



Patterns of mortality in a cold-climate population of garter snakes (*Thamnophis sirtalis parietalis*)

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Abstract

The causes, magnitude and phenotypic determinants of mortality are central features of population demography. Although critical to effective conservation planning, these attributes remain poorly understood for most wild vertebrates. Exceptionally dense aggregations of garter snakes (*Thamnophis sirtalis parietalis*) in and around communal overwintering dens in central Manitoba provide an exceptional opportunity to enumerate these factors. Over the course of long-term field studies we obtained data on mortality of snakes in autumn as they migrated back from their summer ranges, and in winter during and after their entry into the underground dens. Some mortality sources were affected by a snake's phenotype: for example, snakes killed by motor vehicles were smaller, on average, than surviving snakes. However, two major episodes of mortality at the dens themselves (freezing during midwinter due to atypically light snow cover; and drowning due to flooding after heavy rains late in autumn) were essentially random with respect to phenotype. Mark-recapture estimates suggest that the winterkill event eliminated >60,000 snakes, comprising almost the entire populations of the three largest dens. Although such events are cryptic because the bodies of frozen animals remain underground, they are of much greater magnitude than overt mortality sources for active snakes (roadkills, predation, etc.). Thus, relatively minor habitat manipulations around the dens may contribute more to conservation of these populations than would extensive efforts to protect active snakes during their spring and autumn migrations.

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1. Introduction

One of the most fundamental questions that one can ask about any natural population involves the causes and magnitude of mortality. Animals in wild populations die for several reasons, such as disease, parasitism, starvation, and predation. Ecological models suggest that rates of mortality are major determinants of demographic processes in animal populations, because of mechanisms acting at two temporal scales. On an immediate level, mortality can substantially affect not only overall abundance and population persistence, but also demographic traits such as the age-structure and adult sex ratio (Caughley, 1977). On a longer (evolutionary)

timescale, patterns of mortality may influence the evolution of species-specific attributes as diverse as anti-predator tactics, seasonal activity schedules and habitat selection, and life-history traits (Roff, 1992; Lima, 1998).

Information on the magnitude, causes and phenotypic correlates of mortality can also be of direct benefit to wildlife resource managers (Caughley, 1977; Caughley and Sinclair, 1994). Anthropogenic activities that add to existing sources of mortality must be viewed within the wider framework of natural survival schedules. Killing by humans often occurs at different times and in different places than most natural mortality, and is directed at subsets of the population that differ phenotypically from those most vulnerable to other mortality sources. For example, hunting may remove large, adult males because of their greater value for trophies (e.g. deer: Caughley and Sinclair, 1994) or because their larger body size provides more meat (e.g. kangaroos:

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Grigg, 1995). Alternatively, reproductive females may be at most risk because they are easier to catch (e.g. watersnakes: Shine, 1986), or juveniles may be targeted for removal because of their value to the pet trade (e.g. pythons: Ross and Marzec, 1990; Groombridge and Luxmoore, 1991). To understand the impact of such selective mortality from human activities, we need to place it within the overall context of mortality from other sources.

Thus, we need to understand more about issues such as the causes of mortality, the magnitude of mortality, and the degree to which different types of mortality impact on different subsets of the population with respect to traits such as sex, age and body size. Despite general agreement as to the importance of this topic, robust empirical data on mortality rates are available for relatively few populations of free-living vertebrates. The reason is straightforward: it is logistically daunting to quantify mortality schedules, because each individual's death provides only a single data point. It is rare to find circumstances in natural populations where we can actually observe mortality events (or more realistically, locate large numbers of dead individuals) and thus, can estimate the magnitude of mortality and its selectivity with respect to the organisms' phenotypes. We have taken advantage of an unusual opportunity in this respect, provided by an exceptionally dense concentration of free-ranging snakes around communal overwintering dens in the prairies of central Canada. In the course of longterm ecological studies on the ecology, physiology and behavior of these snakes, we have gathered several data sets that illuminate patterns of mortality. The present paper provides these data.

2. Materials and methods

2.1. Study species and area

Red-sided garter snakes (*Thamnophis sirtalis parietalis*) are small (males to 0.8 m, females to 1.0 m total length) non-venomous colubrid snakes (Rossman et al., 1996). In severely cold northern parts of their range, these snakes rely upon relatively deep crevices for overwintering, to escape lethally low temperatures close to the soil surface. Because suitable sites are rare, snakes gather in very large numbers in such dens (Gregory, 1974; Hawley and Aleksyuk, 1975, 1976). This situation facilitates scientific study, so that snake dens near the town of Chatfield in central Manitoba (100 km north of Winnipeg) have been the focus of considerable research over many years. The Narcisse Community Pasture (50°44'N 97°34'W; see Mason and Crews, 1985; Mason, 1993 for details) contains three main dens with very large numbers of snakes. Each den is about 1 km from each of the others. The dens themselves are rocky depressions

(ranging from 2×10 to 5×10 m in size), and about 2 m deep. The sides and base of the dens contain many small holes into which the snakes disappear in autumn and from which they reappear in spring. The limestone underlying these dens is riddled with crevices that allow the snakes to penetrate deep underground. As well as these three major dens, several superficially similar locations within the same general area (<1 km from the main dens) also contain thousands of snakes during winter. Many even smaller dens are scattered throughout the surrounding pastures, sometimes comprising small (1×1 m) sinkholes in open grassy areas.

Juvenile snakes do not use these dens in their first winter of life, but apparently find their way to dens in later years by following pheromonal trails deposited by adult snakes (Gregory, 1974, 1977; Gregory and Stewart, 1975; Mason, 1992; Lawson, 1994). Courtship and mating occur at the den prior to dispersal. Adult males remain near the den for about two weeks whereas females disperse within a day or two of emerging; thus, the operational sex ratio in the den area is highly male-biased during spring (Shine et al., 2001a) and the area immediately surrounding the den can contain many thousands of mate-searching male snakes. Snakes may disperse up to 20 km from the den to their summer feeding ranges (Gregory and Stewart, 1975; Larsen, 1987; Larsen and Gregory, 1989; Lawson, 1989). After their relatively brief (four-month) activity period, the snakes migrate back to the den and remain active near the den entrance for a week or two before going underground.

In a previous study of the Chatfield dens, we documented several sources of mortality for snakes in spring (May) and identified phenotypic biases in vulnerability (Shine et al., 2001b). Predation by crows (*Corvus brachyrhynchos*) killed 590 snakes, primarily smaller animals. Suffocation inside massive courting groups killed 42 females (mostly large animals) plus 259 males (mostly small animals). Depletion of energy reserves may have contributed to mortality of an additional 142 snakes, especially females in poor body condition.

2.2. Methods

The present paper combines data sets taken over several years at the Chatfield dens. We combined these data to look at changes through time, but each of our analyses of phenotypic biases in mortality is based on information gathered during only a single season to avoid combining data from seasons with different sex ratios or body sizes in the samples. Our data clarify mortality acting over winter and during autumn, as follows:

2.2.1. Mortality due to freezing in winter

We conducted mark-recapture studies on male snakes at the three large Chatfield dens in spring (May)

of 1997 and 1998. We also recorded sexes and body sizes of snakes from these dens over the period from 1992 to 2002, although sample sizes varied considerably. Because these den populations experienced catastrophic mortality over the winter of 1998–99 (see below), these data enable us to characterize the numbers and phenotypes of snakes that died during this event, and the attributes of survivors and recolonizers after that time. Our recapture data also enable us to explore the degree of den fidelity, relevant to the potential rate of recolonization. Specific methods were as follows:

- (a) *Phenotypes* – In the course of several studies since 1992, we collected, sexed, measured and weighed samples of snakes from the Chatfield dens. We have combined these data (mostly from pairs of snakes found mating at the dens) to examine year-to-year changes in mean body sizes and body condition (mass relative to length, analysed using ANCOVA).
- (b) *Population estimates* – In 1997 and 1998, immediately prior to the massive winterkill, we obtained Bailey's Triple-Catch estimates (Caughley, 1977) of the numbers of male snakes at each of the large dens. The procedure was to collect 500 male snakes at each den on a single day, and mark them ventrally with a colored pen. The snakes were then released. We repeated the procedure the following day (or two days later, if cold weather intervened), marking with another color and recording the number of recaptured snakes. The third day saw another repeat of this procedure, yielding data on the numbers of males caught once, twice and three times at each of the dens. Because the snakes were marked on their ventral surfaces, we could not distinguish marked from unmarked animals until we picked them up and hence, our recapture rates were not biased by previous marking. We also conducted a triple-catch estimate at one of the Chatfield dens in 2001, but marking only 100 rather than 500 snakes per day.
- (c) *Den fidelity* – We scale-clipped male snakes in both spring and autumn in 1995 through 1997 to provide individual identification, and examined the source den for each snake recaptured in a subsequent season.

2.2.2. Mortality due to den flooding

We identified two major sources of mortality during autumn, and gathered separate data sets to quantify these processes. The first event involved flooding around a small den in autumn 2000. This den (the "south pasture den") lies in a small wooded area among pastureland less than 300 m from one of the main Chatfield dens (the "south den"). When we visited the den early in spring (2 May 2001), soon after the snow had melted from the surrounding area, we found the bodies of many snakes that had drowned while entering the den the

previous autumn (see Section 3.2 for evidence that flooding was responsible for this mortality). We collected, sexed and measured these snakes, as well as a sample of live snakes from the nearby "north pasture den" 30 m away.

2.2.3. Mortality due to motor vehicles

The other obvious source of mortality in autumn is that snakes returning to the dens are killed by motor vehicles on Highway 17. Tunnels constructed under the roadway have substantially reduced this carnage (Shine and Mason, 2001), but many snakes are still killed by vehicles. In September 2002, we collected all freshly killed snakes along the highway adjacent to the Chatfield dens, as well as a sample of live snakes from the dens themselves.

3. Results

3.1. Mortality due to freezing in winter

3.1.1. The winterkill event of 1998–99

Snakes have emerged from the Chatfield dens in large numbers by mid-May during annual fieldwork over more than 20 years (R.T. Mason, personal observation). However, virtually no snakes were seen throughout May 1999, despite daily checks of the dens. Excavation at the "north den" in June 1999 revealed masses of dead snakes close to the ground surface (D. Roberts, personal communication). The winter of 1998–99 was unusual in that snow cover was much lighter than usual during midwinter (A. Johnson, personal communication) and thus, the ground froze much deeper. Sewage in underground tanks in the area was still frozen solid in late May 1999, long after the usual date of thawing. It thus seems that the snakes froze to death inside their dens because deep-soil temperatures fell to lethally low levels, due to the lack of insulating snow cover in midwinter.

3.1.2. Snake abundances before and after the winterkill event

Bailey's Triple-Catch estimates for numbers of male snakes at each of the Chatfield dens prior to the 1998–99 winterkill ranged from 3196 to 5751 per den (mean of six estimates = 4497). The total number of male snakes emerging from each den would be much greater than this number because (1) many males disperse after about two weeks, and new males continue to emerge throughout a period of about six weeks in May–June (Gregory, 1974; Shine et al., 2001a); and (2) radiotelemetry shows that at least one-third of males spend most of their time more than 20 m from the dens (Shine et al., 2001a). Thus, the total population of male garter snakes at each den probably was greater than 10,000 animals. Approximately equal numbers of males and females use the dens

(Shine et al., 2001a,b), so the total number of snakes in each den would have been around 20,000 (and thus, the three dens in total contained about 60,000 snakes). We note that Bailey's method assumes equal catchability and a closed population, so the estimates may be imprecise if these assumptions were violated. Nonetheless, all that is required for the current analysis is the general order of magnitude of population numbers.

In the spring following this winterkill event (May 1999), the maximum number of snakes that we recorded active at the main dens on a single day (counted directly not subsampled, because of the lower numbers) was 168 (48 males, 120 females). Numbers have increased slightly in subsequent years, and by 2001 were high enough at one den (the south den) for us to attempt another Triple-Catch estimate. We recaptured 16 of the 200 marked snakes, for an overall population estimate of 337 males.

3.1.3. Body sizes and body condition of snakes before and after the winterkill event

We collated data on snout-vent lengths (SVLs) and masses for 5541 snakes over 10 years. We analyzed data

on SVL using three-factor nested ANOVA with sex, year nested within time period (before vs. after the winterkill event) and time period as the factors; effects involving time period were tested against the nested factor rather than the residual error term. Data on body condition were analyzed with a similar design but using ANCOVA not ANOVA, by including SVL as a covariate and ln mass as the dependent variable. These analyses revealed that the mean SVLs of snakes differed between the sexes ($F_{1,5529} = 910.82$, $P < 0.0001$) and varied significantly among years ($F_{8,5529} = 9.13$, $P < 0.0001$). Snakes were consistently larger before the winterkill event than afterwards, in both sexes ($F_{1,5529} = 6.08$, $P < 0.04$) but the magnitude of the size decrease was greater in females than in males (interaction between time period and sex, $F_{1,5529} = 29.80$, $P < 0.0001$; see Fig. 1). Body condition of snakes (mass relative to length) also varied according to sex ($F_{1,5529} = 55.88$, $P < 0.0001$) and year ($F_{8,5529} = 352.57$, $P < 0.0001$) but was not affected by the winterkill event ($F_{1,5529} = 0.24$, $P = 0.64$; interaction sex vs. time period, $F_{1,5529} = 1.84$, $P = 0.18$; see Fig. 1). Sex ratios of the

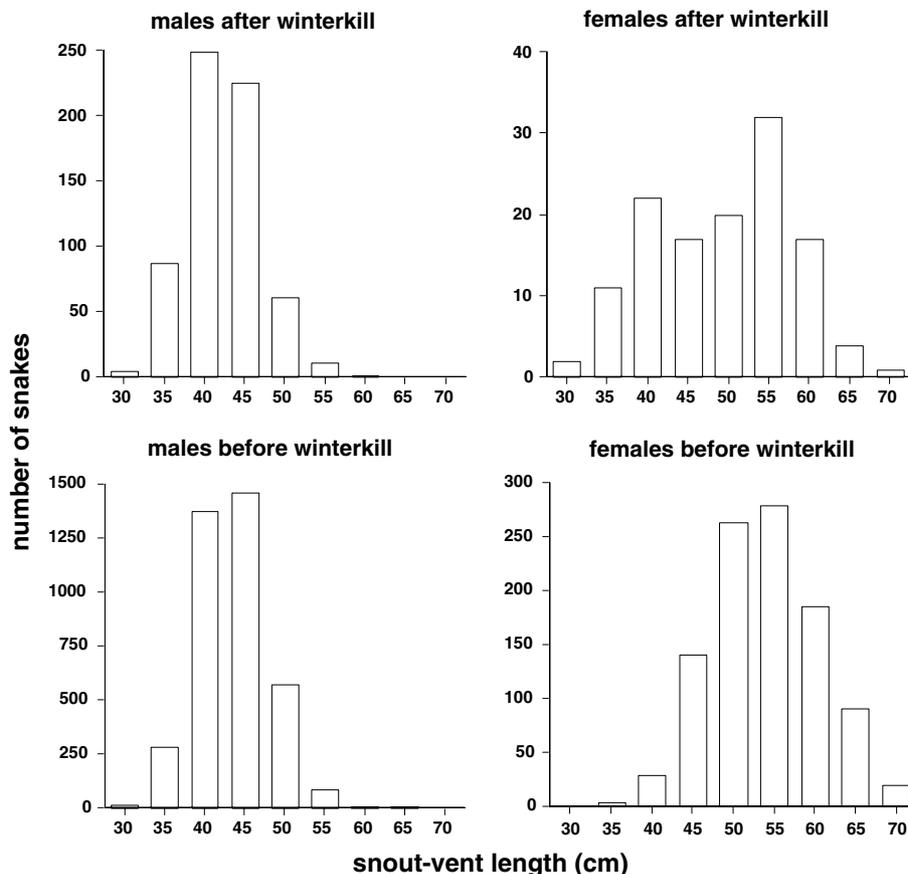


Fig. 1. Body sizes of male and female garter snakes (*T. sirtalis parietalis*) at three large communal overwintering dens near Chatfield, Manitoba. The upper graphs show data for samples taken after the major winterkill event of 1998–99, and the lower graphs show data for snakes collected prior to that event. Sample sizes were 3790 males and 1018 females sampled prior to the winterkill (1992–1998), and 637 males and 126 females sampled after the winterkill (1999–2002).

samples differed significantly before vs. after the winterkill ($\chi^2 = 8.66$, 1 df, $P = 0.0033$) but the disparity was small (79.1% vs. 83.8% male) and is difficult to interpret given that data were gathered for different purposes at different times (e.g. pre-winterkill data often included mating pairs and thus included a higher proportion of females than would be true of random collections).

3.1.4. Den fidelity

The numbers and source of recolonizing animals after a catastrophic mortality event will depend upon the degree to which snakes return to the same dens to overwinter each winter. If den fidelity is strong, recruitment after mass mortality may be very slow. We can assess this parameter with our mark–recapture data from the main Chatfield dens prior to the mortality event. These three dens are separated by less than 1 km, and radiotracked male snakes sometimes moved between dens within a day during courtship activities in spring (Shine et al., 2001a). Thus, we might expect snakes to use different dens in successive winters unless they display active philopatry. Of 191 adult male snakes that were individually marked in one year and recaptured after one to three summer seasons, 167 (87%) had returned to the same den in which they were marked. We conclude that these animals display high philopatry and effective homing, with most snakes returning each year to the same den in which they had spent their previous winter. This result reinforces the conclusion that the massive decline in snake numbers at the main dens after the 1998–99 winter was due to mortality rather than emigration.

3.2. Mortality due to den flooding

When we visited the north pasture den on 2 May 2001, we found many dead snakes. Some were actually within the den entrance with their heads inside ingress holes, whereas others were up to 20 m away. Most were in lifelike poses; several times we thought that we had found live animals rather than dead ones. Closer inspection revealed that the animals had been dead for several months, and under water or snow for most of that time. There was little obvious decomposition, but many of the dead snakes were coated in algae, and had attracted numerous notonectid (water) beetles. Of the 123 dead snakes that we recovered (many others could be seen further down inside the den entrance but were inaccessible), 79 (64%) were female. A sample of live snakes from the adjacent north pasture den had only 20% female (36 of 177). Autumn surveys (which are not affected by differences between the sexes in duration of residency at the den: Shine et al., 2001a) show a 50:50 sex ratio (Shine et al., 2001b). Comparing the observed sex ratio to a 50% null expectation confirms that the sample of dead snakes was disproportionately female-

biased ($\chi^2 = 9.96$, 1 df, $P < 0.01$). However, body-size distributions of the dead snakes did not differ from those of live snakes collected in the adjacent den (Fig. 2). Log-likelihood tests from a logistic regression on these two samples (live vs. dead as dependent variable) confirmed that dead snakes were more likely to be females than males ($\chi^2 = 32.75$, 1 df, $P < 0.0001$) but that body-size distributions did not differ between the victims and the survivors ($\chi^2 = 0.26$, 1 df, $P = 0.61$).

What killed these snakes? Drowning due to a sudden onset of cold weather, heavy rainfall and consequent flooding provides the likely explanation. The autumn of 2000 was unusual (unique in the previous 60 years: A. Johnson, personal communication) in that weather conditions in autumn abruptly changed from very warm to cold, coincident with very heavy rain turning to snow after two days. Many low-lying areas flooded, and then the water in these areas froze solid down to ground level. Because of local topography, the paddocks adjacent to the south pasture den collect rainfall such that it flows down into the den. Marks and mud on the surrounding vegetation suggest that water and snow lay up to approximately 20 cm deep over the whole area through much of winter. The nearby north pasture den is on slightly higher ground, and so was not flooded.

3.3. Mortality due to motor vehicles

A busy rural highway (#17) runs north–south approximately 1 km from the three main Chatfield dens, and many snakes are killed by vehicles as the animals disperse from the dens in spring and when they return in autumn. In autumn (September) 2002, we collected 129 road-killed snakes along Highway 17 adjacent to the main Chatfield dens, as well as 99 live snakes randomly sampled from the main dens. Sex ratios differed significantly between the two samples; females comprised only 50 of 129 dead snakes (39%) but 54 of 99 live snakes (55%; $\chi^2 = 5.01$, 1 df, $P < 0.025$), and most road-killed snakes were smaller than the live animals sampled at the same time (Fig. 3). Interpretation of these results is complicated by the covariation between sex and body size: females grow larger than males, so that the apparent sex effect on survival could be a secondary consequence of the body-size effect (or vice versa). A multivariate test that includes both independent variables can clarify this possibility. Log-likelihood ratio tests from a multiple logistic regression showed that dead snakes were smaller than live animals ($\chi^2 = 8.17$, 1 df, $P < 0.005$). Males and females were equally vulnerable ($\chi^2 = 0.37$, 1 df, $P = 0.54$) but an animal's body length affected its vulnerability more in females than in males (interaction, $\chi^2 = 6.17$, 1 df, $P < 0.02$). Thus, the largest snakes (large females) were less at risk from motor vehicles than were smaller snakes of either sex within this population.

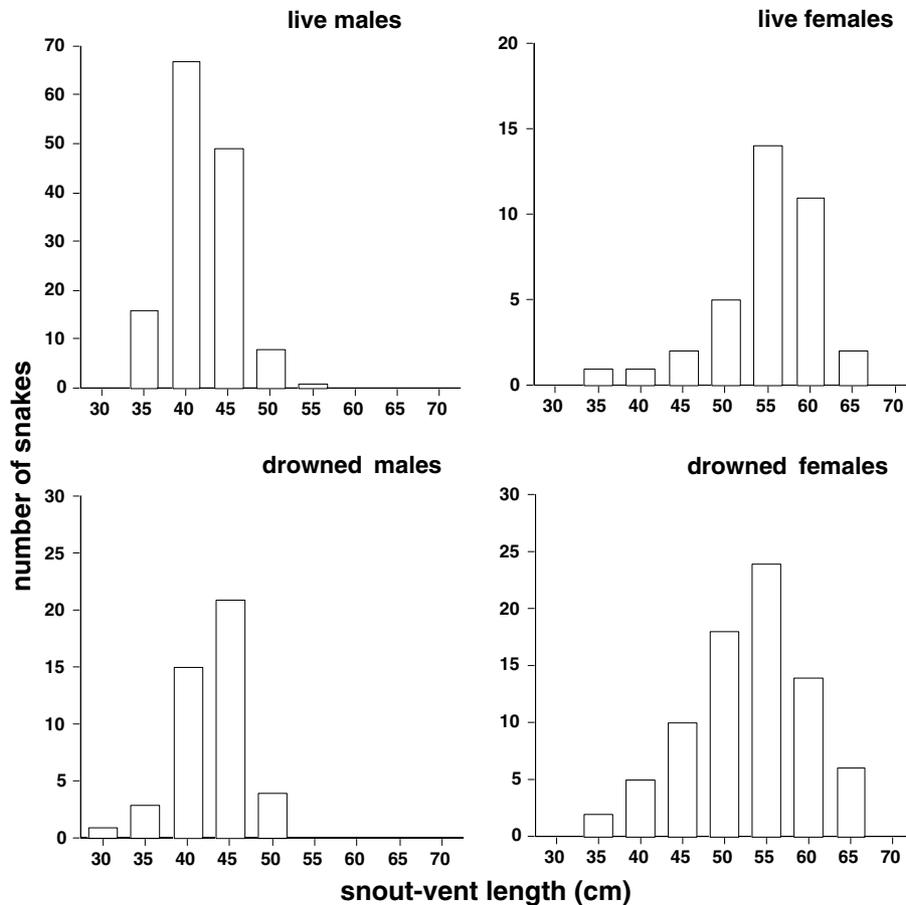


Fig. 2. Body sizes of male and female garter snakes (*T. sirtalis parietalis*) at a communal overwintering den near Chatfield, Manitoba (live snakes) and at a nearby den where all snakes were drowned during autumn floods (drowned snakes). Both samples were collected on the same day in spring (2 May 2001). Sample sizes were 141 live males and 36 live females, and 44 dead males and 79 dead females.

4. Discussion

In combination with our previous analyses of mortality in courting aggregations of snakes at the Chatfield dens in spring (Shine et al., 2001b), the present study provides an unusually extensive data set with which to evaluate mortality patterns in this population. Information on mortality during summer would also be valuable, but is logistically more challenging because the snakes are widely dispersed at this time of year. Substantial differences are evident between patterns of mortality in spring and those in autumn. These involve three attributes: (1) the causes of mortality; (2) the degree to which an animal's phenotype (its sex and body size) influenced its vulnerability; and (3) the numbers of snakes that were killed.

4.1. Causes of mortality

The primary causes of mortality identified by our study in spring were predation by crows and suffocation by other snakes inside the massive "mating balls" that sometimes form during courtship. Neither of these

causes was significant in autumn. Courtship and mating are seen only rarely in autumn (Gregory, 1977), but crows are present at this time (R. Shine, personal observation). Why do crows not take many snakes in autumn, as they do in spring? The answer involves the snake's behavior (undistracted by courtship, they are much more wary in autumn than in spring; R. Shine, personal observation) and locomotor abilities (lower in spring because of cooler weather and the need to recover from the long period of winter inactivity; Shine et al., 2001a), as well as the crow's own energy needs (they raise offspring in spring but not in autumn). Roadkills are common at both times of year, but more obvious in autumn than spring because snakes returning to the den tend to follow consistent migration routes whereas dispersing snakes in spring head off in all directions (Shine et al., 2001a). Thus, roadkills in autumn are concentrated in relatively short stretches of the road (Krivda, 1993). Mortality at the den itself is much less obvious, because most of the dead snakes are hidden below-ground. Floods can cause mortality in spring as well as in autumn (Gregory, 1977).

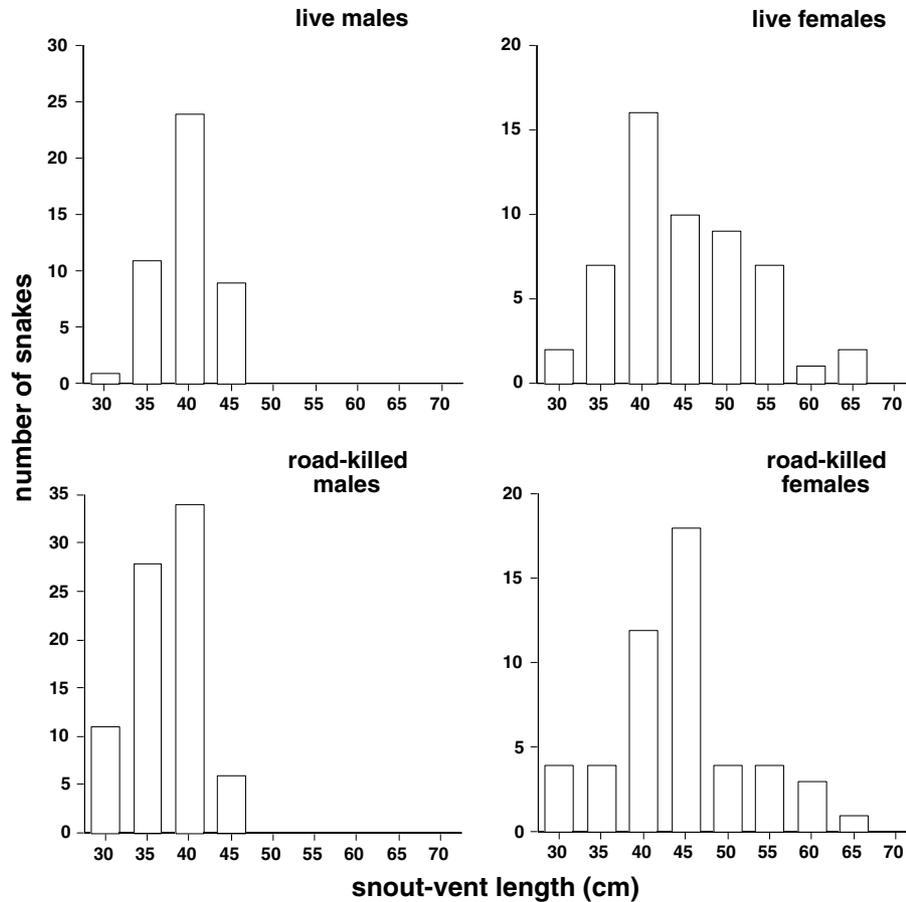


Fig. 3. Body sizes of male and female garter snakes (*T. sirtalis parietalis*) at communal overwintering dens near Chatfield, Manitoba (live snakes) and from a nearby highway where these snakes were killed by motor vehicles (road-killed snakes). Both data sets were collected in September 2002. Sample sizes were 45 live males and 36 live females, and 79 dead males and 50 dead females.

Although the exact numbers of snakes killed within the den during winter necessarily remain unclear, the causal mechanisms seem straightforward. It remains possible that some other event (disease? blocking of egress holes?) within a den was involved, but the circumstantial evidence for freezing is strong. Laboratory and field experiments confirm that few red-sided garter snakes can survive temperatures below freezing for more than a few hours (Bailey, 1949; Churchill and Storey, 1992). Gregory (1977, p. 37) describes exactly the same kind of winterkill scenario as we encountered and at one of the same dens, albeit based only on anecdotal information (“Hawley [personal communication] found large numbers of dead snakes below ground, in a den at which he was working at Narcisse, Manitoba, in the spring of 1973. Apparently, many of these had been frozen. . . Snowfall was light in the winter of 1972–73; this lack of insulation might have accounted for the snakes freezing underground”). Longterm records of snow cover in Canada reveal major changes over recent decades, notably a decrease in the mid-1970s that has continued through to the present day (Brown and

Braaten, 1998). In support of Hawley’s interpretation, snow cover in the Canadian prairies was lower in the winter of 1972–73 than in any year back to 1955 when records began; but fell below this level in seven of 19 years since 1973 (Brown and Braaten’s Fig. 7).

4.2. Phenotypic determinants of vulnerability

The major sources of mortality for snakes at the den were likely to strike snakes equally, irrespective of traits such as sex and body size. Except for juveniles, all snakes overwinter in the same dens and presumably, occupy similar sites within the den. Thus, neither flooding or freezing is likely to serve as a selective force on phenotypic traits. Why, then, were snakes at the Chatfield dens smaller after the 1998–99 winterkill event than had been the case before (Fig. 1)? The answer almost certainly involves a shift in age structure, with the post-winterkill population dominated by young animals entering the den population for the first time. This pattern was particularly evident among female snakes (Fig. 1).

In contrast, mortality occurring during spring, while the snakes are active, provides a greater opportunity for a snake's sex and body size to influence its behavior and thus, its vulnerability to mortality. Although we documented a sex bias in mortality due to flooding (more females died), this may simply reflect sex differences in the times of ingress to the den. Assuming that most or all snakes using the den were drowned (as is strongly suggested by the dearth of live snakes emerging from the den in spring 2001), this apparent sex bias in vulnerability is likely to be an artifact of behavioral differences between the sexes in autumn. The body-size bias in roadkills (larger snakes survived better than small snakes) cannot be dismissed in this way, and there are at least three plausible (and non-exclusive) explanations for this pattern. The first is that motorists can see bigger snakes and thus, avoid them. The second is that snakes of different body sizes use different migration routes or move at different times of day and thus encounter traffic at different times or places. The third is that larger body size enables a garter snake to maintain a higher body temperature (Seebacher and Shine, unpublished data) and thus, to escape more rapidly from an approaching vehicle. Further data are needed to test these alternative (and complementary) ideas.

The survival advantage conferred by larger body size in encounters with motor vehicles is interesting, in that fitness advantages to larger body size have already been documented in this population via other pathways. For example, larger females produce more offspring (Gregory, 1977), and larger males obtain more matings (Shine et al., 2000c), are less likely to be killed by crows, and are less likely to suffocate within mating balls (Shine et al., 2001b). Thus, several selective forces favor large body sizes in this population, possibly explaining why snakes attain larger sizes in this region than in most of the rest of their extensive geographic range (Rossman et al., 1996).

4.3. Magnitude of mortality

Although our evidence is indirect (primarily, the lack of emerging animals in spring), it seems likely that two of the mortality events that we recorded for snakes in the den area (flooding and freezing) extirpated the entire den populations in each case. Thus, this relatively non-selective form of mortality may have eliminated more than 60,000 snakes during the brief duration of our study. Anecdotal reports of freezing and flooding of dens in the same area in the 1970s, as well as low survival rates of snakes over winter even in the absence of such profound impacts (Gregory, 1977) suggest that such events may be common. Winterkill may also occur in other areas within the range of *T. sirtalis* (Michigan: Carpenter, 1952), and may be caused by more than one set of climatic circumstances. For example, the spring flood that killed all the snakes in Gregory's (1977) study

den in Manitoba was caused by snowmelt after unusually heavy winter snows (Gregory, 1977; Macmillan, 1995). Thus, overwintering snakes in the Manitoba Interlake may experience massive mortality either if snow cover is unusually light (causing freezing) or unusually heavy (causing flooding). Such sensitivity may have catastrophic consequences for denning populations, especially in a time of changing global climates (Brown and Braaten, 1998).

What are the long-term population consequences of such massive (albeit episodic) mortality events? The high philopatry of adult snakes to specific dens (Gregory, 1977; this study) suggests that garter snakes exhibit a strong metapopulation structure in the Interlake. Thus, separate dens may comprise relatively discrete populations, with frequent extinctions followed by low rates of recolonization (Macmillan, 1995). Exchange of individuals among dens may be most common for the youngest age classes, with juvenile snakes following the pheromonal trails of conspecific adults to locate communal dens (Lawson, 1994). If an entire den population is extirpated, however, there will be no pheromonal trails for the juveniles to follow, and the offspring of previous years' reproduction by animals from a given den will be "captured" by nearby dens with continuing viable adult populations. We believe that this occurred in the Chatfield area, with numbers of snakes at the "pasture dens" increasing dramatically in the autumn of 1999, after winterkill virtually eliminated snakes at the three "main" dens (personal observation). Ironically, many of these snakes then drowned a year later, when one of the two pasture dens flooded in the autumn of 2000.

The severe and variable climate of Manitoba imposes major challenges to garter snakes, generating substantial year-to-year variation in mortality and recruitment within populations of these animals (Gregory, 1977). The life-history attributes of *T. sirtalis* (fast growth, early maturation, and high fecundity: Gregory, 1977) enable populations to persist despite such variations. The tendency for juveniles to overwinter away from the main dens is critical in this respect, because otherwise an entire population could be wiped out by a single unfavorable weather event. Although the avoidance of dens by juveniles may thus facilitate population persistence, the behavior presumably has evolved for reasons related to advantages experienced by individuals and not populations (Williams, 1966). One likely reason is avoidance of substantial sexual harassment by hordes of reproductive males which court newly emerged males as well as females, and juvenile as well as adult conspecifics (Shine et al., 2000a,b). Such courtship may inflict significant costs to juvenile snakes (Shine et al., 2000b).

The clear implication from our data is that conservation and management of this snake population must give careful thought to the cryptic mortality that occurs inside the underground dens during winter, as well as to the

much more overt mortality (due to roadkills and predation, etc.) that occurs while the snakes are active in warmer times of year. In saying this, we do not wish to denigrate the outstanding accomplishments of the Manitoba Department of Natural Resources, ably assisted by local residents, to stop commercial exploitation of these snakes and to reduce roadkill mortality in this system. In earlier years, the highway carnage was so great that the road became slippery due to the crushed bodies of snakes; a bulldozer was brought from Winnipeg to scrape the bodies off the road so that cars could safely negotiate the highway (A. Johnson, personal communication). The construction of tunnels beneath the highway, combined with drift fences to direct the snakes into these tunnels, has massively reduced the numbers of snakes that are killed in this way (Shine and Mason, 2001).

Ameliorating the massive road toll of migrating snakes was clearly a high priority, from ethical as well as conservation perspectives (Krivda, 1993). However, the numbers of snakes now killed by vehicular traffic may be lower than those that drown or are frozen to death inside the dens during winter. We might usefully try to reduce this source of mortality also. For example, the generally flat topography would facilitate construction of small levee banks to prevent major flooding at vulnerable dens. Such barriers might also reduce the flow of eroded soil (especially from tourist activities) down into the dens; such material otherwise accumulates and will eventually block the snake's egress holes (R. Shine, personal observation). A more ambitious plan would be to provide additional insulation above the main dens, so as to reduce the depth of frost penetration during winter. The feasibility of such manipulations would require careful thought and additional data. For example, we have no clear idea of the spatial dispersion of snakes inside the den during winter. If they are concentrated in small areas close to the den entrance, then manipulation of the habitat above such areas might be feasible. On the other hand, snakes might be widely dispersed through underground cavities, such that any manipulation would have to occur at a greater spatial scale. We need innovative technologies (perhaps ground-penetrating radar) to quantify the distribution of these underground crevices and hence, the feasibility of modifying overwinter conditions for snakes in these systems.

More generally, should we attempt to modify these conditions? Many people would argue that ameliorating overt anthropogenic mortality (such as roadkills) is desirable, but that interference with "natural" events (such as freezing during winter) is ethically unacceptable. This argument runs into problems if anthropogenic activities (such as greenhouse gas production) have contributed to fluctuations in weather conditions, in turn affecting the probability of lethal conditions inside the dens. The difficulty of defining "natural" conditions is exacerbated by the readiness of *T. sirtalis* to use manmade structures

such as old wells and gravel quarries as overwintering sites. Another objection to devoting resources to conserving this system is the lower conservation priority generally accorded to snakes than to most other vertebrates (Mittermeier et al., 1992). We would argue that this simply reflects a lack of understanding, and should not be used to determine conservation priorities. Lastly, the species involved (*T. sirtalis*) is abundant over a very wide geographic range and hence, cannot be considered as threatened on a wider spatial scale. However, the phenomenon of massive congregations of animals around a few sites is unparalleled, and hence one can argue that this unique ecological phenomenon warrants careful management. Maintaining large numbers of snakes at the main Chatfield dens clearly offers advantages to local industries (via tourism) and education (via school tours to the dens).

Ultimately, the answers to these debates will hinge upon value judgements, and thus need to come from the local community rather than from scientists. Our contribution to this debate is to provide information. In the present example, perhaps our most important result is to show that overt sources of mortality (such as roadkills) may be less important to long-term persistence of these populations than the much less obvious mortality that occurs deep inside the overwinter dens. To conserve garter snake populations in the Interlake of Manitoba effectively, we need to consider mortality sources in as broad a context as possible.

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References

- Bailey, R.M., 1949. Temperature tolerance of gartersnakes in hibernation. *Ecology* 30, 238–242.
- Brown, R.D., Braaten, R.O., 1998. Spatial and temporal variability of Canadian monthly snow depths, 1946–1995. *Atmosphere–Ocean* 36, 37–54.

- Carpenter, C.C., 1952. Comparative ecology of the common garter snake (*Thamnophis s. sirtalis*), the ribbon snake (*Thamnophis s. sauritus*) and Butler's garter snake (*Thamnophis butleri*) in mixed populations. *Ecological Monographs* 22, 235–258.
- Caughley, G., 1977. *Analysis of Vertebrate Populations*. John Wiley and Sons, New York.
- Caughley, G., Sinclair, A.R.E., 1994. *Wildlife Ecology and Management*. Blackwell Scientific Publications, Boston.
- Churchill, T.A., Storey, K.B., 1992. Freezing survival of the garter snake *Thamnophis sirtalis parietalis*. *Canadian Journal of Zoology* 70, 99–105.
- Gregory, P.T., 1974. Patterns of spring emergence of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake region of Manitoba. *Canadian Journal of Zoology* 52, 1063–1069.
- Gregory, P.T., 1977. Life-history parameters of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in an extreme environment, the Interlake region of Manitoba. *National Museum of Canada, Publications in Zoology* 13, 1–44.
- Gregory, P.T., Stewart, K.W., 1975. Long-distance dispersal and feeding strategy of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba. *Canadian Journal of Zoology* 53, 238–245.
- Grigg, G.C., 1995. Sustainable use of wildlife: a new direction in conservation? In: Grigg, G., Hale, P., Lunney, D. (Eds.), *Conservation Through Sustainable Use of Wildlife*. Centre for Conservation Biology, University of Queensland, Brisbane, pp. 3–5.
- Groombridge, B., Luxmoore, R., 1991. *Pythons in South-East Asia. A Review of Distribution, Status and Trade in Three Selected Species*. World Conservation Monitoring Centre, Cambridge, UK.
- Hawley, A.W.L., Aleksiuik, M., 1975. Thermal regulation of spring mating behavior in the red-sided garter snake (*Thamnophis sirtalis parietalis*). *Canadian Journal of Zoology* 53, 768–776.
- Hawley, A.W.L., Aleksiuik, M., 1976. Sexual receptivity in the female red-sided garter snake (*Thamnophis sirtalis parietalis*). *Copeia* 1976, 401–404.
- Krivda, W., 1993. Road kills of migrating garter snakes at the Pas, Manitoba. *Blue Jay* 51, 197–198.
- Larsen, K., 1987. Movements and behavior of migratory garter snakes, *Thamnophis sirtalis*. *Canadian Journal of Zoology* 65, 2241–2247.
- Larsen, K.W., Gregory, P.T., 1989. Population size and survivorship of the common garter snake, *Thamnophis sirtalis*, near the northern limit of its distribution. *Holarctic Ecology* 12, 81–86.
- Lawson, P.A., 1989. Orientation abilities and mechanisms in a northern population of the common garter snake (*Thamnophis sirtalis*). *Musk-Ox* 37, 110–115.
- Lawson, P.A., 1994. Orientation abilities and mechanisms in nonmigratory populations of garter snakes (*Thamnophis sirtalis* and *T. ordinoides*). *Copeia* 1994, 263–274.
- Lima, S.L., 1998. Nonlethal effects in the ecology of predator–prey interactions. *Bioscience* 48, 25–34.
- Macmillan, S., 1995. Restoration of an extirpated red-sided garter snake *Thamnophis sirtalis parietalis* population in the Interlake region of Manitoba, Canada. *Biological Conservation* 72, 13–16.
- Mason, R.T., 1992. Reptilian pheromones. In: Gans, C., Crews, D. (Eds.), *Biology of the Reptilia*. In: *Hormones, Brain and Behavior*, vol. 18. University of Chicago Press, Chicago, pp. 114–228.
- Mason, R.T., 1993. Chemical ecology of the red-sided garter snake, *Thamnophis sirtalis parietalis*. *Brain Behavior and Evolution* 41, 261–268.
- Mason, R.T., Crews, D., 1985. Female mimicry in garter snakes. *Nature* 316, 59–60.
- Mittermeier, R.A., Carr, J.L., Swingland, I.R., Werner, T.B., Mast, R.B., 1992. Conservation of amphibians and reptiles. In: Adler, K. (Ed.), *Herpetology. Current Research on the Biology of Amphibians and Reptiles*. Society for the Study of Amphibians and Reptiles, Oxford, OH, pp. 59–80.
- Roff, D.A., 1992. *The Evolution of Life Histories*. Chapman and Hall, New York.
- Ross, R.A., Marzec, G., 1990. *The Reproductive Biology of Pythons and Boas*. Institute for Herpetological Research, Stanford, CA.
- Rossman, D.A., Ford, N.B., Seigel, R.A., 1996. *The Garter Snakes. Evolution and Ecology*. University of Oklahoma Press, Norman, Oklahoma.
- Shine, R., 1986. Predation upon filesnakes (*Acrochordus arafurae*) by aboriginal hunters: selectivity with respect to size, sex and reproductive condition. *Copeia* 1986, 238–239.
- Shine, R., Mason, R.T., 2001. Serpentine cross-dressers. *Natural History* 110, 56–61.
- Shine, R., Harlow, P.S., LeMaster, M.P., Moore, I., Mason, R.T., 2000a. The transvestite serpent: why do male gartersnakes court (some) other males? *Animal Behaviour* 59, 349–359.
- Shine, R., O'Connor, D., Mason, R.T., 2000b. Sexual conflict in the snake den. *Behavioral Ecology and Sociobiology* 48, 392–401.
- Shine, R., Olsson, M.M., Moore, I., Le Master, M.P., Greene, M., Mason, R.T., 2000c. Body size enhances mating success in male gartersnakes. *Animal Behaviour* 59, F4–F11.
- Shine, R., Elphick, M.J., Harlow, P.S., Moore, I.T., LeMaster, M.P., Mason, R.T., 2001a. Movements, mating and dispersal of red-sided gartersnakes from a communal den in Manitoba. *Copeia* 2001, 82–91.
- Shine, R., LeMaster, M.P., Moore, I.T., Olsson, M.M., Mason, R.T., 2001b. Bumpus in the snake den: effects of sex, size and body condition on mortality in red-sided garter snakes. *Evolution* 55, 598–604.
- Williams, G.C., 1966. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton University Press, New Jersey.