,42} = 18.56$, $P = 0.0001$, $R^2 = 0.31$). The higher repeatability of females is inconsistent with the preparation-for-reproduction hypothesis.

DISCUSSION

We observed substantial variation in emergence timing at both temporal and spatial scales. Snakes had mean emergence dates that differed from year to year and from hibernaculum to hibernaculum. We found that snakes in the St. Lawrence region had significantly later emergence dates than snakes in the other two regions. Maximum daily air temperature was positively correlated with the number of snakes emerging on that day, and differences in annual patterns of air temperature partially explained the observed yearly variation in emergence patterns. At the individual level, only SVL had a consistently strong effect, with larger individuals emerging earlier than smaller individuals. There was a consistent tendency across years for females to emerge slightly before males, but this relationship was not significant in any given year. Finally, male and female black rat snakes were found to have low, but statistically significant, repeatability in their emergence behavior. This pattern was stronger among mature snakes.

We found strong evidence that the mean

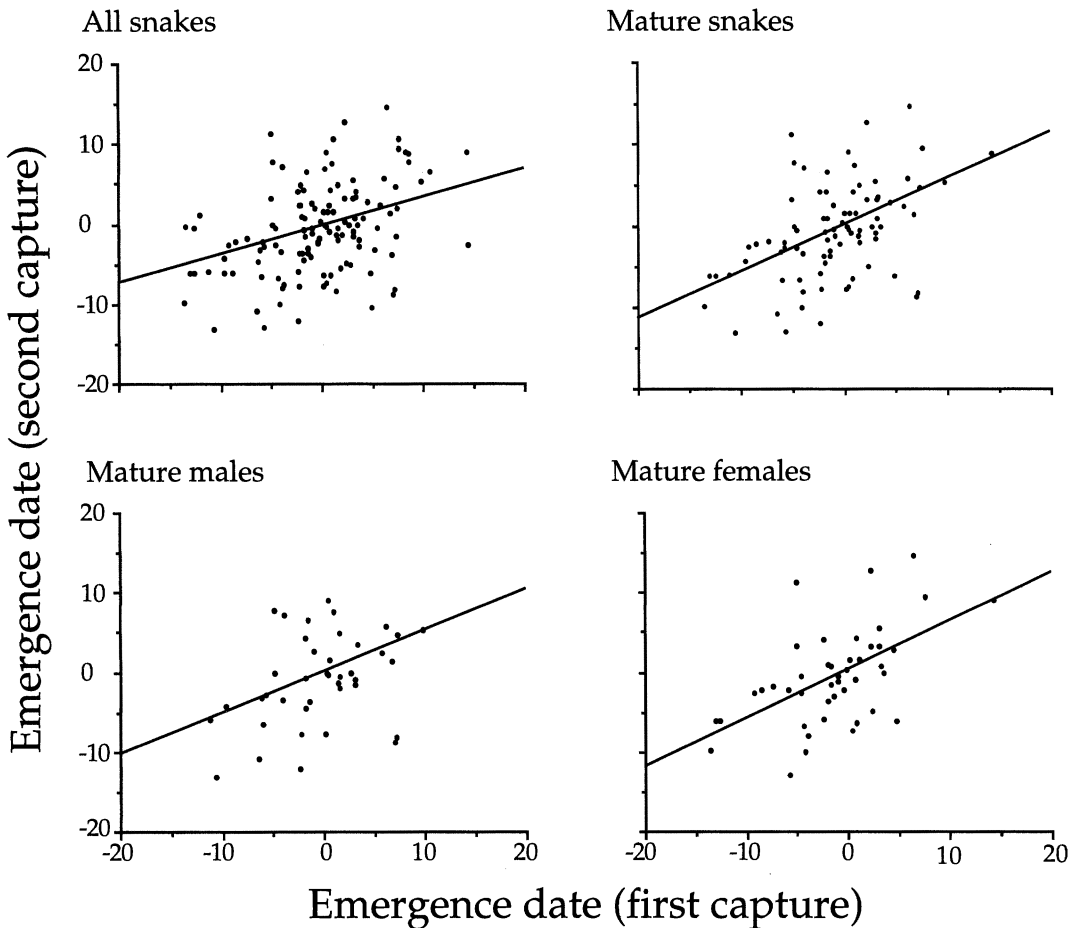


FIG. 4.—Relationships between emergence dates (standardized for hibernacula and SVL, see text) for first and second capture for all snakes ($F_{1,125} = 11.93$, $P = 0.0008$, $R^2 = 0.09$), for mature snakes ($F_{1,83} = 20.29$, $P = 0.00001$, $R^2 = 0.20$), for mature males ($F_{1,39} = 5.33$, $P = 0.03$, $R^2 = 0.12$), and for mature females ($F_{1,42} = 18.56$, $P = 0.0001$, $R^2 = 0.31$).

spring emergence dates of black rat snakes differed among years, regions, and hibernacula across the Frontenac Axis in eastern Ontario. Peak emergence occurred on days with the highest maximum temperatures throughout the emergence period. Microclimatic conditions may contribute to reversals in the thermal gradient inside hibernacula, thereby cueing snakes to initiate emergence (Sexton and Hunt, 1980). However, Weatherhead (1989) found that the hibernaculum that he was studying (i.e., Curtis, see Table 1) was completely buffered from outside temperatures and that snakes' body temperatures did not change until they emerged. He also presented ev-

idence that some individuals might emerge very early and then re-enter the hibernaculum. He concluded that emergence behavior was driven by an internal rhythm. The results of our study seem to contradict this conclusion, because we observed substantial variation among years and hibernacula and found a strong positive relationship between maximum daily temperature and the number of snakes emerging. However, it is possible that an internal rhythm triggers arousal, but that outside temperatures dictate actual emergence.

When we combined climatic data and annual variation in spring emergence, we found that both maximum air temperature

and year were significant in the model, indicating that there was some yearly variation not explained by climatic differences among years. An obvious limitation of this analysis is that our climatic data were obtained from a single location in the center of the study area (at Queen's Station, see Fig. 1). Although these data provide a reasonable indication of the average climatic conditions across the study area on any given day, they do not offer specific information on the microclimatic conditions prevailing at each hibernacula. Because the study area was large and different hibernacula had distinct habitat features (Prior and Weatherhead, 1996), the microclimatic conditions probably differed considerably among sites. The use of hibernacula-specific microclimatic data in our model might have allowed us to explain the annual variation in the timing of emergence more accurately, and also perhaps to explain the regional and hibernacula variation that we observed. For example, hibernacula within the St. Lawrence region, being proximate to the St. Lawrence River, may experience relatively cool conditions in the spring. That this region had significantly later emergence dates than either of the other two regions is consistent with the hypothesis that local and/or microclimatic conditions influence the emergence patterns.

We found that smaller snakes emerged later than larger individuals. This result was contrary to the thermal-inertia hypothesis, but it supported the preparation-for-reproduction hypothesis and the predation-risk hypothesis. Because adults of all temperate-zone snakes complete at least part of gonad development in the spring (Aldridge, 1979a,b), they might need to emerge as early as possible in order to be ready to reproduce. However, the fact that emergence dates of reproductive and non-reproductive females were not significantly different, and that the repeatability of timing of emergence was higher for mature females than for mature males, was not consistent with this hypothesis. Thus, the best explanation for these observations is that larger snakes emerge earlier because their risk of predation in the spring is lower than that of smaller snakes.

The mating system of black rat snakes suggested that males and females should not differ with respect to their average time of emergence. Indeed, we were unable to detect any significant effect of sex on emergence dates for any given year in our study. A slight deviation toward earlier emergence by females was consistent across all 6 yr of the study, but there was only a one day difference between the mean emergence dates of males and females in our population. These results indicate that sex was not a strong predictor of emergence date. In addition to being predicted from the mating system, the similar emergence time of males and females was also consistent with the predation-risk hypothesis.

Although body condition has been suggested by many authors to influence the timing of spring emergence, we are unaware of any study that has documented a significant effect of condition on timing of spring emergence. We found no evidence that condition was important in explaining variation in emergence date in our population of black rat snakes. This conclusion assumes that our index of condition correctly reflected body fat reserves. This might not always be the case when one generates a condition index for individuals spanning a large size range (Weatherhead and Brown, 1996). However, the fact that our results did not change qualitatively when we repeated the analysis using only individuals from a small size range supports our conclusion that condition is not an important factor affecting emergence behavior in our snake population.

We investigated individual repeatability in emergence behavior to assess the possibility that some intrinsic factor underlies individual variation in timing of emergence, independent of phenotypic factors. We found that there was significant individual repeatability, but that this repeatability was relatively low (approximately 10%). This result, combined with the result that we obtained for the effect of size, suggests that both phenotypic and intrinsic factors affect emergence behavior. A result that awaits explanation is why older snakes became more consistent in their timing of emer-

gence, and why that pattern was more pronounced for females than for males.

At the population level, we found that maximum daily temperature was the only significant variable that we examined that explained variation in annual mean emergence dates. However, approximately 60% of the annual variation in mean emergence dates remained unexplained by maximum daily temperature. At the individual level, SVL and intrinsic factors were the only significant predictors of emergence date. Once again, however, approximately 80% of the variation in individual emergence dates standardized for hibernacula remained unexplained by SVL, and approximately 90% of the individual variation in emergence date standardized for hibernacula and SVL remained unexplained by individual repeatability. These results indicate that despite including most of the obvious predictor variables in our analyses, much of the total variation in emergence timing remains unexplained. This substantial unexplained variation in emergence timing is at odds with our expectation that emergence should be highly synchronous because of time constraints in our northern population, and it suggests that selection might not be acting as strongly on emergence timing as we had assumed. A possible explanation for our results is that there is little difference in length of "actual" active season between individuals emerging early and individuals emerging late. This could happen if individuals emerging early do not initiate activity immediately, while individuals emerging late become active soon after emergence. This hypothesis awaits formal testing, but preliminary results from an ongoing telemetry study tend to support this hypothesis (G. Blouin-Demers, unpublished data). Even if this proves to be the case, it is not clear why some individuals should await the start of the active season above ground, while other individuals remain in their hibernacula.

Our results have several management implications. First, region-wide management programs need to be flexible in setting hibernaculum monitoring schedules, because starting and ending dates vary from year to year and site to site. Also, if

resources are limited and monitoring cannot be conducted daily, monitoring should be concentrated on warm days, because that is when most snakes emerge and, thus, more snakes could be sampled. Finally, if one is mostly concerned in monitoring reproductive individuals, sampling effort should be concentrated in the first part of the emergence period.

RÉSUMÉ

On a rapporté d'importantes variations individuelles quant à la date d'émergence d'hibernation parmi les reptiles. Cependant, bien peu d'études se sont penchées sur les causes de ces variations individuelles. Dans la présente étude, nous relatons les patrons dans l'émergence d'hibernation chez les élaphes ratières noires (*Elaphe obsoleta obsoleta*) observées à 13 hibernacula communautaires dans l'est de l'Ontario de 1992 à 1997. Parce que notre aire d'étude est située à l'extrême nord de la distribution de l'espèce, nous nous attendions à ce que les serpents émergent de façon synchronisée puisque leur saison d'activité est très courte. Malgré ces contraintes temporelles, la période d'émergence d'hibernation a duré en moyenne 40 jours. Nous avons découvert une variation significative dans les dates moyennes d'émergence d'une année à l'autre ainsi que d'un hibernaculum à l'autre. Cependant, il ne s'agissait pas d'un simple gradient en latitude des dates d'émergence moyennes des hibernacula. Significativement plus de serpents sortaient d'hibernation les jours où la température maximale de l'air était élevée, mais les différences de températures d'une année à l'autre n'ont expliqué que partiellement les variations annuelles dans les dates d'émergence moyennes. Les individus plus longs émergeaient plus tôt que les individus plus courts, comme prédit si le risque de prédation durant les conditions climatiques printanières plus froides est moins élevé pour les individus plus longs. Les femelles avaient tendance à émerger légèrement plus tôt que les mâles. La condition physique des individus n'était pas un facteur significatif dans la détermination des patrons d'émergence dans notre population d'élaphes ratières noires. Les individus avaient une tendance significative à

émerger au même moment année après année par rapport aux autres individus de leur hibernaculum.

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THE PECTORAL GIRDLES OF *RANA RUGULOSA* (RANIDAE) AND *NESOMANTIS THOMASSETI* (SOOGLOSSIDAE)

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ABSTRACT: Although the pectoral-girdle of sooglossids and the ranid taxa *Rana rugulosa*, *R. tigerina*, and *R. occipitalis* have been considered to be morphologically unique among anurans, two recent studies suggest they are not. The ventromedial parts of the pectoral girdles of adults of *R. rugulosa* (Ranidae) and *Nesomantis thomasseti* (Sooglossidae) were studied using histological sectioning. The pectoral girdle of *N. thomasseti* is arciferal with epicoracoid cartilages that are fused anteriorly but free and overlapping posteriorly; epicoracoid horns are present. The pectoral girdle of *R. rugulosa* is unique among anurans because the epicoracoids are fused anteriorly and posteriorly and overlapping, but not free, in between. However, the nature of the overlap of the epicoracoids in *R. rugulosa* differs morphologically from that of arciferal taxa.

Key words: Pectoral girdle architecture; Sooglossidae; Epicoracoid horns; Ranidae

THE pectoral girdles of anurans commonly are categorized as either firmisternal or arciferal, depending on the relationship of the midventral epicoracoid cartilages to one another. Firmisterny is associated

with complete fusion of the epicoracoids, whereas arcifery describes a condition in which the epicoracoids are fused anteriorly, but are free and usually overlapping posteriorly (Ford and Cannatella, 1993).