

## BUMPUS IN THE SNAKE DEN: EFFECTS OF SEX, SIZE, AND BODY CONDITION ON MORTALITY OF RED-SIDED GARTER SNAKES

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**Abstract.**—Huge breeding aggregations of red-sided garter snakes (*Thamnophis sirtalis parietalis*) at overwintering dens in Manitoba provide a unique opportunity to identify sources of mortality and to clarify factors that influence a snake's vulnerability to these factors. Comparisons of sexes, body sizes, and body condition of more than 1000 dead snakes versus live animals sampled at the same time reveal significant biases. Three primary sources of mortality were identified. Predation by crows, *Corvus brachyrhynchos* (590 snakes killed), was focussed mostly on small snakes of both sexes. Crows generally removed the snake's liver and left the carcass, but very small snakes were sometimes brought back to the nest. Suffocation beneath massive piles of other snakes within the den (301 dead animals) involved mostly small males and (to a lesser extent) large females; snakes in poor body condition were particularly vulnerable. Many emaciated snakes ( $n = 142$ , mostly females) also died without overt injuries, probably due to depleted energy reserves. These biases in vulnerability are readily interpretable from information on behavioral ecology of the snakes. For example, sex biases in mortality reflect differences in postemergence behavior and locomotor capacity, the greater attractiveness of larger females to males, and the high energy costs of reproduction for females.

**Key words.**—Mating, natural selection, predation, sexual selection, size-dependent mortality.

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Although differential survival with respect to phenotype has been demonstrated in many studies, the reason for the mortality and the mechanism causing the fitness differences remain unclear in most of these cases (Endler 1986). The problem involves logistics: It is simpler to quantify differential mortality by assessing phenotype distributions in living animals before and after the mortality event than it is to directly observe mortality or to measure the attributes of dying versus living animals. Unfortunately, detailed data on mortality are difficult to gather in nonhuman populations. Because each individual provides only a single datapoint, very large sample sizes are needed for robust tests of alternative hypotheses about nonrandom patterns in mortality (e.g., Daly et al. 1990). If such samples are available, they can provide unusually direct evidence on the phenotypic targets and potential magnitude of natural selection in wild populations.

Perhaps the most celebrated analysis of the cause and phenotypic correlates of mortality in natural populations is also the earliest such analysis. In 1898, Hiram Bumpus described nonrandom mortality within a sample of house sparrows. He quantified attributes of birds killed by a severe winter storm and compared the distribution of these traits with that of another group of conspecifics that survived the storm (Bumpus 1899). With these data, Bumpus showed that mortality was random with respect to some traits but nonrandom with respect to others. Reanalyses have modified some of his conclusions, but confirmed that much of the mortality was nonrandom (e.g., Buttemer 1992; Pugsek and Tomer 1996; Janzen and Stern 1998). Similar analyses have since been conducted on other taxa (Janzen 1993; Holland and Yalden 1995; Brown and Brown 1998). However, logistical difficulties have precluded such analyses on most kinds of organisms. Because snakes are generally rare and live in relatively low densities, quantitative information on sources of mortality is virtually nonexistent for this group (Turner 1977; Parker and

Plummer 1987). We took advantage of an exceptional opportunity, involving large overwintering aggregations, to quantify sources and determinants of mortality in a garter snake population in central Canada.

### MATERIALS AND METHODS

The red-sided garter snake (*Thamnophis sirtalis parietalis*) is a northern subspecies of a very widely distributed species. These small, nonvenomous snakes (in our population, males average 48 cm snout-vent length [SVL]; females average 58 cm SVL) gather together in autumn to enter communal overwintering dens, then disperse into the surrounding countryside in spring. Only adult snakes spend winter in the dens; the location of juveniles remains unclear (Gregory 1974, 1977). The snakes do not feed while they are at the dens, but participate in intense courtship and mating activity during the month-long period of spring emergence (Gregory and Stewart 1975). Males remain near the den for days or weeks after emerging, but females disperse within a few days (Gregory 1974; Hawley and Alekskiuk 1975, 1976; Shine et al. 2000c).

Den sizes vary considerably, but in one area within the species' range (southern Manitoba), dens may contain many thousands of snakes (Aleksiuk and Stewart 1971; Gregory 1974). The spectacular aggregations of courting snakes in the vicinity of these large dens during springtime provide a unique opportunity to quantify many aspects of the biology of these animals. We have conducted studies on several aspects of garter snake biology at these dens, including work on chemical communication, behavior, and the mating system (e.g., Mason and Crews 1986; Mason 1993; Shine et al. 1999, 2000a,b,c). The area (Chatfield Community Pasture, 50°44'N, 97°34'W) includes three large dens located several hundred meters apart. We have combined data from these three dens, because preliminary analyses revealed no differences among

the dens in terms of sex ratios, body sizes, or body conditions of either live or dead snakes. Radiotelemetry of free-ranging snakes showed that males move between dens from day to day (Shine et al. 2000c), so there is little opportunity for local differentiation.

Each den consists of a shallow (2-m) rocky depression approximately 10–20 m long and 3 m wide. In spring, the snakes emerge from numerous small crevices on the floor of the den. In one year of these studies (May 1997), we took the opportunity to collect all dead snakes that we found near the dens. We patrolled the den floor and areas within 100 m twice each day, and collected all dead and dying snakes that we encountered. These animals were taken back to the laboratory, where they were sexed (by tail shape and the presence of hemipenes) and measured (SVL). Specimens that were undamaged and only recently dead were also weighed. In a few cases (<50) where the bodies of the snakes had been torn apart by predators, we used the intact tails to determine the sex of the animal. We could then estimate its SVL from regressions of SVL against tail length in intact specimens. To compare these dead snakes with live conspecifics, we collected a random sample of live snakes in the morning (0900–1000 h) and afternoon (1700–1800 h) each day. These animals were sexed, measured, and weighed that evening and then released after we took the morning sample the following day. Given the large numbers of snakes at each den and the relatively brief duration of stay at the den by individual animals (Gregory 1974; Shine et al. 2000c), it is unlikely that we sampled any individual snake on more than one occasion.

We use these data to answer two main questions:

What were the major causes of mortality for garter snakes during the spring emergence period? In most cases, these causes could be confidently inferred from the circumstances in which we located bodies.

What factors (sex, body size, and/or body condition) influenced the vulnerability of individual snakes to each of these sources of mortality? This comparison is relatively straightforward for body size and condition, but is more complex for sex. Male garter snakes tend to remain close to the den for weeks after emerging, whereas females generally disperse from the den within a few days (Gregory 1974; Shine et al. 2000c). Thus, samples of the snakes around a den include many more males than females, despite the fact that approximately similar numbers of each sex may disperse from the den over the entire mating season. To take this factor into account, we use two estimates of sex ratio of live snakes: one based on the numbers encountered during our sampling periods in spring (as above) and another based on relative numbers of males and females actually dispersing from the den overall (based on sex ratios in autumn, as the snakes enter the den).

## RESULTS

Over the course of two weeks in May 1997, we obtained data on sexes and sizes of 1033 dead and dying snakes and on 1980 live snakes with which to compare them.

### *Sources of Mortality*

We classified the dead snakes into three main categories, based on their location and appearance.

*Killed by predators.*—Of the 1033 dead and dying snakes that were found in and near the dens, 590 had severe lacerations due to predator attack. Most of these cases involved a midbody wound through which the snake's liver had been removed. Some snakes had been pecked on the head as well. The only predators seen near the dens were American crows (*Corvus brachyrhynchos*). Based on direct observations of crows attacking snakes, crows carrying off snakes, the nature of the wounds on the snakes, and crow footprints in fresh snow leading to torn and dying snakes, we conclude that almost all of this predation was due to crows. A crow nest (with four unhatched eggs) that we located 25 m from one den was surrounded by the remains of 24 snakes within a 10-m circle. Unlike the near-den snakes (that were generally intact except for their missing livers), the bodies of these snakes near the nest had been partially consumed. We include this sample within the predator-killed snakes, but also compare it to the other snakes within this sample.

Undoubtedly, crows are not the only predators. One radiotracked snake that we followed in May 1998 was killed by a hawk as she dispersed from the den. This snake displayed multiple shallow lacerations, very different from the single liver-removal gash evident in crow-killed snakes. We did not see this kind of injury in any other snake, possibly because raptors take snakes as they disperse rather than close to the den.

*Suffocated.*—On three occasions, we found large piles of freshly killed snakes in the floor of the dens. On each occasion, the dead snakes were in a single heap, had died very recently, and showed no external wounds. Instead, they were flattened and appeared to have been crushed beneath other snakes. In the case of the largest mass kill of this kind (169 snakes, on 8 May), the dead snakes were still beneath a pile of many hundreds of live snakes when found and removed. The other suffocation kills involved 81 snakes on 6 May, and 51 snakes on 9 May. We spent hours each day at the dens, and thus can be sure that all of these snakes (total  $N = 301$ ) had died within a very short period, within the preceding few hours of their discovery.

*Unknown causes.*—Another 142 snakes with no overt injuries were found dead either on the den floor or in the surrounding aspen woodland and clearings. These animals were always scattered in space and time, unlike the piles of suffocated snakes. Some of the live snakes that we encountered were so weak that they were close to death. Some died as we picked them up, and others were seen alive but immobile for a day or two before being found dead in the same location. Based on the emaciated appearance of many of these animals, we speculate that they died from nutritional stress or from a susceptibility to other mortality sources (e.g., pathogens, thermal stress, or the weight of courting males) brought about by starvation.

### *Biases Involved with Each Cause of Mortality*

We used logistic regression to analyze determinants of vulnerability to mortality. In each case, the dependent vari-

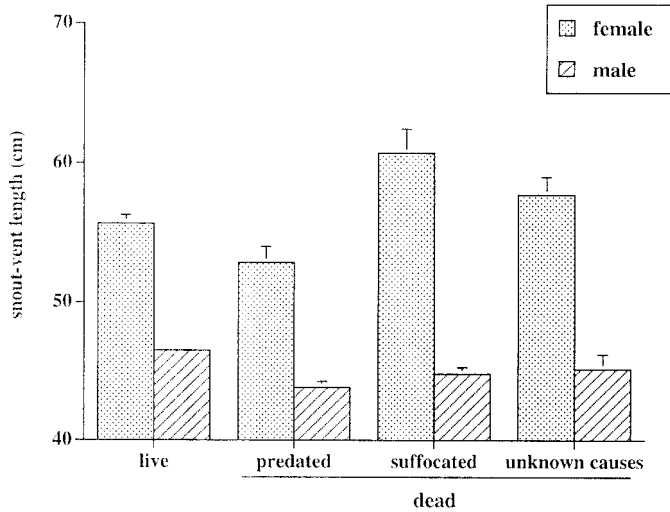


FIG. 1. Body sizes (snout-vent lengths) of red-sided garter snakes (*Thamnophis sirtalis parietalis*) measured in spring (May 1997) at communal dens in Manitoba. The histograms show means (and two associated standard errors) for mean body sizes of male and female snakes that were found either alive (live) or dead from various causes (predation, suffocation, and unknown).

able was whether the snake was dead or alive, and the independent variables were factors such as sex, body size, and body condition. We used residual scores from the general linear regression of ln-transformed body mass against SVL as our size-independent measure of body condition. Comparison of the 1980 live snakes with each of the groups of dead snakes described above revealed significantly nonrandom patterns with respect to mortality.

**Killed by predators.**—We could not include body condition in these analyses because the predator-killed snakes were damaged so badly that we could not estimate their original mass. Thus, only sex and body size (SVL) were included as independent variables in the logistic regression to compare live versus predator-killed animals. Both were highly significant; log-likelihood ratio tests yielded chi-square values of 118.63 for body length ( $df = 1$ ,  $P < 0.0001$ ) and 47.80 for sex ( $df = 1$ ,  $P < 0.0001$ ). Predator-killed snakes were smaller than live animals, and this was true within each sex (Fig. 1). That is, sex as well as size affected a snake's vulnerability to predation. If crows were selective with respect to size alone, then females (the larger sex) would be taken only rarely. This was not the case. The sex ratio of crow-killed snakes was approximately the same as in live snakes encountered near the den at the same time of year ( $\chi^2 = 0.77$ ,  $df = 1$ ,  $P = 0.38$ ; see Fig. 2).

As noted above, behavioral differences between males and females mean that the sex ratio of live snakes around the den at any one time in spring (the sex ratio used in the comparisons above) differs substantially from the proportions of males and females that emerge over the entire spring period. The latter characteristic is best quantified by samples taken in autumn, when the sexes do not exhibit these behavioral differences. Counts of live snakes near the den, shortly before ingress, reveal a sex ratio close to 50:50 (45% male in 635 snakes sampled in September 1997). Thus, the proportion of

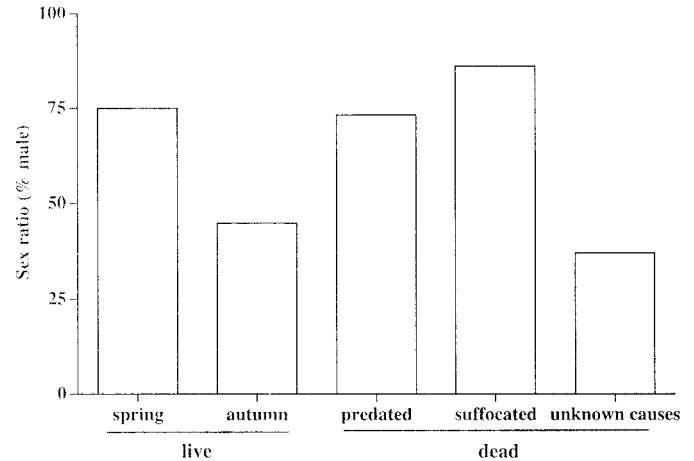


FIG. 2. Sex ratios (percentage of the samples composed of males) of red-sided garter snakes (*Thamnophis sirtalis parietalis*) measured in spring (May 1997) and autumn (September 1997) at communal dens in Manitoba. The histograms show sex ratios for samples of snakes that were found either alive (live) or dead from various causes (predation, suffocation, and unknown). All of the dead snakes were recorded in spring.

snakes using the den that were killed by predators was much lower for females than for males (using autumn counts to provide the expected proportions; contingency-table analysis:  $\chi^2 = 105.5$ ,  $df = 1$ ,  $P < 0.0001$ ). Consequently, the sex ratio of snakes taken by predators was similar to that in samples of live snakes taken at the same time, but the sex ratios in both of these samples were highly skewed by differences between the sexes in the duration of residency near the den after emergence.

The carcasses (minus livers) of most snakes that were attacked by crows were left at the site of the attack, but some snakes were brought back to the crows' nest. The small sample ( $n = 24$ ) of dead snakes found near the crows' nest differed significantly from the larger sample ( $n = 566$ ) of dead snakes left in situ. Snakes brought back to the nest were smaller than the other predator-killed animals (for males, means of 39.6 vs. 44.0 cm SVL; for females, 43.5 vs. 53.0 cm SVL; two-factor ANOVA with sex and location as factors and SVL as the dependent variable: for location of body,  $F_{1,586} = 17.62$ ,  $P < 0.0001$ ; interaction between sex and location not significant). The sample of snakes brought back to the nest was more highly male biased (21 of 24 = 88% male) than the sample of dead snakes found near the den (411 of 566 = 73% male), but sample sizes were too small for statistical significance in the comparison between the two ( $\chi^2 = 1.90$ ,  $df = 1$ ,  $P = 0.17$ ).

**Suffocated.**—Because the suffocated snakes were collected shortly after they died and were not torn apart like the predator-killed snakes, we could weigh as well as measure and sex them. Thus, our logistic regression incorporated mass as well as SVL and sex; the dependent variable was whether the snake was found alive (i.e., in our regular sampling) or suffocated. Log-likelihood ratio tests showed that an animal's vulnerability to suffocation depended on its SVL ( $\chi^2 = 18.27$ ,  $df = 1$ ,  $P < 0.0001$ ) and body condition ( $\chi^2 = 67.44$ ,  $df = 1$ ,  $P < 0.0001$ ), but not its sex ( $\chi^2 = 0.20$ ,  $df = 1$ ,  $P = 0.66$ ).

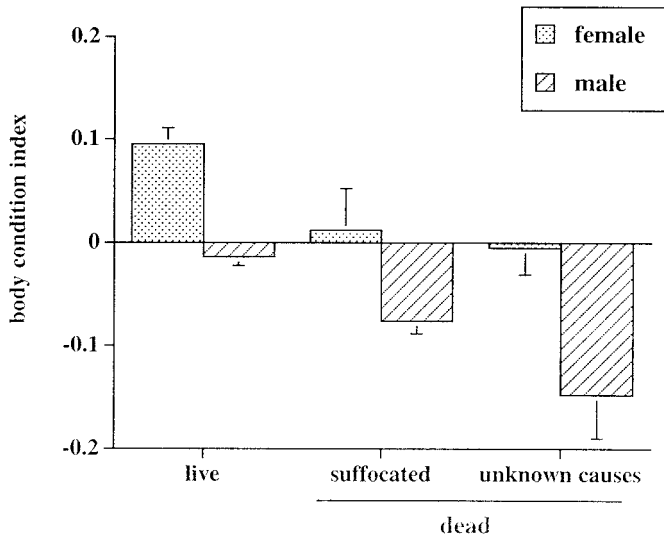


FIG. 3. Body condition (mass relative to snout-vent length) of red-sided garter snakes (*Thamnophis sirtalis parietalis*) measured in spring (May 1997) at communal dens in Manitoba. The values shown are residual scores from the general linear regression of  $\ln$ -transformed body mass against snout-vent length. The histograms show means (and two associated standard errors) for mean body condition scores of male and female snakes that were found either alive (live) or dead from various causes (suffocation and unknown). Predator-killed snakes are not included in this figure because they were too badly damaged for us to obtain reliable measures of body mass.

The apparent lack of a sex difference in this respect, however, masks strong but contrasting patterns involving mortality in each sex. Animals in poorer body condition were more vulnerable to suffocation in both sexes (Fig. 3), but body size affected vulnerability differently in males and females (Fig. 2). Larger body size (SVL) reduced vulnerability to suffocation in males, but increased it in females (Fig. 1; two-factor ANOVA with factors being sex and live vs. suffocated, with SVL as the dependent variable: interaction between sex and body size:  $F_{1,2277} = 58.70$ ,  $P < 0.0001$ ).

Unlike the comparison involving predator-killed snakes, the conclusions with respect to suffocation vulnerability of males versus females do not depend on whether the sample of live snakes is based on collections made in spring or autumn. In both cases, males comprised a higher proportion of the suffocated snakes than they did among live specimens. The sex ratio in the sample of suffocated snakes (42 females, 259 males) was more highly male biased (86% male) than that in either the spring-collected sample of live snakes (75% male; comparing the two,  $\chi^2 = 17.11$ ,  $df = 1$ ,  $P < 0.0001$ ) or the sample of autumn-collected live snakes (45% male;  $\chi^2 = 145.5$ ,  $df = 1$ ,  $P < 0.0001$ ; see Fig. 2).

*Unknown causes.*—Logistic regression (with live vs. dead of unknown causes as the dependent variable) showed that vulnerability to this cause of mortality was a function of a snake's sex (based on log-likelihood ratios,  $\chi^2 = 70.20$ ,  $df = 1$ ,  $P < 0.0001$ ) and body condition ( $\chi^2 = 54.94$ ,  $df = 1$ ,  $P < 0.0001$ ), but not its SVL ( $\chi^2 = 1.63$ ,  $df = 1$ ,  $P = 0.20$ ). In both sexes, thinner snakes were more likely to be found dead rather than alive (Fig. 3). The sex ratio bias was even stronger. Females constituted most of the snakes found dead

of unknown causes (90 females, 42 males = 37% male), in strong contrast to the male-biased sample of live snakes (75% male). The female-biased sex ratio of these dead snakes also differed significantly from the more even sex ratio found among live snakes collected in autumn (45% male;  $\chi^2 = 6.38$ ,  $df = 1$ ,  $P < 0.012$ ; see Fig. 2). Thus, this mortality due to unknown causes chiefly affected emaciated animals, especially females.

## DISCUSSION

Studies on a diverse array of organisms have revealed that mortality is often highly nonrandom with respect to attributes such as sex, body size, body condition, and location (e.g., Holomuzki and Short 1990; Acharya 1995; Villafuerte et al. 1997; Brown and Brown 1998). Much of this research, however, has concentrated on a relatively small number of systems. For example, avian predation on mammals has attracted considerable attention (e.g., Daly et al. 1990; Dickman et al. 1991; Koivunen et al. 1996; Rohner and Krebs 1996), whereas predation on reptiles has not (but see Christian and Tracy 1981; Jayne and Bennett 1990; Janzen 1993). As far as we are aware, our dataset is the most extensive ever gathered on the way in which phenotypic attributes (sex, body size, body condition) influence a snake's vulnerability to various sources of mortality. Previous studies on natural selection within snake populations have generally involved the frequency of alternative color patterns and have relied on inferences rather than direct measurements. Such inferences have been based on ontogenetic shifts in trait frequencies (e.g., Ehrlich and Camin 1960) or predator responses to artificial models of various colors and patterns (e.g., Andren and Nilson 1981; Madsen 1987; Brodie 1993).

For most snakes, direct quantification of mortality would be logistically prohibitive (but see Bronikowski and Arnold 1999). The huge aggregations of courting garter snakes in Manitoba provide a rare opportunity for such an analysis, but the unusual nature of the system might generate patterns that do not occur in smaller populations. To what degree can our results be generalized to other snake species or, indeed, to other populations of the same species? Plausibly, ecological processes operating at these massive communal dens may differ in important ways from the conditions that apply to the more typical situation, where snakes occur at much lower densities (e.g., Rossman et al. 1996). We cannot evaluate this proposition directly because there are no analogous datasets on other snake populations. However, intuition suggests that some sources of mortality will be strongly affected by the size of the aggregations, whereas others will not. Most obviously, it is difficult to imagine that courting snakes will suffocate in other snake populations because the numbers of rival males in a single group are generally much less than can occur in the Manitoba dens. Predation by crows occurs at small as well as large dens in the Chatfield area (pers. obs.), so is less likely to be affected by den size. However, the situation is complex. The large snake dens may be a focus for crows because of prey availability, but at the same time these dens attract many tourists whose presence discourages crows from frequenting the large dens. Thus, predation rates may not differ between the large dens and the smaller ones.



TABLE 1. Calculation of directional selection coefficients for body size (ln snout-vent length) and body condition (residual scores from the general linear regression of ln mass vs. ln snout-vent length) for female and male garter snakes during spring 1997 at a communal den in Manitoba. See Janzen and Stern (1998) for method of calculating the selection gradient ( $\beta_{\text{avgrad}}$ ) from the results of logistic regression analysis.

Sex	Trait	Selective force	Logistic regression analysis			Selection gradient ( $\beta_{\text{avgrad}}$ )
			Coefficient	SE	<i>P</i>	
female	body size	predation	2.720	0.765	0.000	0.474
female	body size	suffocation	-10.605	3.449	0.002	-1.519
female	body size	unknown	-3.333	1.163	0.005	-0.520
female	body condition	suffocation	3.566	1.681	0.034	0.962
female	body condition	unknown	7.310	1.543	0.000	1.530
male	body size	predation	5.813	0.617	0.000	0.743
male	body size	suffocation	5.326	0.874	0.000	0.542
male	body size	unknown	3.628	1.725	0.035	0.372
male	body condition	suffocation	8.231	1.047	0.000	1.276
male	body condition	unknown	7.317	1.708	0.000	0.994

Each of the three major causes of mortality that we identified operated nonrandomly with respect to some of the variables that we measured. This evaluation depends on comparisons between live versus dead animals. Characterising phenotypic traits of the live snakes proved to be more complex than doing so with the dead animals, because the composition of the den population differed between sampling times. In particular, sex differences in the duration of near-den residency meant that the population of snakes near the den during spring was heavily male biased, although the absolute numbers of males and females dispersing from the den over the entire spring period were similar. Comparisons of both of these sex ratios with the sample of dead snakes is informative. The overall numbers tell us that females experience proportionately less mortality than do males. The spring sample of live snakes tells us that crows take male and female snakes in approximately the same proportions as we encounter them at that time of year. In combination, the two comparisons suggest that crows exert sex-biased predation because of sex differences in behaviors (especially, duration of postemergence residency) that determine a snake's vulnerability to any predator—humans as well as crows.

The considerable body of research carried out at the Manitoba dens allows us to interpret mechanisms responsible for the biases we see in mortality patterns. For example, the tendency for crows to kill small rather than large snakes (of both sexes) probably reflects simple preference by the birds. Extensive data show that small snakes do not differ substantially from larger conspecifics in traits such as times of emergence, body temperatures, alertness (as judged by posture or response to human approach) or locomotor speed (Shine and Mason 2001). The tendency for crows to carry exceptionally small snakes back to their nest is likely to reflect the greater ease of transporting these snakes. The opposite bias—for birds to carry large items back to the nest, but consume smaller items in situ—has been documented in other birds (e.g., Sonnerud 1989).

Because male and female garter snakes differ in body size as well as behavior, the influence of sex on vulnerability to mortality sources is complex. Females were taken by crows more often than would be expected from their larger body size. Plausibly, this bias reflects the fact that most females

near the den are newly emerged, and hence are likely to be colder, less alert, and with lower crawling speeds than the male snakes around them (R. Shine et al. 2000a). Most males near the den have been out and about for a longer period than these females. Also, the livers of females might provide a more nutritious meal to a crow (Mason 1993; Bonnet et al. 1998). On the other hand, the lower residency period of females near the den substantially reduces their vulnerability to this form of mortality.

Suffocation kills mostly males because most courting aggregations contain only one female and several males (Mason and Crews 1986). Smaller males experienced disproportionately higher mortality, presumably because they found it more difficult to escape from the pile of snakes. In contrast, it was larger rather than smaller females that died from suffocation. Enclosure studies offer a reason for this bias: Larger females attract larger numbers of courting males (Hawley and Aleksyuk 1976; Joy and Crews 1985; R. Shine et al., 2001) and thus are more likely to find themselves crushed beneath an excessive mass of suitors. Suffocation mortality was also biased toward thinner-bodied snakes, in both sexes; these animals may have been weaker and thus less able to escape their doom. Suffocation events occur infrequently, because they depend upon weather conditions concentrating all the snakes within a den into small patches of sunlight (pers. obs.).

Body condition was also the most important determinant of mortality due to unknown causes, presumably involving depletion of energy reserves past some critical threshold. Females were the sex most often involved (Fig. 2). Female garter snakes are generally more heavily bodied than males, but all of the snakes dying from this cause were extremely thin (Fig. 3). Females reproduce less than annually in this population (Gregory 1977). Females of viviparous snake species are often emaciated after giving birth, and many die before they can recover body condition (e.g., Madsen and Shine 1993; Luiselli 1995; Luiselli et al. 1996). The long migration back to the den typical of cold-climate garter snake populations (up to 20 km; Larsen 1987) may well have contributed to the poor body condition of these animals.

Although the causes of these patterns of mortality are relatively straightforward, their consequences are less clear. Overall, the probability of a snake's survival depended on

its body size and condition, but in different ways for different kinds of mortality and for the two sexes (Table 1). The role of body condition seems relatively straightforward. Snakes in better body condition tended to survive better than thinner animals for at least two of the three mortality sources identified in our analysis; this was true within both males and females (Table 1). We do not know if body condition also affected an animal's vulnerability to predators. Predation is biased toward animals in poor condition in some systems (e.g., Koivunen et al. 1996), but the reverse is true in others (e.g., Rohner and Krebs 1996).

A snake's body size also affected its probability of survival, but differently in males and females. Larger body size significantly enhanced survival prospects for male garter snakes in terms of all three mortality sources that we documented (i.e., suffocation, predation, and unknown causes; Table 1). Larger body size also enhances mating success of male snakes within this population (Shine et al. 2000b; contra Joy and Crews 1988), suggesting that larger male size may be under strong positive selection. However, larger snakes will also tend to be older snakes, and thus our estimates of the survival advantages to larger body size (Table 1) are confounded with age. The effects of body size on survival rates of female garter snakes were more complex. Larger body size made a female less vulnerable to predation (as was the case for males), but increased rather than decreased mortality due to suffocation (larger females attracted more males and thus were more likely to be crushed) and unknown causes (possibly due to higher maintenance metabolic costs).

These mortality patterns may generate selective forces not only on the traits themselves (body size and condition), but also on more general aspects of spatial ecology. For example, predator preferences for small snakes may be one of the factors responsible for small (juvenile) snakes overwintering away from the large communal dens. Mortality through suffocation may impose a density-dependent upper limit on the numbers of snakes using any particular den and may favor males that join small courting groups around the den's perimeter, rather than joining larger groups within the den itself.

Clearly, we need more studies before we can interpret the significance of these findings. Our results are based on only a single population over a few weeks in one year. Even during this period, other sources of mortality were undoubtedly at work but were not detected by us. For example, the stench of rotting snakes from inside the den in late spring suggests that many animals may die during winter (for further reports of this phenomenon, see Gregory and Stewart 1975; Gregory 1977). Other mortality sources will operate as the snakes disperse to their summer ranges and as they move around those areas. Studies at other times and on other systems will be needed to see if the patterns detected in our analyses are of general importance or specific to red-sided garter snakes as they court and mate around their dens in central Manitoba.

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#### LITERATURE CITED

- Acharya, L. 1995. Sex-based predation on moths by insectivorous bats. *Anim. Behav.* 49:1461-1468.
- Aleksiuik, M., and K. Stewart. 1971. Seasonal changes in the body composition of the garter snake (*Thamnophis sirtalis parietalis*) at northern latitudes. *Ecology* 52:485-490.
- Andren, C., and G. Nilson. 1981. Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, *Vipera berus*. *Biol. J. Linn. Soc.* 15:235-246.
- Bonnet, X., R. Shine, G. Naulleau, and M. Vacher-Vallas. 1998. Sexual dimorphism in snakes: different reproductive roles favour different body plans. *Proc. R. Soc. Series B* 265:179-183.
- Brodie, E. D. I. 1993. Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* 47:227-235.
- Bronikowski, A. M., and S. J. Arnold. 1999. The evolutionary ecology of life history variation in the garter snake *Thamnophis elegans*. *Ecology* 80:2314-2325.
- Brown, C. R., and M. B. Brown. 1998. Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. *Evolution* 52:1461-1475.
- Bumpus, H. 1899. The elimination of the unfit as illustrated by the introduced sparrow, *Passer domesticus*. *Mar. Biol. Lab., Biol. Lect.* (Woods Hole, 1898):209-228.
- Buttemer, W. A. 1992. Differential overnight survival by Bumpus' house sparrows: an alternate interpretation. *Condor* 94:944-954.
- Christian, K. A., and R. Tracy. 1981. The effect of the thermal environment on the ability of hatchling land iguanas to avoid predation during dispersal. *Oecologia* 49:218-223.
- Daly, M., M. Wilson, P. R. Behrends, and L. F. Jacobs. 1990. Characteristics of kangaroo rats, *Dipodomus merriami*, associated with differential predation risk. *Anim. Behav.* 40:380-389.
- Dickman, C. R., M. Predavec, and A. J. Lynam. 1991. Differential predation of size and sex classes of mice by the barn owl, *Tyto alba*. *Oikos* 62:67-76.
- Ehrlich, P., and J. Camin. 1960. Natural selection in Middle Island water snakes (*Natrix sipedon*). *Evolution* 14:136.
- Endler, J. A. 1986. *Natural selection in the wild*. Princeton Univ. Press, Princeton, NJ.
- Gregory, P. T. 1974. Patterns of spring emergence of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake region of Manitoba. *Can. J. Zool.* 52:1063-1069.
- . 1977. Life-history parameters of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in an extreme environment, the Interlake region of Manitoba. *Nat. Mus. Canada, Publ. Zool.* 13: 1-44.
- Gregory, P. T., and K. W. Stewart. 1975. Long-distance dispersal and feeding strategy of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba. *Can. J. Zool.* 53: 238-245.
- Hawley, A. W. L., and M. Aleksiuik. 1975. Thermal regulation of spring mating behavior in the red-sided garter snake (*Thamnophis sirtalis parietalis*). *Can. J. Zool.* 53:768-776.
- . 1976. Sexual receptivity in the female red-sided garter snake (*Thamnophis sirtalis parietalis*). *Copeia* 1976:401-404.
- Holland, P. K., and D. W. Yalden. 1995. Who lives and who dies?

- The impact of severe April weather on breeding common sandpipers, *Actitis hypoleucos*. *Ring and Migration* 16:121–123.
- Holomuzki, J. R., and T. M. Short. 1990. Ontogenetic shifts in habitat use and activity in a stream-dwelling isopod. *Holarctic Ecol.* 13:300–307.
- Janzen, F. J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. *Ecology* 74:332–341.
- Janzen, F. J., and H. S. Stern. 1998. Logistic regression for empirical studies of multivariate selection. *Evolution* 52:1564–1571.
- Jayne, B. C., and A. F. Bennett. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44:1204–1229.
- Joy, J. E., and D. Crews. 1985. Social dynamics of group courtship behavior in male red-sided garter snakes (*Thamnophis sirtalis parietalis*). *J. Comp. Psychol.* 99:145–149.
- . 1988. Male mating success in red-sided garter snakes: size is not important. *Anim. Behav.* 36:1839–1841.
- Koivunen, V., E. Korpimäki, and H. Hakkarainen. 1996. Differential avian predation on sex and size classes of small mammals: doomed surplus or dominant individuals? *Ann. Zool. Fennici* 33:293–301.
- Larson, K. 1987. Movements and behavior of migratory garter snakes, *Thamnophis sirtalis*. *Can. J. Zool.* 65:2241–2247.
- Luiselli, L. 1995. The mating strategy of the European adder, *Vipera berus*. *Acta Oecol.* 16:375–388.
- Luiselli, L., M. Capula, and R. Shine. 1996. Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps. *Oecologia* 106:100–110.
- Madsen, T. 1987. Are juvenile grass snakes, *Natrix natrix*, aposematically coloured? *Oikos* 48:265–267.
- Madsen, T., and R. Shine. 1993. Costs of reproduction in a population of European adders. *Oecologia* 94:488–495.
- Mason, R. T. 1993. Chemical ecology of the red-sided garter snake, *Thamnophis sirtalis parietalis*. *Brain Behav. Evol.* 41:261–268.
- Mason, R. T., and D. Crews. 1986. Pheromone mimicry in garter snakes. Pp. 279–283 in D. Duvall, D. Muller-Schwarze, and R. M. Silverstein, eds. *Chemical signals in vertebrates*. Vol. 4. Plenum, New York.
- Parker, W. S., and M. V. Plummer. 1987. Population ecology. Pp. 253–301 in R. A. Seigel, J. T. Collins, and S. S. Novak, eds. *Snakes: ecology and evolutionary biology*. Macmillan, New York.
- Pugsek, B. H., and A. Tomer. 1996. The Bumpus house sparrow data: a reanalysis using structural equation models. *Evol. Ecol.* 10:387–404.
- Rohner, C., and C. J. Krebs. 1996. Owl predation on snowshoe hares: consequences of antipredator behavior. *Oecologia* 108:303–310.
- Rossman, D. A., N. B. Ford, and R. A. Seigel. 1996. *The garter snakes: evolution and ecology*. Univ. of Oklahoma Press, Norman, OK.
- Shine, R., and R. T. Mason. 2001. Courting male garter snakes use multiple cues to identify potential mates. *Behav. Ecol. Sociobiol.* *In press*.
- Shine, R., M. M. Olsson, I. T. Moore, M. P. LeMaster, and R. T. Mason. 1999. Why do male snakes have longer tails than females? *Proc. R. Soc. Ser. B* 266:2147–2151.
- Shine, R., P. S. Harlow, M. P. LeMaster, I. Moore, and R. T. Mason. 2000a. The transvestite serpent: why do male garter snakes court (some) other males? *Anim. Behav.* 59:349–359.
- Shine, R., M. M. Olsson, I. Moore, M. P. LeMaster, M. Greene, and R. T. Mason. 2000b. Body size enhances mating success in male garter snakes. *Anim. Behav.* 59:F4–F11.
- Shine, R., M. J. Elphick, P. S. Harlow, I. T. Moore, M. P. LeMaster, and R. T. Mason. 2000c. Movements, mating and dispersal of red-sided gartersnakes from a communal den in Manitoba. *Copeia* 2000: *In press*.
- Shine, R., D. O'Connor, M. P. LeMaster, and R. T. Mason. 2001. Pick on someone your own size: ontogenetic shifts in mate choice by male garter snakes result in size-assortative mating. *Anim. Behav.*: *In press*.
- Sonerud, G. A. 1989. Allocation of prey between self-consumption and transport in two different-sized central place foragers. *Ornis Scand.* 20:69–71.
- Turner, F. B. 1977. The dynamics of populations of squamates, crocodylians and rhyncocephalians. Pp. 157–264 in C. Gans and D. W. Tinkle, eds. *Biology of the Reptilia*. Academic Press, New York.
- Villafuerte, R., J. A. Litvaitas, and D. F. Smith. 1997. Physiological responses by lagomorphs to resource limitations imposed by habitat fragmentation: implications for condition-sensitive foraging. *Can. J. Zool.* 75:148–151.

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