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Mortality Patterns and the Cost of Reproduction in a Northern Population of Ratsnakes, *Elaphe obsoleta*

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ABSTRACT.—A recent study of Ratsnakes (*Elaphe obsoleta*) in Texas found that adult mortality was higher for females than males, consistent with the cost of reproduction in snakes being higher for females. To determine whether the same pattern prevailed in a northern population of Ratsnakes, we used data collected using radio-telemetry to test several predictions of the cost-of-reproduction hypothesis. Contrary to there being a cost to reproduction, mortality rates did not differ between juvenile and adult snakes and, contrary to females having a higher cost of reproduction, mortality rates among adults did not differ between males and females. The only evidence consistent with reproduction increasing mortality risk was higher winter mortality for females in poor condition following egg laying. Mortality did not vary with activity but increased with time spent basking, although group differences in basking were not sufficient to produce differences in mortality. High risk of winter mortality in this population may require all Ratsnakes to behave in ways that mask mortality costs associated with reproduction. To determine whether our results for Ratsnakes in Ontario are anomalous or reflect something more substantial about the cost of reproduction in snakes, details of mortality patterns from more species, ideally with diverse ecologies, are needed.

Reproduction entails costs, including an increased risk of mortality (Williams, 1966). If different costs of reproduction for males and females result in sex-biased mortality, there may be important life history, demographic, and sexual selection consequences (Magnhagen, 1991; Andersson, 1994). Differences in mortality between males and females appear to be common. In birds and mammals, the prevalent pattern is for male mortality to exceed that of females (Promislow, 1992; Promislow et al., 1992). This bias is associated with differences in appearance and reproductive behavior that make males more vulnerable than females to predators (Christe et al., 2006). Among snakes, however, female mortality generally appears to exceed male mortality (Madsen and Shine, 1993, 2000; Luiselli et al., 1996; Bonnet et al., 2002), although specific causes of mortality can be higher for males (e.g., Aldridge and Brown, 1995; Bonnet et al., 1999). Given that some reproduction-related mortality for female snakes is associated with spending more time basking (e.g., Shine, 1980; Brown and Weatherhead, 2000; Blouin-Demers and Weatherhead, 2001), and with impaired locomotion when gravid (Shine, 1980; Brown and Shine, 2004), it might be expected that the sex bias in mortality would be lower for oviparous than for viviparous snakes because eggs are carried for a much shorter time than are embryos. That was not the case for Water Pythons (*Liasis fuscus*) in tropical Australia (Madsen and Shine, 2000), however, although extended fasting and some parental care by reproductive females could counter any reduced reproductive costs associated with oviparity. In a recent study of Ratsnakes (*Elaphe obsoleta*) in Texas, Sperry and Weatherhead (2009) also found that the mortality of adult females was greater than that of adult males, consistent with reproduction imposing a higher mortality cost on females of an oviparous snake species in which females do not undergo extensive fasting or provide care for their eggs. In that study, the reproductive status of most females was unknown, however, so the evidence was indirect. Here we test the cost-of-reproduction hypothesis with another population of Ratsnakes in which female reproductive status is known and where rates of mortality can be compared among males and females before and after sexual maturation.

For free-living snakes, the only feasible approach for documenting the cost of reproduction is to use correlational evidence (Madsen and Shine, 2000). Using this approach, we

test the following predictions. If higher female mortality is a cost of reproduction, then the sex bias in mortality should be found only in adult snakes and should arise primarily from an increase in female mortality beginning at the time of sexual maturation (Madsen and Shine, 2000). Furthermore, among reproductive females, mortality should be higher for females that are in poorer condition following egg laying–parturition (Madsen and Shine, 1993, 2000; Luiselli et al., 1996). Finally, for species in which adult females do not reproduce every year, mortality may be higher for reproductive than for nonreproductive females (Bonnet et al., 2002). Increased foraging to replace the energy capital expended on reproduction, and to prepare for breeding again, could spread the cost of reproduction over an extended period (Sperry and Weatherhead, 2009), however, blurring the distinction between reproductive and nonreproductive females.

We also consider the proximate factors that could contribute to mortality differences between males and females. Mortality of Ratsnakes in Texas increased with both activity (mean distance moved per day) and time spent basking, and higher mortality of females, particularly later in the season, was associated with more movement and basking (Sperry and Weatherhead, 2009). Here, we determine if mortality is associated with movement and basking in Ontario Ratsnakes and whether such patterns explain any differences in mortality observed between males and females.

MATERIALS AND METHODS

Study Species and Area.—Data used here were collected as part of a long-term study of Black Ratsnakes (*Elaphe obsoleta*) at the Queen's University Biological Station in eastern Ontario (44°34'N, 76°19'W). Ratsnakes are oviparous colubrids that reach sexual maturity in our study population at 7–9 years old (Blouin-Demers et al., 2002). We defined juveniles of both sexes as individuals <1,050 mm snout–vent length (SVL) based on the size of the smallest known reproductive female and the smallest male observed mating. Paternity data indicate that some males may mature at a somewhat smaller size (Blouin-Demers et al., 2005), so our estimate of the size at maturation should be considered only a reasonable approximation for the population. Males and females follow similar growth trajectories until sexual maturation, after which females grow slightly slower than males, producing weak male-biased sexual size dimorphism among adults (Blouin-Demers et al., 2002).

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Radio-Telemetry.—We estimated survival directly from radio-tracked individuals caught at hibernacula during spring emergence. We tracked 92 adult snakes between 1996 and 2004 and 35 juveniles between 2001 and 2004 (Blouin-Demers et al., 2007). Radio-transmitters (Model SB-2T [5.5 g, 12-month battery life at 20°C] and SI-2T [12.0 g, 24-month battery life at 20°C], Holohil Systems, Carp, Ontario) were implanted surgically in snakes using isoflurane anesthesia (Weatherhead and Blouin-Demers, 2004). Transmitters represented, at most, 4% of the snake's mass. Snakes were kept overnight in the laboratory and then released at their point of capture. Following release, we located snakes using hand-held receivers and antennas every 2–3 days until the snakes entered hibernation. Tracking was resumed the following spring when snakes became active. To obtain data on reproduction from females, we tracked gravid females to nest sites. Once a female had laid her eggs (determined by palpation after she moved away from the nest), we weighed her. We did not have data to estimate male reproductive effort and assumed that all adult males were reproductive.

Statistical Methods.—Because females that are tracked over multiple years often changed status (e.g. nonreproductive to reproductive) between years, we considered observations from each year as separate individuals. Within years, however, a female that reproduced was considered “reproductive” for that year (i.e., even after she had laid her eggs). Although juveniles and males did not change status yearly, for consistency we separated these groups into yearly observations as well. Because this approach results in some individuals being represented multiple times in our analyses, we also ran separate analyses with only one year of observation per snake to ensure that individuals tracked for several years did not affect the overall outcome. The year used in the analysis was determined using a random number generator.

Snakes that had their transmitters removed and snakes alive at the end of the study were considered to have survived (i.e., right censored). We also assumed that, when we lost a snake with a transmitter, that the snake had survived (i.e., loss was due to transmitter failure rather than the transmitter being damaged when the snake was depredated or moved out of range by a predator). In some cases, we later recaptured the lost snake, confirming that it was still alive. Note that predation was often easily identified as such because the transmitter continued to function and was located along with the remains of the snake. In those cases, the snake was therefore known to have died. We assessed the effect of the assumption that lost snakes were alive by also running analyses in which those snakes were assumed to have died. Because the results were qualitatively the same, we present only results using the assumption that those snakes survived. For snakes that died in hibernation, we assumed that death occurred midway between when the snake entered the hibernaculum and the mean date that other snakes emerged from that hibernaculum. Because of the relative infrequency of mortality events, we collapsed our 48-h telemetry data into monthly or yearly sampling intervals, depending on the analysis.

We used an information-theoretic approach (Burnham and Anderson, 2002) to examine relative support for candidate models that represented our hypotheses regarding the relationship between reproductive effort and survival. We used the known-fate procedure in the program MARK (White and Burnham, 1999) to model survival in terms of our explanatory variables and to calculate annual survival rates. We used the sine link function to generate maximum likelihood estimates of regression coefficients and associated confidence intervals for our variables. Models were ranked according to Akaike's information criterion for small sample sizes (AIC_c ; Burnham and Anderson, 2002).

TABLE 1. Annual survival estimates and associated lower (L) and upper (U) 95% confidence intervals for reproductive female, nonreproductive female, adult male, and juvenile male and female Black Ratsnakes in Ontario, Canada (1997–2005).

Group	Annual survival	L 95% CI	U 95% CI
Reproductive female	0.80	0.62	0.91
Nonreproductive female	0.62	0.50	0.73
Male	0.75	0.61	0.85
Juvenile female	0.76	0.51	0.91
Juvenile male	0.80	0.58	0.92

To address our specific predictions, we ran two analyses. The first was designed to examine whether the age (adult or juvenile) or sex of an individual affected its survival, controlling for annual variation in overall survival. For this analysis, we included observations from all snakes, and the candidate models included reproductive group (reproductive female, nonreproductive female, male, juvenile male, or juvenile female), year, and the interaction between year and group. The second analysis was designed to determine whether female survival was affected by their body condition after laying eggs, again controlling for annual variation in overall survival. We used a subset of snakes based on the availability of body-condition data. We included models with condition as a continuous covariate, year, and the interaction between year and condition. Condition was estimated as the residuals from a regression of SVL on mass (Weatherhead and Brown, 1996) with positive residuals indicating good condition and negative residuals indicating poor condition.

Distance moved between observations was calculated using Geospatial Modelling Environment (Beyer 2010) in ESRI ArcGIS version 9 (Redlands, CA) and was standardized as the mean distance moved per day. We quantified basking as the percentage of relocations at which each snake was observed basking, averaged across all snakes. Monthly mean daily distances traveled and mean monthly percent time basking were compared among groups using ANOVA. We used linear regression to determine whether survival varied with seasonal activity and percent time basking. Means are presented ± 1 SE.

RESULTS

We obtained sufficient data to estimate survival for 118 Ratsnakes (61 adult females, 28 adult males, 13 juvenile females, and 16 juvenile males). Following the separation of individuals monitored over multiple years into yearly categories, we had 39 annual survival estimates for reproductive females, 94 for nonreproductive females, 69 for adult males, 28 for juvenile females, and 31 for juvenile males.

Overall annual survival was similar among the four groups (nonreproductive females, reproductive females, adult males, and juveniles; Table 1), although survival for nonreproductive females appeared to be slightly lower than for the other groups. Survival models indicate only weak support for an effect of group on survival (Table 2). Inclusion of only 1 yr of observation per individual yielded similar results, with the group model again receiving little support (AIC_c weight = 0.08) and overlapping estimates of annual survival for all groups. Monthly patterns of survival differed only slightly among groups, with higher early season survival for reproductive females and juveniles compared to males and nonreproductive females (Fig. 1).

We measured SVL and mass for 28 females immediately following egg laying. Four of those females died before or during the subsequent winter. Those in relatively good body condition (positive residuals based on SVL–mass regression) had a mean SVL of 1.24 ± 0.02 m and a mean mass of 541.3 ± 26.1 g. Those in relatively poor body condition had a mean SVL

TABLE 2. Model selection (S) results describing survival of Black Ratsnakes in Ontario, Canada from 1997–2005. For each model, ΔAIC_c is the difference between each model and the model with the lowest AIC_c score, w describes the relative support for each model, and np is the number of parameters. The group variable indicates whether a snake was a reproductive female, nonreproductive female, adult male, juvenile male, or juvenile female.

Model	AIC_c	ΔAIC_c	w	np
S (constant)	470.15	0.00	0.70	1
S (group)	473.14	2.98	0.16	5
S (year)	473.39	3.23	0.14	10
S (group \times year)	530.66	60.50	0.00	50

of 1.20 ± 0.03 m and a mean mass of 427.7 ± 22.2 g. All four snakes that died following egg laying were in relatively poor condition. The effect of body condition on survival was positive ($\beta = 1.40$, 95% CI = 0.69–2.11) and the model containing the interaction of body condition and year received the most support (AIC_c weight = 0.93); all other models were not supported ($\Delta AIC_c > 6.25$, AIC_c weight < 0.05). Results were similar when we included only 1 yr of observation per individual (body condition $\beta = 3.06$, 95% CI = 1.73–4.39).

We had movement and basking data for 22 reproductive females, 41 nonreproductive females, 16 males, and 34 juveniles. Overall, all groups moved similar distances over the season ($F_{3,366} = 1.86$, $P = 0.14$). We did not find a relationship between activity and survival for any of the groups (all $R^2 < 0.70$, all $P > 0.16$) or for all groups combined ($R^2 = 0.01$, $P = 0.67$; Fig. 2).

Overall time spent basking differed among groups ($F_{3,352} = 8.57$, $P < 0.001$), with Tukey-Kramer analysis indicating that reproductive females and juveniles were observed basking less than were males and nonreproductive females. We did not find a significant relationship between basking and survival within any group (all $R^2 < 0.30$, all $P > 0.38$). With all groups combined, however, monthly survival declined with mean time spent basking ($R^2 = 0.35$, $P = 0.02$; Fig. 3).

DISCUSSION

Our data for Ratsnakes in Ontario were inconsistent with most of the patterns expected if the cost of reproduction is higher for females than for males (Madsen and Shine, 2000) or, indeed, with there being a mortality cost to reproduction. Mortality rates of males and females were not significantly different among adults and we found no evidence that mortality rates increased with sexual maturation. Among adult

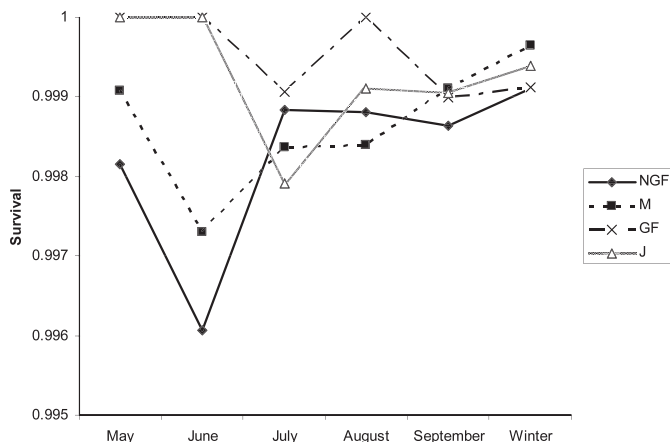


FIG. 1. Monthly and over-winter (October–April) survival for reproductive female (RF), nonreproductive female (NRF), male (M), and juvenile (J) Black Ratsnakes in Ontario, Canada (1997–2005).

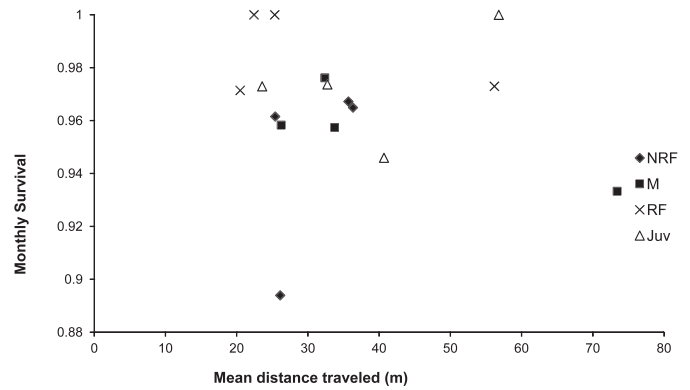


FIG. 2. Monthly survival relative to mean distance traveled (m) per day each month for reproductive female (RF), nonreproductive female (NRF), male (M), and juvenile (J) Black Ratsnakes in Ontario, Canada (1997–2005).

females, mortality rates did not differ between reproductive and nonreproductive individuals and the trend was actually for reproductive females to survive better. The only evidence consistent with reproduction increasing female mortality was that females in poorer condition following egg laying were less likely to survive over winter. Proximately, mortality was unrelated to movement, but mortality increased with time spent basking. Although we found differences among groups in the amount of time spent basking, these differences were not sufficient to produce differences in mortality.

A shortcoming of the correlational approach we used here is that the patterns of interest could potentially be confounded by other factors. For example, if mortality risk decreases with size, the size advantage of adults might mask their increased risk of mortality associated with reproduction. Nonetheless, other studies using the same general approach used here have found evidence that reproduction increases mortality in snakes and, usually, more-so for females than for males (Madsen, 1987; Madsen and Shine, 1993, 2000; Luiselli et al., 1996; Bonnet et al., 2002; Sperry and Weatherhead, 2009). It is, therefore, reasonable to conclude that our study population of Ratsnakes is different from the other species–populations studied.

A question arising from our results specific to the Ratsnake population we studied is, given that survival appears not to decrease at sexual maturation, why do these snakes not mature sooner than 7–9 years (Blouin-Demers et al., 2002)? The probable explanation is that maturing sooner would entail

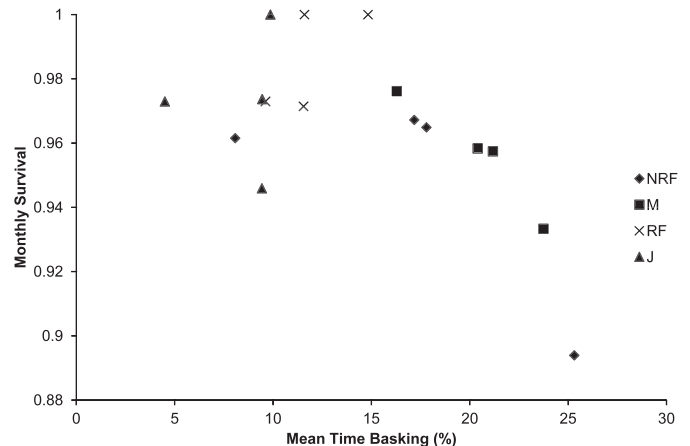


FIG. 3. Monthly survival relative to mean percent time observed basking per month for reproductive female (RF), nonreproductive female (NRF), male (M), and juvenile (J) Black Ratsnakes in Ontario, Canada (1997–2005).

fecundity costs (Roff, 1992). Fecundity increases with size for both male (Blouin-Demers et al., 2005) and female (Blouin-Demers and Weatherhead, 2007) Ratsnakes. Because diverting energy to reproduction is likely to constrain growth (even sperm production has non-trivial costs in snakes; Olsson et al., 1997), Ratsnakes that matured too young (=small) would not realize the size-related fecundity advantages that would result from channeling energy into growth for more years.

A broader question stemming from our results is why Ratsnakes in Ontario are different from Ratsnakes in Texas. It is possible that higher mortality of female Ratsnakes in Texas was unrelated to reproduction. We are unaware of any aspect of the snakes' natural history that could produce such an effect, and an analysis of parasite loads, hematological characteristics, and corticosterone concentrations provided no evidence of health differences between males and females (Sperry et al., 2009). An alternative explanation for the difference between Ontario and Texas Ratsnakes is that some difference in the ecology of the two populations causes reproduction to be costly for female Ratsnakes in Texas but not in Ontario. One obvious ecological difference is in the length of the active season. Ratsnakes are active for 5–6 months in Ontario vs. year-round in Texas, although winter activity in Texas is much reduced (Sperry et al., 2010). Associated with the difference in activity is a difference in the timing of mortality, with winter mortality accounting for 37% of mortality in Ontario and 0% in Texas (Sperry et al., 2010). Given the challenge that surviving winter presents to Ontario Ratsnakes, all individuals, regardless of age, sex, or reproductive status may be forced to behave in ways that maximize the probability of winter survival. This could result in similar exposure to predators during the active season and, thus, similar rates of mortality. How do Ontario females avoid the cost of reproduction under these circumstances? One strategy is to breed only when adequate reserves have been accumulated to allow females to reproduce and still survive the following winter. Intervals between breeding attempts for females vary from 1 to >3 years, with evidence indicating the interval is determined by condition (G. Blouin-Demers, unpubl. data). The higher winter mortality we observed for females in poor condition after egg laying suggests that females sometimes "miscalculate" the appropriate level of investment in reproduction.

The preceding explanation might account for differences between Ratsnakes in Ontario and Texas but does not explain why other species of snakes, some of which live in highly seasonal environments similar to Ontario, all provide evidence that reproduction is costly to females (Madsen, 1987; Madsen and Shine, 1993, 2000; Luiselli et al., 1996; Bonnet et al., 2002). The fact that most of the other species studied at higher latitudes are viviparous could indicate that higher fixed costs of reproduction (Madsen and Shine, 1993) for viviparity, relative to oviparity, afford viviparous females less scope for avoiding reproductive costs at higher latitudes. Details of mortality patterns from more species, ideally with diverse ecologies, are needed to help understand whether Ontario Ratsnakes are anomalous or reflect something more general about the cost of reproduction in snakes.

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