

Temporal dynamics of emergence and dispersal of garter snakes from a communal den in Manitoba

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Abstract. Although garter snakes at communal overwintering dens on the Canadian prairies have attracted considerable behavioural ecology research, previous studies have relied upon sampling of active animals to describe broad patterns of distribution and abundance of snakes within the den population. We conducted a mark–recapture study to directly quantify temporal and spatial variation in the phenotypic traits (sex, size, body condition) of snakes at the den itself, and those dispersing through woodland 50 m away. Captures of 909 snakes on the days they emerged, and 6653 snakes as they dispersed, revealed massive spatiotemporal heterogeneity in phenotypic traits among samples. Day-to-day variation in weather conditions affected numbers and sex ratios of emerging and dispersing snakes; for example, small females dispersed in greater numbers after unusually cold nights, when harassment by courting males was reduced. Most snakes stayed at the den only briefly (<5 days) prior to dispersal, so that sampling at the den itself (the only evidence available from most previous studies) underestimates the number of animals in the population, as well as the proportions of females, of small adult males and of juvenile animals. Overall, the heterogeneous and temporally dynamic distributions of phenotypic traits (such as sex and size) among our samples are predictable on the basis of the central roles of male–male competition and sexual conflict in the mating system of these snakes. Surprisingly, however, many of the snakes that overwinter at this den play no part in den-based breeding aggregations

Introduction

The spatial and temporal distribution of individuals of different phenotypic traits (sex, body size, body condition, etc.) within a population reflect many factors, including mating systems and environmental heterogeneity. For example, species that exhibit territorial defence often exhibit overdispersion of the territorial sex across the landscape (Verner and Willson 1966; Jarman 1983; Davies and Lundberg 1984); harem-based systems involve aggregations of several females plus single large males (Le Bouef 1974; Harper 1986); and lek systems are associated with phenotype-structured aggregations of males (Payne 1984; Wikelski *et al.* 1996). Thus, we expect to see correlations between the mating system of a population and the temporal and spatial patterns of distribution of individuals of different phenotypic traits within that population.

In order to explore such relationships, we need a system where the mating system is well understood. A good opportunity in this respect comes from communal overwintering dens of garter snakes (*Thamnophis sirtalis parietalis*) on the Canadian prairies. Courtship and mating occur around the den, facilitating detailed research (Mason 1993). In consequence, we have a more detailed understanding of sexual interactions in red-sided garter snakes than in any other snake species. Most of this work has been based on observa-

tions and experiments on individual snakes rather than broad patterns in the distribution of animals; for example, snakes have been placed in small groups within outdoor arenas to monitor courtship intensity, copulatory success, and the like (Shine *et al.* 2000c, 2000d, 2001a). These studies have revealed intense male–male competition and sexual conflict. Larger males obtain more matings than their smaller rivals (Shine *et al.* 2000d); accordingly, smaller males allocate less effort to courtship when larger rivals are present (Shine *et al.* 2000b, 2003b). Males force copulations upon newly emerged females by inducing hypoxic stress (Shine *et al.* 2003a); some females are suffocated during courtship (Shine *et al.* 2001b). Even small (immature) females are courted and sometimes mated (Shine *et al.* 2000c, 2004). On the basis of the results of this work, we can make specific predictions about the spatiotemporal distribution of male and female garter snakes of different body sizes at and around the den:

- (1) males will emerge from the overwinter den before females (because of intense male–male rivalry for mating opportunities);
- (2) large males will emerge earlier in the season than small males (because larger males are more likely to win in male–male rivalry);

- (3) males will remain longer at the den than will females (because mating opportunities are greatest near the den);
- (4) small males will disperse from the den sooner than will large males (because the small animals are less able to compete in large multi-male courting aggregations, and should either forego mating or concentrate their activities in peripheral areas where the intensity of male–male rivalry is reduced);
- (5) small females will disperse sooner than large females (because small females gain no benefit from mating, but face a significant risk of injury or death due to intense prolonged courtship); and
- (6) weather conditions will affect numbers and types of snakes emerging and dispersing, with small females emerging and dispersing under weather conditions that minimise the numbers of courting males.

Previous reports are consistent with these predictions, but are generally not quantified; even Gregory's (1974) pioneering study did not include data from large samples of animals taken both from the den and from the surrounding woodland, at regular intervals throughout the spring emergence period. To remedy this gap, we took such samples throughout spring at a large communal den in Manitoba.

Methods

Study species and area

Red-sided garter snakes (*Thamnophis sirtalis parietalis*) penetrate further north into severely cold areas than do any other North American snakes (Rossman *et al.* 1996). The harsh winter temperatures in Manitoba force adult snakes into deep caverns to avoid freezing, so that snakes from a wide area congregate in communal dens in autumn (Gregory and Stewart 1975). Some dens contain thousands of snakes (Gregory 1974; Gregory and Stewart 1975). Courtship and mating occur early in spring, before the snakes disperse to their summer feeding ranges (Gregory 1974). Adult males average smaller than females (mean snout–vent lengths [SVLs] 45 v. 60 cm respectively) and radio-telemetric monitoring shows that males remain longer near the den after spring emergence than do females (Shine *et al.* 2001a). Thus, courting aggregations near the den are highly male-biased, with any emerging female immediately courted by many males (Gregory 1974; Shine *et al.* 2001a).

We worked in May 2003 at a large communal den 1.5 km north of Inwood in central southern Manitoba (50°31.58'N, 97°29.71'W). The main den lies in an open rocky area beside a limestone quarry; the snakes emerge from between the rocks. The surrounding area is dominated by aspen woodland, extending to within 5 m of the den. During the spring emergence period, courting groups of snakes can be found both within the den itself, and up to 200 m away through the woodland (Shine *et al.* 2001a, 2003b). Our study encompassed the major period of emergence and dispersal in spring 2003: <20 snakes were visible at the den on most days over a two-week period prior to our work, and numbers had decreased to <500 by the end of the main study period (versus many thousands during peak activity).

Measurement of vegetation and abiotic factors

To test the prediction that abiotic (weather) conditions will affect snake movements, we need to quantify the conditions experienced by emerging and dispersing snakes. Because snake emergence from the dens occurs at the same time of year as the leafing-out of aspens, the degree

of shading changes dramatically during the snakes' emergence period. Accordingly, we took daily measurements of canopy cover, incident radiation levels and substrate temperatures in open and shaded habitats at daily intervals throughout the study period. For logistical convenience we measured these variables near our field laboratory 20 km from the Inwood den rather than at the den itself. To ensure that the laboratory site accurately mimicked conditions at the den, we measured the same variables at the den and its surrounds on three occasions (at the beginning, middle and end of the study period). The results from the two sites were almost identical, and so we use the more extensive dataset from the field-laboratory site for analyses in this paper. Six replicate sites were selected within each of the two major habitat types present near the den (open v. woodland). We used hemispherical photography to make these measurements; a digital camera with fish-eye lens took 180° photographs pointing straight upwards, and these images were examined using gap-analysis software to calculate canopy cover and incident radiation levels (Frazer *et al.* 1999). Thermal data-loggers (thermochron iButtons, Dallas Semiconductor, Dallas, TX, USA; diameter 15 mm, height 6 mm, mass 3.3 g) placed at the same sites recorded temperatures at 15-min intervals.

Mark–recapture study

We patrolled the den each day to collect newly emerged snakes (i.e. those on their first day out after their eight-month winter inactivity). Females disperse soon after emergence, and attract intense courtship (Whittier *et al.* 1985); thus, newly emerged females were easy to locate. Newly emerged males also attract courtship by other males for the first day after emergence (Shine *et al.* 2000c) and thus surveys for courted snakes were effective in locating new-emergers of both sexes. Hundreds of individually marked male snakes were seen again the day after their initial emergence, and none were attracting courtship from other males by this time. Hence, we are confident that our criterion (attracting courtship) was a reliable indicator of recent emergence for male snakes in this system. We measured SVL of all of the newly emerging snakes that we found, gave each an individual painted number on the dorsal surface, and then released most of them in the den on the same day. The non-toxic paint marks were generally readable for ~2 weeks, so that recaptures of these animals provided data on the timing of den residency and dispersal. In a few cases, especially with females, we retained snakes for experimental studies and thus they were released a few days after emergence. We do not use data from these animals to assess dispersal times.

To capture dispersing animals, we set up a 60-m drift-fence of wire mesh ('hardware cloth') 20 cm high, with six evenly spaced funnel traps beside the fence. The drift-fence was erected among aspen woodland 50 m from the den, oriented to catch snakes dispersing away from the den. Traps were checked and cleared twice daily (or more often when capture rates were high), yielding data on 6653 animals. All snakes were taken back to the field laboratory where they were measured before release the following morning on the opposite side of the fence. On four evenly spaced days within the 19-day study period we also weighed all snakes that we captured (emergers as well as dispersers); logistics prevented us recording mass any more often.

Results

Temporal shifts in vegetation cover and abiotic factors

Unsurprisingly, canopy cover was lower in the open (den) areas than in adjacent aspen woodland, but the magnitude of that disparity changed through time when the aspen began leafing out (Fig. 1a). This shift is evidenced by a significant interaction term between date and location in a repeated-measures ANOVA with day as the repeated factor, location

(den *v.* woodland) as the factor and canopy openness as the dependent variable ($F_{18,180} = 4.86$, $P < 0.0001$). The seasonal decrease in woodland canopy openness caused an equivalent change in the amount of incident radiation reaching ground level (interaction, $F_{18,180} = 12.66$, $P < 0.0001$; see Fig. 1*b*). Thermal regimes showed less overall change over the course of the study, but exhibited marked day-to-day variation and, again, a significant interaction between sampling date and location (for minimum temperature, $F_{18,180} = 4.79$, $P < 0.0001$; for maximum temperature, $F_{18,180} = 6.13$, $P < 0.0001$; see Fig. 1*c, d*). Despite these interactions, there was a clear thermal difference between locations: temperatures at the exposed (den) site were lower by night ($F_{1,180} = 74.40$, $P < 0.0001$) but higher by day ($F_{1,180} = 8.40$, $P < 0.02$) than in the adjacent woodland (Fig. 1*c, d*).

Daily variation in the numbers, sexes, and body sizes of emerging snakes

The number of newly emerging snakes of both sexes peaked a few days after emergence commenced (dotted lines in Fig. 2*a, b*). The number of emerging males fell precipitously thereafter (Fig. 2*a*), whereas numbers of females remained at relatively high levels throughout the study period (Fig. 2*b*).

To statistically evaluate the roles of weather conditions and seasonal factors on rates of emergence, we used multiple regression with time in season (number of days since 5 May) and weather conditions (minimum and maximum air temperatures) as independent variables, and the daily number and sex ratio of emerging snakes as the dependent variables. The total number of snakes found emerging each day ranged from 41 to 416, was higher after colder nights (number emerged *v.* minimum temperature, $n = 16$, $t = 2.44$,

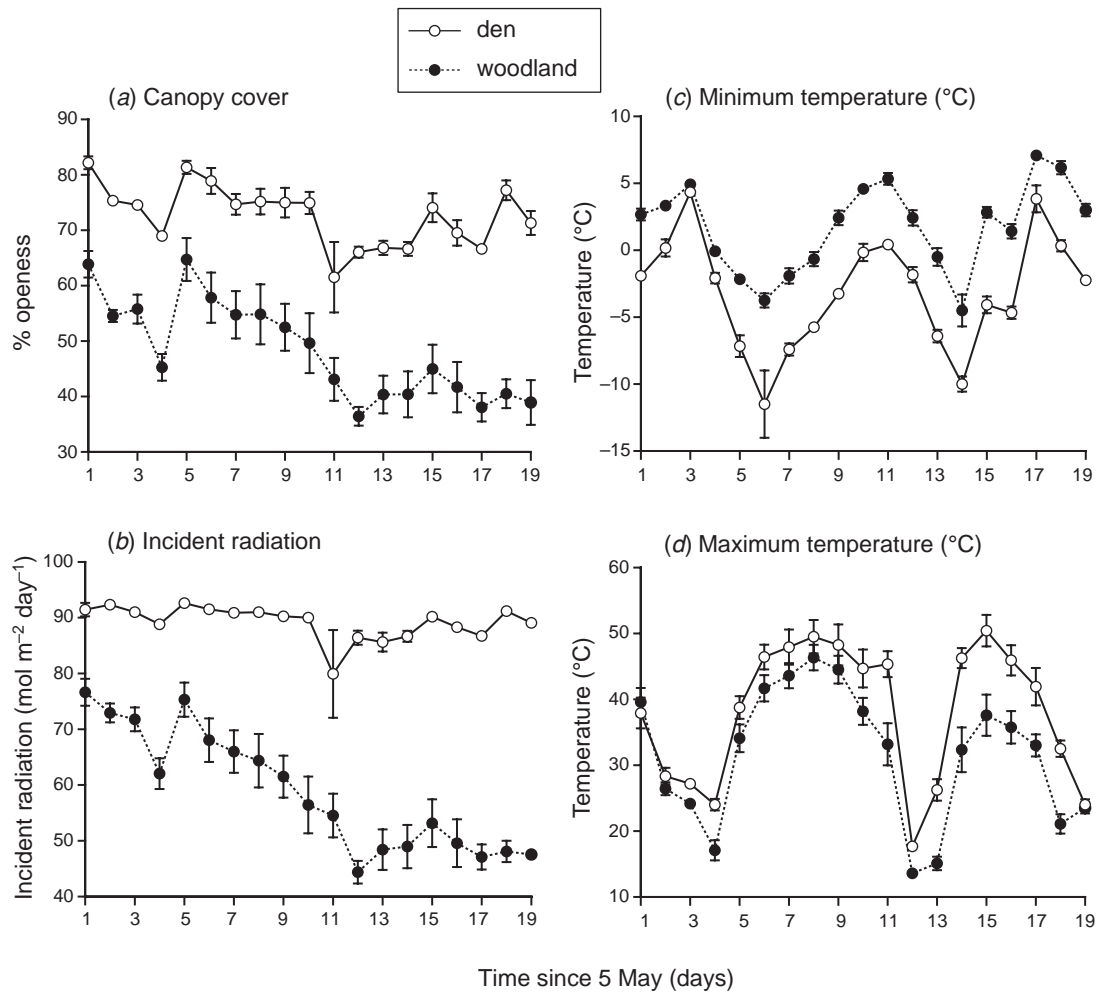


Fig. 1. Canopy cover, incident radiation and substrate temperatures in two habitat types (open den and aspen woodland) during May 2003 near the town of Inwood in Manitoba, Canada: (a) canopy cover as measured using hemispherical photography, (b) total incident radiation as estimated by specialised gap-analysis software (see text for details), (c) minimum, and (d) maximum daily temperatures as recorded by miniature thermal data-loggers placed on the ground surface. All graphs show mean values and associated standard errors. All variables were measured at six sites per habitat per day.

$P < 0.035$) but was not significantly related either to seasonal timing ($t = 1.14, P = 0.28$) or daily maximum temperature ($t = 0.75, P = 0.47$). In contrast, the daily sex ratio of emerging snakes ranged from 19.2 to 97.7% male, and was significantly linked to all three of the variables we tested. The proportion of males was higher early in the emergence season ($t = 8.84, P < 0.0001$), was higher on days with higher maximum temperatures ($t = 2.20, P < 0.05$) and, especially, was higher when minimum air temperatures did not fall too low at night ($t = 3.55, P < 0.005$). A similar multiple-regression analysis on mean body lengths of emerging snakes showed that larger males emerged earlier in the season than did smaller conspecifics (daily range of mean values 43.6–48.7 cm SVL; $t = 2.91, P < 0.015$; see Fig. 2c), with no effects of minimum or maximum temperatures on this variable (respectively, $t = 0.28, P = 0.78$; $t = 1.80, P = 0.10$). Mean body sizes of females emerging each day were not significantly associated with seasonal timing (daily range of

mean values 49.9–60.0 cm SVL; $t = 0.71, P = 0.49$; see Fig. 2d), nor with minimum temperature ($t = 0.35, P = 0.73$), or maximum temperature ($t = 1.37, P = 0.19$).

Daily variation in the numbers, sexes, and body sizes of dispersing snakes

To our surprise, snakes began dispersing (as indicated by captures at the drift fence) almost as soon as emergence commenced (Fig. 2a, b). That is, some snakes left the den almost as soon as they emerged, rather than waiting near the den. This rapid dispersal involved males as well as females (Fig. 2a, b). Indeed, the numbers of males leaving the den (as evidenced by their capture at the fenceline) exceeded the numbers emerging for all but the first two days of our study (Fig. 2a). On 10 of those days (out of 19), 300 or more males were captured at the fence, compared with less than half this number recorded as new emergers (Fig. 2a). Numbers of emergers and dispersers were more similar in females (Fig. 2b).

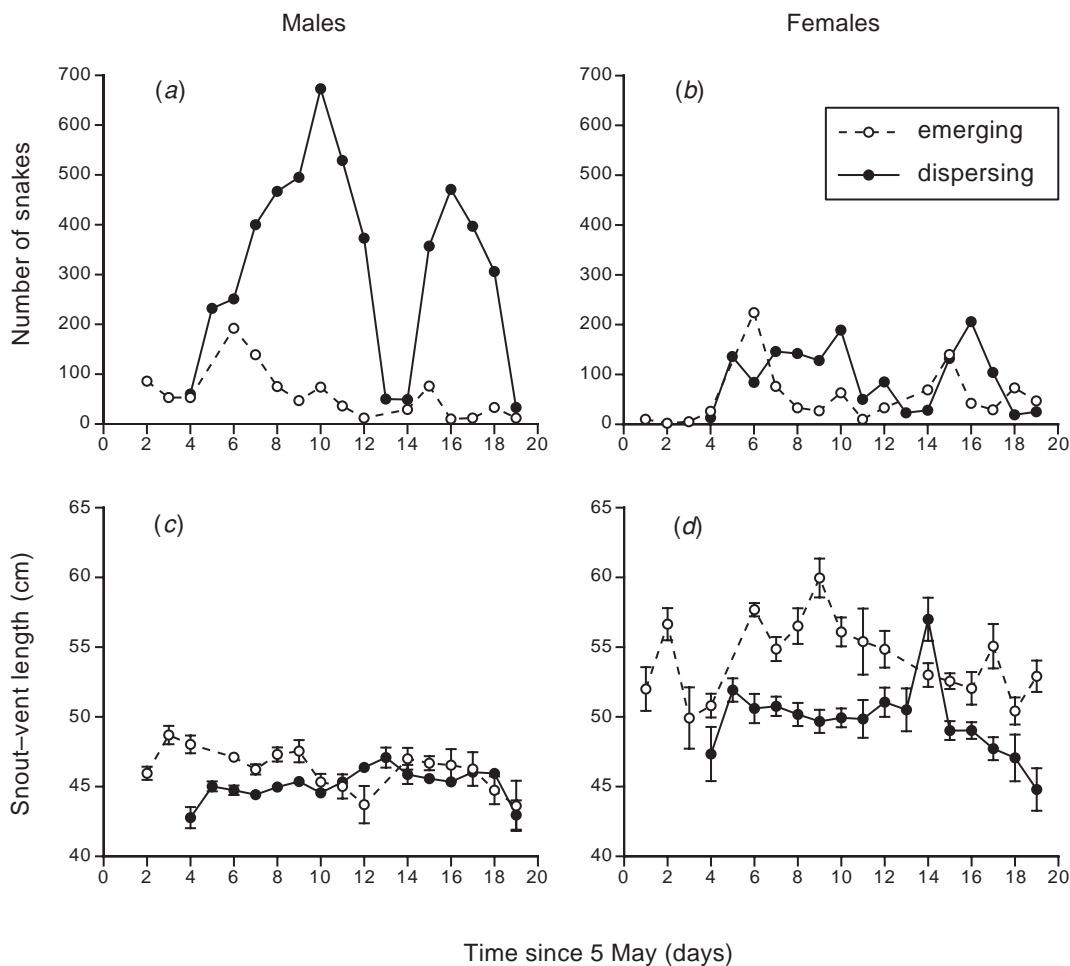


Fig. 2. Shifts in the numbers and mean body sizes (snout–vent lengths) of garter snakes as a function of time since the beginning of the springtime emergence period. Data are shown separately for males and females, and for two categories of snakes: those captured on the day they first emerged from winter inactivity (emergers) and those that were trapped at a fenceline 50 m from the den (dispersers).

To clarify the roles of weather conditions and seasonal factors on dispersal rates, we used multiple regression with time in season (number of days after 5 May) and daily weather conditions (minimum and maximum temperatures) as independent variables, and the daily numbers and mean body sizes of dispersing snakes of each sex as the dependent variables. The number of snakes captured at the fenceline each day (daily range 0–862 animals) was highest on warm days (versus maximum air temperature, $t = 2.86$, $P < 0.015$) but was not related either to seasonal timing ($t = 1.33$, $P = 0.21$) or minimum air temperature ($t = 0.96$, $P = 0.36$). The sex ratio of snakes captured at the fenceline each day varied from 54 to 97% male, but did not change significantly through the season ($t = 1.90$, $P = 0.09$) and was unaffected by maximum air temperature ($t = 0.45$, $P = 0.66$). However, sex ratios of dispersing snakes were significantly correlated with overnight minimum air temperatures, with a higher proportion of female snakes captured after very cold nights ($t = 2.69$, $P < 0.025$).

Mean body sizes of dispersing male snakes (daily range of mean values 42.8–47.1 cm SVL) were not significantly associated with any of the variables we included in our multiple-regression analyses of day-to-day variation (seasonal timing, $t = 1.36$, $P = 0.20$; minimum temperature, $t = 0.44$, $P = 0.67$; maximum temperature, $t = 0.39$, $P = 0.71$). Similarly, sizes of dispersing females varied considerably among days (daily range of mean values 44.8–57.0 cm SVL) but were not significantly linked to seasonal timing, despite an exodus of small females in the last few days of the study (Fig. 2d; but $t = 0.22$, $P = 0.83$). There was a marginally significant trend for smaller females to be captured at the fence after colder nights (mean SVL *v.* minimum temperature, ($t = 2.18$, $P = 0.05$), but no relationship with maximum daily temperature ($t = 0.82$, $P = 0.43$).

*Comparisons between phenotypic traits of emerging *v.* dispersing snakes*

Despite the close proximity of the den and the fenceline (50 m apart), our samples of snakes from these two areas differed dramatically in several aspects. First, similar numbers of males and females were captured emerging at the den (939 and 956 animals respectively, = 50% male) whereas males outnumbered females at the fenceline (5143 and 1510 animals respectively, = 78% male; see Fig. 2a *v.* Fig. 2b). Contingency-table analysis confirms the statistical significance of this disparity in sex ratios ($\chi^2 = 552.05$, d.f. = 1, $P < 0.0001$). Second, the mean body sizes of snakes differed significantly between the two sets of samples, especially in females (Fig. 2c, d and Fig. 3a, b). Two-factor ANOVA with sex and location (den *v.* fence) as factors thus shows a significant interaction term ($F_{1,8544} = 81.52$, $P < 0.0001$), reflecting the greater spatial disparity for mean body size in females (49.93 *v.* 54.38 cm: see Fig. 3b) than in males (45.25 *v.* 46.61 cm: see Fig. 3a). However, separate analyses of data

for each sex confirm that mean body sizes were significantly lower at the fence than at the den in both sexes (males, $F_{1,6080} = 58.73$, $P < 0.0001$; females, $F_{1,2464} = 170.59$, $P < 0.0001$).

Analyses of body condition (residual scores from the general linear regression of $\ln(\text{mass})$ *v.* $\ln(\text{SVL})$) using a two-factor ANOVA showed a significant interaction between sex and location ($F_{1,2911} = 14.43$, $P < 0.0001$), and a trend in both sexes for snakes captured at the fence to be in lower body condition than snakes captured as they emerged at the den (Fig. 3c, d). However, when the data were analysed separately for each sex, there was no significant difference in body condition between females captured at the den and those captured at the fenceline ($F_{1,457} = 0.76$, $P = 0.38$: see Fig. 3d) whereas the difference was highly significant for males ($F_{1,2454} = 315.22$, $P < 0.0001$: see Fig. 3c). This difference between the sexes in spatial variation in body condition may partly reflect disparities in the amount of time that individuals spent at the den prior to dispersing to the fenceline (Fig. 4; $F_{1,197} = 21.37$, $P < 0.001$).

Estimating the total number of snakes using the den

We can use our data on snakes marked at emergence and then recaptured at the fenceline to estimate the total number of snakes using the den. We restrict analysis to snakes that emerged early enough in the study to have dispersed before the end of trapping (first 13 days only) and further restrict the dataset to animals that were released immediately after they were marked on the day of emergence (some snakes were kept for experimental work and thus not released until a few days after they initially emerged). Of 743 newly emerged male snakes, we recaptured 151 animals (20.32%) in traps along the drift-fence 50 m away. Of 166 similarly marked females, we recaptured 30 (18.07%). Thus, recapture rates did not differ significantly between the two sexes ($\chi^2 = 0.32$, d.f. = 1, $P = 0.58$). The overall mean probability of recapture (19.2%) gives a measure of the likelihood of any given snake at the den being captured in our traps, under the assumption that paint-marking did not influence an individual's probability of recapture (which is reasonable, given that the traps captured all snakes attempting to disperse from the den in the region of the fenceline). The estimate that we captured about 20% of dispersing snakes fits well with the fact that our fenceline probably covered ~20% of the circumference through which snakes would be likely to disperse from the den. If the 6653 animals captured in our traps represent 19.2% of all snakes that actually used the den, about 35000 snakes must have dispersed from the Inwood den during May 2003.

Discussion

Communal dens of garter snakes in Manitoba are perhaps the most intensively studied snake populations worldwide, and mark–recapture methods are among the most widely used methods in the study of snake populations (Fitch 1987;

Mason 1993). It is thus surprising that the current study is the first attempt since Gregory's (1974) pioneering study to combine these two major themes by collecting and marking a large sample of newly emerging snakes at such a den, and then recapturing those animals as they dispersed. Presumably, such a project has rarely been attempted because processing and measuring up to 1000 snakes per day poses a considerable logistical challenge. The resultant dataset provides a quantitative picture of spatial and temporal heterogeneity in the sexes and body sizes of snakes in and near a large communal garter snake den. It thus provides a useful background to the many detailed studies that have been conducted at this and other dens. All of the predictions outlined in the Introduction to this paper were supported:

(1) males tended to emerge from the den before females, with the proportion of males among emerging snakes

declining steadily through the emergence season (Fig. 2a *v.* Fig. 2b) (however, both sexes continued to emerge throughout the study period);

- (2) larger males tended to emerge sooner than did small males, so mean body size of emerging males declined through the emergence season (Fig. 2c);
- (3) on average, males remained longer at the den than did females prior to dispersing (Fig. 4);
- (4) small males dispersed from the den sooner than did large males (Fig. 2c);
- (5) small females dispersed sooner after emergence than large females, as reflected in the disparity in mean body sizes between emerging and dispersing females (Fig. 2d);
- (6) weather conditions affected numbers and types of snakes encountered, with small females emerging and dispersing under weather conditions (following very low

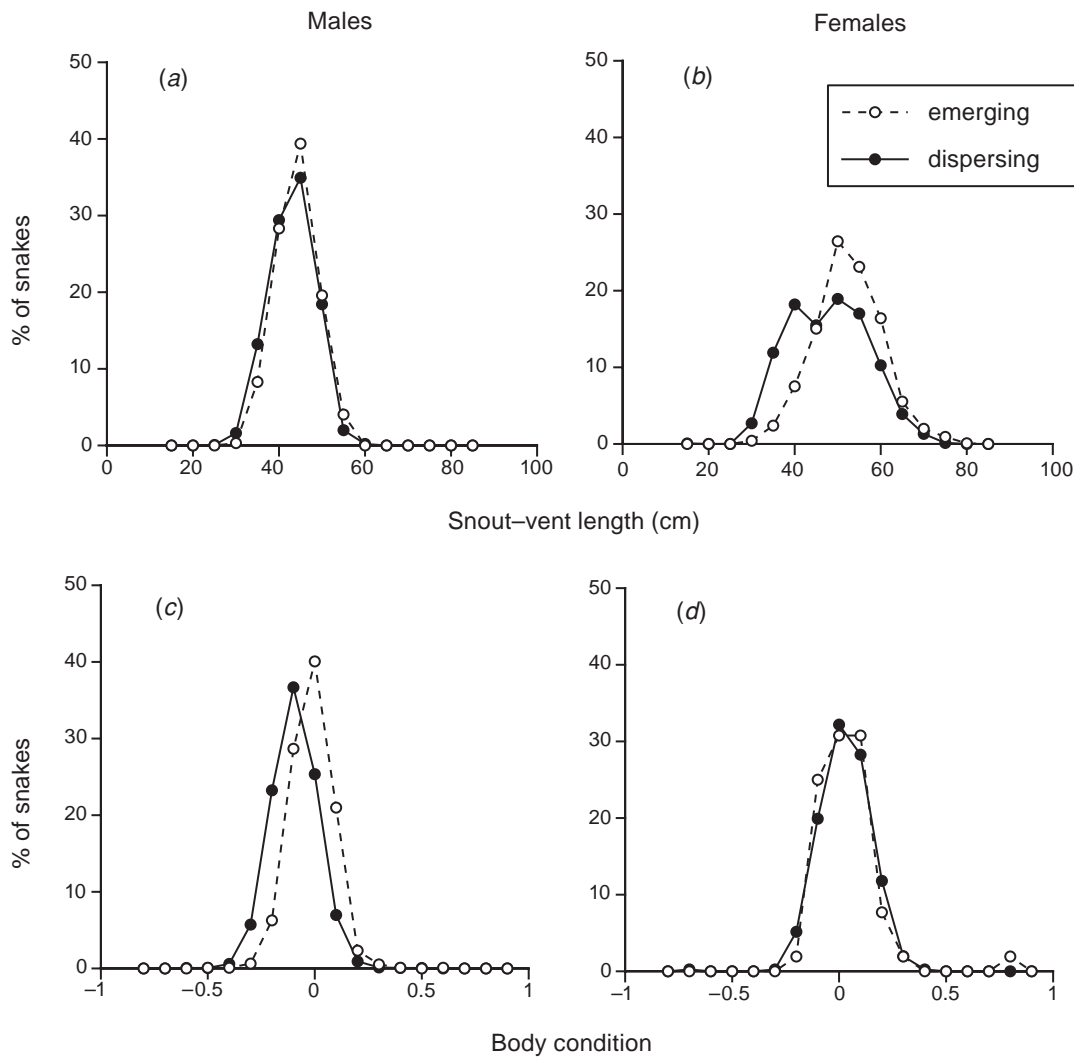


Fig. 3. Frequency distributions of body sizes (snout-vent lengths) and body condition scores (residuals from linear regression of $\ln(\text{mass})$ *v.* $\ln(\text{snout-vent length})$) of male and female garter snakes at a communal den in Manitoba, and 50 m away at a drift-fence that caught snakes as they dispersed away from the den towards their summer ranges.

overnight minimum temperatures) that minimised the numbers of courting males (Fig. 1c v. Fig. 2d). [Also, some small females remained within the den (and presumably, did not emerge) until late in the season (note reduced mean body size of females towards the end of the study period: Fig. 2d), perhaps avoiding sexual harassment in this way.]

The most surprising aspects of our results were: (1) the immediate dispersal of many snakes after emergence; (2) the large numbers of small females captured at the fence, but not at the den; (3) the marked variation in the sex and body-size composition of our samples taken on successive days; and (4) the difference in overall sex ratio of emerging versus dispersing snakes. We discuss these results in more detail below.

First, many snakes of both sexes dispersed as soon as they emerged (Fig. 2a, b). Gregory (1974) had suggested that males emerge and disperse gradually, rather than emerging simultaneously and waiting until the end of the reproductive season to disperse. Nonetheless, we were surprised that such

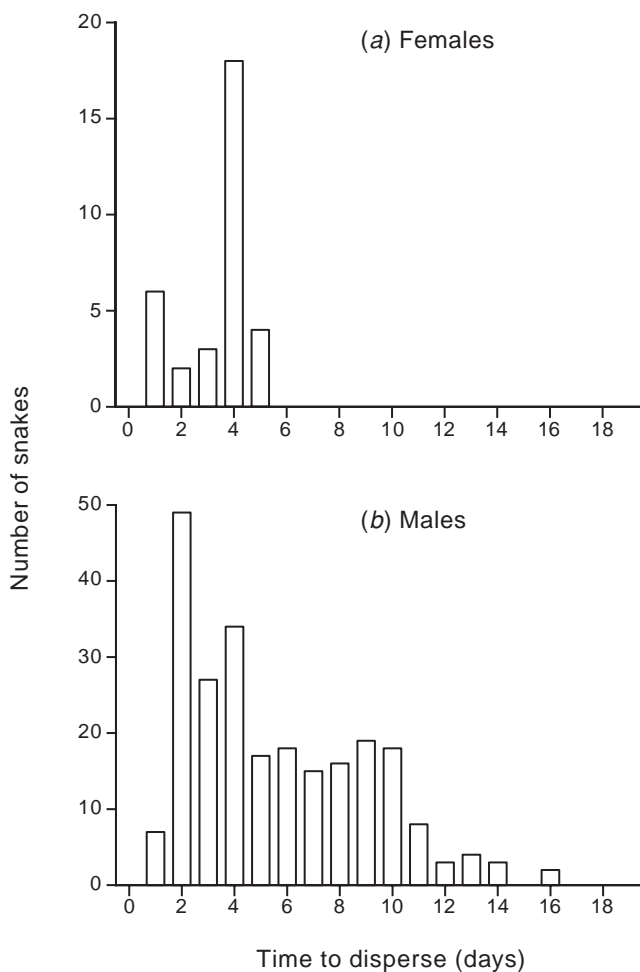


Fig. 4. Frequency distributions of the delay between emergence and dispersal of individually paint-marked male and female garter snakes at a communal den in Manitoba.

a high proportion of the male population dispersed so rapidly: we expected most adult males to participate in courtship activities prior to dispersing to their summer range. Part of the answer to this paradox lies in the fact that many 'dispersing' males were, in fact, engaged in reproductive activities, but did so in the woodland rather than at the den itself. Radio-telemetric monitoring has shown that some male snakes remain in the woodland, intercepting dispersing females (Shine *et al.* 2001a). Thus, although some of the males that we captured at the fenceline presumably were travelling directly towards their summer range, others were not. Multiple recaptures of some individuals on the other side of the fenceline show that some males remained in the woodlands around the den (Shine *et al.* 2005). Thus, male garter snakes that overwinter at the Inwood den fall into three main groups: large animals that emerge early and tend to remain at the den, participating in the vigorous male–male rivalry that occurs there; smaller animals that disperse to nearby woodland areas to court dispersing females; and smaller animals that leave the den immediately to travel to the summer range. Some of these latter snakes may continue to court females that they encounter (confirmed by trials in which these animals were captured hundreds of metres away, and placed in arenas with females: Shine *et al.* 2003c) but rates of such encounters will be very much lower than in the vicinity of the den (Shine *et al.* 2005).

Second, our drift-fence captures revealed that many small snakes, especially females, overwinter in the den despite the fact that we have rarely encountered such animals in the course of our research at the dens over many years. Clearly, these animals were highly cryptic at emergence, and dispersed soon afterwards, perhaps in the early morning or late evening when few males are active. Certainly, these small females emerged and dispersed in large numbers in unusually cold weather (following low overnight temperatures). The non-random association between visibility at the den and an animal's sex and body size means that surveys at the den will underestimate both the total numbers of snakes that overwinter at that site, and the relative proportions of smaller (including, juvenile) animals within the den population.

Third, samples of snakes taken on consecutive days, or at the fenceline versus the nearby den, often showed substantial disparities in sex ratios and mean body sizes (and for males, in body condition: Fig. 3c). Like the spatial heterogeneity discussed above, the temporal (day-to-day) variation arises at least partly because small females disperse at times when they are least likely to attract vigorous courtship. A major exodus of small female snakes during cold weather was previously documented at another den (Shine *et al.* 2000c). Because males are actively courted for the first day after they emerge (Mason and Crews 1985; Shine *et al.* 2000a), sexual conflict (due to excessively vigorous courtship: Pfrender *et al.* 2001; Shine *et al.* 2003a) may induce small animals of both sexes to disperse rapidly from the den.

The significant day-to-day changes in the sizes, numbers and sex ratios of snakes in our samples reflect the variable weather conditions experienced in this area in spring. Commonly, both thermal maxima and minima vary by $>10^{\circ}\text{C}$ over a one- or two-day period (Fig. 1), frequently associated with snowfall. The consequent changes in snake activity patterns are superimposed on a more gradual seasonal shift, whereby the sex ratio and mean body sizes of snakes (especially males) shift through time. Concurrently, vegetation cover in the woodland (and thus, incident radiation levels and operative temperatures) shifts with the leafing-out of the aspen (Fig. 1). Thus, snakes that emerge later in the season have access to shadier conditions, providing cover against predatory crows (Shine *et al.* 2001b) as well as buffering thermal conditions during dispersal. However, there is substantial annual variation in the timing of the aspen leafing-out relative to emergence and dispersal of snakes. In some years the aspen has not even begun to leaf-out by the end of May, by which time all of the snakes have left the dens (e.g. 1997: R. Shine, unpublished data) whereas in other years the aspen leafs-out in April, before snakes begin to emerge (e.g. 1998: R. Shine, unpublished data).

Fourth, the sex ratio of dispersing snakes was much more male-biased than that of emerging snakes (Fig. 2a, b). Some of the males that we captured at the drift-fence may have emerged prior to our main study, whereas others presumably emerged during our study but were not detected as emergers. Newly emerged males are more difficult to detect than newly emerged females because they elicit less vigorous courtship, especially when females are present (Shine *et al.* 2000b), and lose their attractiveness rapidly in warm weather (Shine *et al.* 2000a). An alternative explanation is that some males may not pass through a 'she-male' stage at emergence, but this possibility is not consistent with direct observations of emerging males (Shine *et al.* 2000a), nor the strong phenotypic similarity between emergers and dispersers. If some subgroup of males had not attracted courtship at emergence, we would have expected a significant divergence in phenotypic traits between these two groups of animals. The only consistent difference was in body condition (Fig. 3c), a disparity expected from the rapid rate of mass loss of courting males (Shine *et al.* 2001a).

In summary, a mark-recapture study at a large garter snake den over a three-week period in spring revealed extensive temporal and spatial heterogeneity in the composition of sampled snakes. For example, large heavy-bodied male snakes emerged early in the season and stayed near the centre of the den for many days, whereas females and smaller males dispersed more rapidly. Thus, samples taken in the woodland 50 m from the den comprised much higher proportions of small snakes, and females than were evident at the den itself. Simply censusing the 'standing crop' of snakes around the den provides a misleading picture both of the total number of

animals overwintering in the den, and the composition of that population in terms of sex and body size. Male-male rivalry and sexual conflict favour avoidance of the crowded den centre by significant segments of the population, generating strong heterogeneity in the ways that individuals with different phenotypic traits were distributed across the landscape, even at the small spatial and temporal scales utilised in the present study. More surprisingly, a high proportion of snakes overwintering at the den play no reproductive role in den-based mating aggregations, instead dispersing almost as soon as they emerge. Thus, simple counts of active animals at or near a den (the sole evidence available from previous work) substantially underestimate the numbers of animals present, as well as providing a highly biased view of the body sizes and sexes of animals using the den as an overwinter refuge.

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