Movements, Mating, and Dispersal of Red-Sided Gartersnakes (*Thamnophis sirtalis parietalis*) from a Communal Den in Manitoba

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We studied the spring emergence of red-sided gartersnakes (*Thamnophis sirtalis parietalis*) from a large communal den in Manitoba to clarify the context in which courtship and mating occur. In particular, is the mating system in such a massive aggregation (> 20,000 snakes) substantially different from that at smaller dens? Radio-tracked female snakes stayed near the den for a few days postemergence, apparently waiting until they recovered locomotor ability after the long hibernation period, before setting out for their summer ranges. Females dispersed from the den in all directions, rather than following distinct migration corridors. Male snakes moved frequently and spent much of their time far from the den in surrounding woodland. Most males remained near the den for only a small proportion of the entire mating season, apparently because of high rates of energy expenditure during mate-searching and courtship. Courting groups contained from 1–62 males and were largest close to the den. Most courting and mating occurred in groups of less than five males, often more than 20 m from the den. These small group sizes resulted from the females' dispersal prior to mating. Larger groups did not induce female cooperation (mating) more quickly than small groups. Despite the spectacular aggregations of courting snakes within the den, most reproductive activity in this population (as in other gartersnake populations) occurs in small groups, widely dispersed over a broad area.

ALTHOUGH research on the ecology of snakes has proliferated in recent years, our knowledge of even the most intensively studied species is generally based on work at only a few locations. In many cases, particular populations have been the focus of a high proportion of all research, even in species with very wide geographic distributions. Perhaps the best example of this phenomenon concerns the most wide-ranging and abundant North American snake species: the common gartersnake, *Thamnophis sirtalis.* Although there is a massive literature on many aspects of the biology of this species, we have detailed ecological investigations for only a few populations. In particular, one population near the northern limit of the species' distribution has attracted disproportionate scientific investigation, because of unique logistical advantages. Unlike the situation in warmer areas, where snakes of this species overwinter in small groups, adult gartersnakes in the Interlake region of central Manitoba gather in huge numbers around limestone sinkholes. These animals mate soon after emerging from the dens, before dispersing to their summer ranges. These aggregations provide a unique opportunity for scientific research.

The Manitoba gartersnakes have thus become a "model system" for studies on a variety of topics relating to life histories (Gregory, 1974, 1977; Gregory and Stewart, 1975), pheromonal communication (Mason and Crews, 1985; Mason et al., 1987; Mason, 1993), and sexual selection (Joy and Crews, 1985, 1988). Indeed, a recent review pointed out that "much of our apparent wealth of knowledge about gartersnake reproductive ecology is based on a single species (*sirtalis*) and (even worse) is mainly from populations of *sirtalis* from the northern portion of their range" (Seigel, 1996:56). This massive bias in the available information makes it important for us to understand the basic ecology of the Manitoba system so that we can compare it to gartersnake populations in other parts of the species' range. Otherwise, there is a real danger that we will accept results from the Manitoba population as representative of gartersnakes in general. Given the severe climate and uniquely large overwintering aggregations of snakes in this area, the Manitoba animals may actually be atypical of the "usual" gartersnake pattern in many respects.

The most obvious difference between the Manitoba snakes and other conspecific populations involves the attribute that has attracted researchers: the huge numbers of animals that congregate at overwintering sites. Plausibly, these large groupings may modify aspects of the mating system, such as the degree of male-male rivalry within "mating balls" (Joy and Crews, 1988). Population sizes have been reported to modify mating systems in other taxa (Warner

and Hoffman, 1980; Lott, 1991). To evaluate this possibility, the first step is to gather data on the size and dispersion of the Manitoba snakes during the mating season. Although writhing masses of courting snakes within the den are a popular subject for photographers, and are shown in many books and magazine articles, it remains possible that much of the mating activity occurs in other places, in situations (and snake densities) more similar to those that occur more generally throughout the species' range. Remarkably, data on these topics are not available. Our knowledge of snake behavior at the dens is based primarily upon pioneering studies by Gregory and coworkers (see above), and these studies were carried out before the availability of miniature radio-transmitters. Because telemetry enables the investigator to follow the movements of specific individuals through time and space, it has revolutionized studies of movements and habitat use by snakes.

To describe the mating system at one of the large Manitoba dens, we provide data from radiotelemetric monitoring of 36 animals, combined with information from mark/recapture and from sampling of courting groups. For cases in which patterns of behavior suggested causal hypotheses, we undertook additional experimental work (on courtship effectiveness vs group size and on locomotor speeds of snakes) to test those ideas.

MATERIALS AND METHODS

Species and study area.—Red-sided gartersnakes (*Thamnophis sirtalis parietalis*) are small nonvenomous colubrid snakes with a broad geographic distribution in North America (e.g., Rossman et al., 1996). At our study population in central Manitoba (Chatfield Community Pasture; 50°44′N 97°34′W), adult males averaged approximately 45 cm snout–vent length (SVL) and 30 g, whereas adult females averaged 55 cm SVL and 80 g. The den where we worked ("North Den") comprises a sinkhole 15 m long, 3 m wide, and 2 m deep, where the limestone "ceiling" over an underground stream has collapsed to provide a point of ingress for snakes into the underlying caverns. The surrounding area consists of a mosaic of open grassy pasture and aspen woodland. The appearance of the area changes dramatically over the month-long period of spring emergence and mating. At the time that snakes first emerge from the den (late April), snowdrifts are common, the grass has not yet begun to grow, and the aspen has not yet commenced budding. By the end of the emergence period (late May), the landscape is

green rather than grey-brown, with a rapid growth of aspen leaves and grasses.

Methods.—We visited the Manitoba dens in May 1997 and May 1998. During the 1997 trip we gathered data on sexes and sizes of snakes in courting groups, conducted a mark/recapture study, and carried out enclosure trials on effects of mating-group size. On the 1998 trip, we undertook a telemetry study as well as gathering additional data on sex ratios and measuring locomotor speed of the snakes. Overall, data were obtained by five methods.

Radiotelemetry—Snakes were collected at the den, fitted with miniature temperature-sensitive transmitters the next day and then released at their original capture site the day after. The transmitters used were Holohil model BD-2GT (mass 1.29 g) for female snakes and Titley Electronics model LTM (mass < 0.4 g) for male snakes. Snakes were anesthetized by subcutaneous injection of Brevital Sodium (0.5%, dosage 0.003 ml/g body mass). Transmitters were surgically implanted in the peritoneal cavity, with the whip antenna threaded back under the skin (Reinert and Cundall, 1982). In each case, the transmitter weighed < 2% of the body mass of the snake into which it was implanted. All snakes were active upon release, and apparently unaffected by the operation; males exhibited courtship < 30 seconds after being released. Telemetry signals were monitored daily or more often, using Telonics TR-2/TS-1 (Telonics, Inc., Mesa, AZ) and Televilt RX-900 (Televilt Intl AB, Lindedsberg, Sweden) receiver/scanners. Exact locations of snakes were plotted onto a map of the den area and displacements calculated from this map. Monitoring ceased when we could no longer locate the snake or after it moved > 500 m from the den in a consistent direction, indicating that it had begun the phase of postemergence dispersal.

Sampling at the den—A high proportion of all snakes at or near the den consisted of courting groups, that is, one or more actively courting males, plus the object of their affections. This focal snake was usually a female, but some groups formed around female mimics ("she-males"; Mason and Crews, 1985). The locations, numbers and body sizes of males in she-male-focused groups were very similar to those in female-focused groups (Shine et al., 2000a), so we have combined these data for the present analysis.

Mark/recapture—Male gartersnakes were captured and individually marked by writing a number on the dorsal surface of their heads. The snakes were measured, weighed, and re-

leased. We periodically attempted to recapture all marked animals that we could find. They were reweighed at recapture. Mass loss over the intervening period might represent dehydration as well as energy expenditure, so we reweighed the recaptured snakes after they had spent 30 min in outdoor enclosures (open-topped nylon arenas, $1.0 \times 1.0 \times 0.8$ m) with access to pools of water. Many of the snakes were observed to drink during this period.

Enclosure trials—We used the same outdoor enclosures to see whether the numbers of males courting a female influenced the time it took before she accepted copulation. A single unmated female was added to each enclosure, together with either two, four, or 24 males. We monitored the enclosures constantly, and recorded the time at which copulation occurred (for more detail on experimental procedures, see Shine et al., 2000b).

Locomotor performance—We noticed that recently emerged female snakes seemed lethargic and relatively slow moving. To quantify this trait, we measured locomotor speeds of snakes. We marked out a 5-m radius circle on a flat open grassy area near the den. Snakes to be tested were kept in cloth bags for 3 h (to enable their body temperatures to equilibrate to 24–26 C; temperatures checked before commencement of trials), and then snakes were placed one at a time in the center of the circle and encouraged (with a leafy aspen twig repeatedly brushed against the tail) to crawl away as rapidly as possible. With a stopwatch, we recorded the time taken for the snake to reach the perimeter. Two groups of females were tested in this respect: some that we collected immediately post-emergence (found inside the den, covered in mud, as they crawled out of cracks in the limestone soil), and others found in the adjacent aspen groves and clearings (with no mud covering, and presumably having emerged at least one day previously).

RESULTS

Sex ratio of snakes near the den.—Sex ratios were highly male-biased overall. In 1997, when our trip coincided with the first half of the mating season, we recorded 495 females and 1485 males in a sample of snakes taken around the den (against a null of 50% male, $\chi^2 = 990.0$, 1 df, $P < 0.0001$). In 1998, warmer weather in spring accelerated reproductive activity. Thus, we were present during the latter half of the mating season. In this year, the sex-ratio bias was even stronger (101 females and 917 males, test-ed against the 1997 sample, $\chi^2 = 103.39$, 1 df, $P < 0.0001$).

Movements and habitat use of telemetered snakes.—Movement patterns differed substantially between the radio-tracked males and females. Male snakes moved frequently but usually over short distances and generally not in a consistent direction (i.e., they often returned to the general area of the den). Some males remained close to the den throughout the time that we monitored them (e.g., Fig. 1A), whereas others centered their activity in areas away from the den (e.g., Fig. 1B). Yet other males made frequent trips away into the surrounding countryside, punctuated with occasional returns to the den. One male moved to another den 500 m away (in a single day's travel) and then returned to the original den two days later. In contrast, females generally moved less than a hundred meters from the den after their release and then remained almost stationary for one to three days before suddenly embarking on a long unidirectional move (at which time we lost contact with most of these animals). Both males and females were typically located in small open clearings among the aspen groves; the den itself was in the center of one such clearing.

These differences in movement patterns generated sex differences in the duration of monitoring and in the distances moved. Twenty-two male snakes fitted with transmitters were monitored for an average of 7.3 days (SD = 2.99) before we lost the telemetry signals, whereas 14 females were monitored for an average of only 4.2 days (SD = 3.04) before we lost touch with them (or recaptured them as they undertook long-distance dispersal). This difference was statistically significant ($F_{1,34} = 9.62$, $P < 0.004$). Although females were generally lost after briefer monitoring periods than were males, their total displacement over the course of monitoring was greater (means + SDs = 185.0 ± 211.9 m for males, 738.0 ± 894.5 m for females, ANOVA on ln-transformed data, $F_{1,34} = 16.83$, $P < 0.001$).

We used nested ANOVAs to compare the sexes in terms of distances moved per day, to overcome the nonindependence of successive measures on the same animal. Snake ID number was nested within sex, and the effect of sex was tested against this nested term rather than the residual term. Females moved away from the den more rapidly than did males (cumulative displacement per hour since release, means = 1.3 m/h for males, 7.8 m/h for females; $F_{1,34} = 9.54$, $P < 0.005$), and, at any given time that the animals were located, females tended to be farther away from the den than were males ($F_{1,34}$
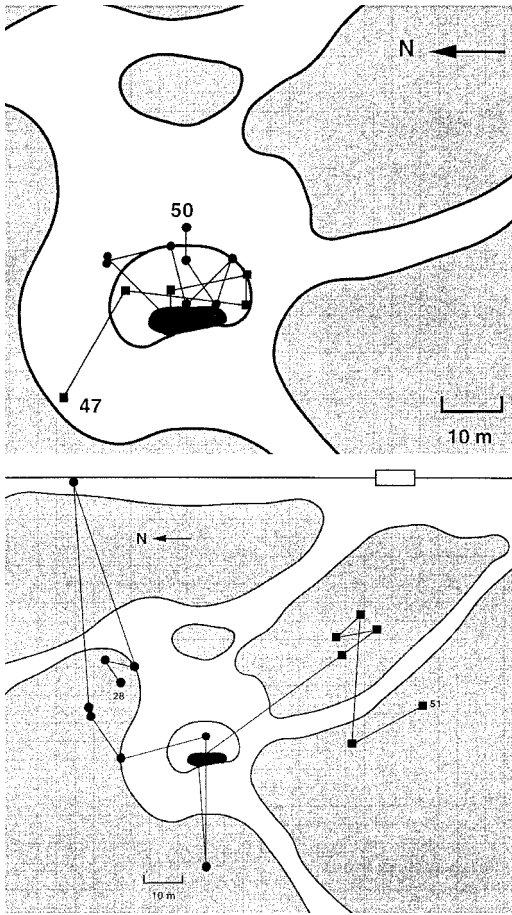
Fig. 1. Movement patterns of four radio-tracked male gartersnakes (*Thamnophis sirtalis parietalis*) in central Manitoba during the spring mating season in 1998. Data for four snakes are shown, as examples of the patterns observed. Some males remained relatively close to the den throughout the monitoring period (numbers 47 and 50, upper diagram), whereas the activity of others was centered away from the den (numbers 28 and 51, lower diagram). The den itself is represented by the black area near the center of each diagram; the circle around it represents a fence (to exclude tourists), and the hatched area represents thick groves of aspen trees. The unhatched area between the aspen groves represents open grassland. Dots show successive daily locations of each telemetered snake, connected by straight lines.
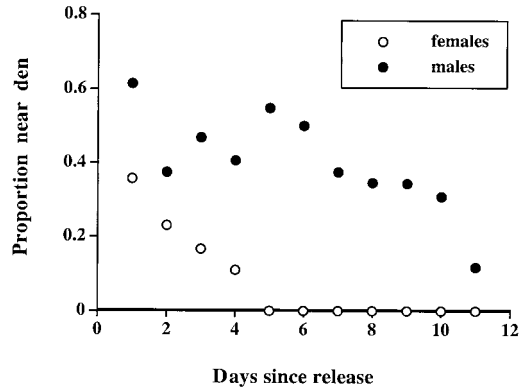

Fig. 2. The proportion of telemetry locations at which radio-tracked gartersnakes were close enough to the den to be within reception range of the telemetry signal, as a function of the time since their release at the beginning of the study. Reception range was typically 20–50 m for males, 50–100 m for females.

tances were not significantly correlated with the animal's body size or condition. We detected no association between mean distance moved per hour and a female's snout–vent length ($n = 14$, $r = 0.04$, $P = 0.88$), mass ($n = 14$, $r = -0.04$, $P = 0.89$) or body condition (residual score from the linear regression of ln mass vs SVL; $n = 14$, $r = 0.36$, $P = 0.21$). Similarly, a male's movements were not significantly correlated with his SVL ($n = 22$, $r = -0.04$, $P = 0.87$), mass ($n = 22$, $r = -0.06$, $P = 0.78$) or body condition ($n = 22$, $r = -0.11$, $P = 0.61$).

Proximity of telemetered snakes to the den.—One consequence of these movement patterns is that many of the telemetered snakes spent relatively little of their time close to the den (e.g., Fig. 1). The transmitters that we used gave an effective reception range of 20–50 m (males) and 5–100 m (females). Thus, whenever we failed to record a signal from the den, but later relocated that snake with a functional transmitter, we could be confident that the snake was > 20 m away from the den at the time of our previous (unsuccessful) attempt at relocation. Figure 2 plots the proportion of "close to den" records as a function of the length of time since the snake was telemetered and released. Two interesting results are apparent. The first is that the snakes spent much of their time away from the den, even in the period immediately after their release (when they were still definitely engaged in mating activities). The second result is that both sexes "disappeared" quite soon after implantation. As noted above (and see Fig. 2), males generally remained near the den longer than females. Even in the

$= 5.67$, $P < 0.03$). Some individuals within each sex moved much more than others. This result is apparent from the above ANOVAs: the factor "snake ID number" was highly significant in both analyses (for cumulative displacement per hour, $F_{34,218} = 19.48$, $P < 0.005$; for distance from den, $F_{34,218} = 26.43$, $P < 0.005$).

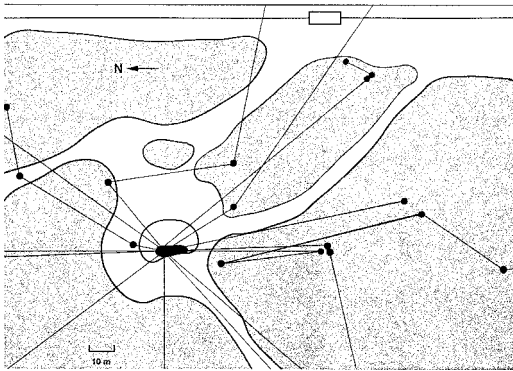Although individual snakes varied considerably in the distances that they moved, these dis-

Fig. 3. Movement patterns and directions of dispersal for radio-tracked female gartersnakes (*Thamnophis sirtalis parietalis*) in central Manitoba during the spring mating season in 1998. Most females stayed for a few days near the den then moved away rapidly in a consistent direction. The figure only shows the first 50 m of their dispersal movement, but in some cases, we followed the animals for > 1 km. See caption to Figure 1 for explanation of symbols and shading.

case of males, however, most left the vicinity of the den within a few days and did not return during the rest of our study (which lasted until the end of the mating period).

Direction of dispersal by female snakes.—Males follow females as they leave the den and court them actively over the next few days (pers. obs.). If all of the female snakes disperse along a narrow "corridor," effective densities in the postemergence mating areas will be much higher than if the snakes disperse randomly in all directions. Our telemetered female snakes provided useful information on this question, because we were able to identify the direction in which they dispersed (as indicated by an abrupt, unidirectional and rapid movement away from the den). Inspection of these locations provides no indication of any "preferred" corridor for dispersal. Females dispersed in all directions (Fig. 3). Contingency table testing (comparing numbers of expected versus observed dispersals in each compass quadrant) shows that female dispersal directions were about as evenly spaced as would be expected by chance ($\chi^2 = 2.57$, 3 df, $P = 0.45$). This behavior resulted in females (and thus, courting groups) being widely distributed throughout a broad area, rather than concentrated in a "migration corridor" near the den.

How tightly are courtship and mating focused on the den?—The fact that many of the radio-tracked snakes were a significant distance away from the den when located, brings into question the im-

portance of the den itself as a focus of reproductive activity. Our observations of the radio-tracked females indicated that they mated either as they emerged from the den (six animals) or over the next one to two days as they basked in small open clearings among the aspen groves 20–50 m from the den (four animals). We did not observe mating by the remaining four females. The sizes of courting groups in which matings occurred ranged from six to 15 males; mated females were later recorded as being accompanied by one to 12 males. These small clearings often contained several females in addition to our telemetered animals. Unmated females in this situation were generally accompanied by one to four males, whereas mated females (as evidenced by the presence of a mating plug; Whittier et al., 1985) were often solitary.

Our survey data on the distribution of snakes around the den (and especially courting groups) provide additional insight into the location of mating activities. Most of the courting groups that we encountered were in the den itself, or very close by, but we also found groups up to 82 m from the den (Fig. 4A). The group's size was a function of its location. Mating groups within the den itself were generally larger than those on the adjacent grassland, with a rapid decline in group size with increasing distance from the den (Fig. 4B).

In one sense, Figure 4B is misleading, because it obscures the many small groups of courting snakes found very close to the den. A plot of the frequency distribution of group sizes (Fig. 4C) is more revealing in this respect. Although we recorded some very large groups (up to 62 males per female), we also recorded many small ones. Among 317 groups, the mean group size was 4.0 males (SD = 7.7). Most groups (62%) contained five or fewer males, and more than three-quarters of the groups (82%) contained 10 or fewer males. Although writhing balls of hundreds of males are a popular subject for photography, relatively few matings actually occur within this context.

Does group size influence latency to copulation?—Above, we have documented a very high variation in numbers of males per courting group (one to 62). Males constantly move among groups (pers. obs.), so group sizes may be influenced by the mating opportunities presented by large versus small groups. Clearly, competition for a mating is higher with a large group; but are there compensating advantages? We might expect copulation to occur more rapidly in larger groups, for two reasons: (1) if total courtship
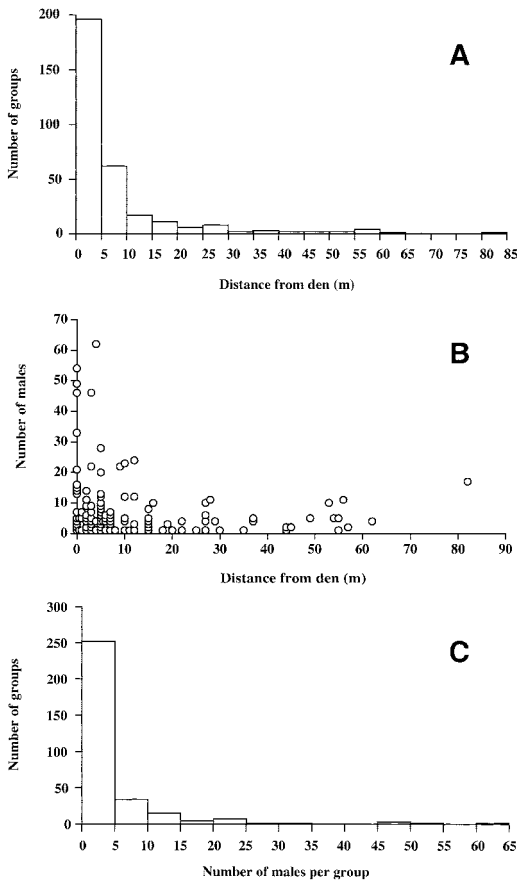
Fig. 4. The distribution and attributes of courting groups of gartersnakes at and near a den in central Manitoba. The upper figure (A) shows that most groups were found very close to the den, but some were a considerable distance away. The middle figure (B) shows that the numbers of males per group declined rapidly with increasing distance from the den. The lower figure (C) shows that group sizes varied considerably, but most groups consisted of < 5 males.
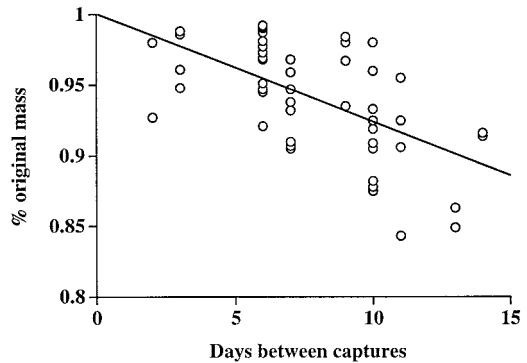

Fig. 5. Rates of loss in body mass of male gartersnakes during the mating season. Each snake is represented by only one data point. The line shows least-squares regression of best fit; see text for statistical results.

intensity is important in stimulating female receptivity, larger groups should provide more stimulation; and (2) if female receptivity depends upon the courtship of the "best" male, a larger group size enhances the probability that the group will contain at least one such male. Our data from enclosure trials falsify this scenario. The mean duration of courtship required prior to copulation was actually greater in trials with 24 males per female than in trials with either two or four males (means of 41.3, 31.9, 39.8 min, respectively). The difference in courtship durations among group sizes was not statistically significant ($F_{2,123} = 1.28$, $P = 0.28$).

Locomotor performance relative to date of emergence.—Male snakes obviously have a reason for remaining close to the den: because they are actively seeking mating opportunities with newly emerged females. But why do females not disperse immediately after emergence, rather than waiting a few days before undertaking their dispersal? The time needed to recover from overwintering may provide an answer. Recently emerged females ($n = 32$) moved less rapidly over a 5-m distance than did conspecific females ($n = 25$) that were collected in areas adjacent to the den (and hence, presumably had been out of the den for at least 24 h). The mean time ($\pm$ SD) taken to cover 5 m was 18.0 ± 9.2 sec for newly emerged animals, versus 13.7 ± 5.6 sec for the other animals ($F_{1,55} = 4.29$, $P < 0.05$).

Mass loss of males during the mating season.—Recaptures of marked male snakes showed that these animals lost mass rapidly. After two weeks, the recaptured males had lost an average of 10% of their initial mass (Fig. 5; recapture interval vs percent of mass loss: $n = 53$, $r = -0.60$, $P < 0.0001$). Recaptured males were given the opportunity to drink ad libitum but did not recover their initial mass (paired t-test comparing initial mass to postrehydration mass at recapture, $t_{44} = 2.81$, $P < 0.007$). We quantified body condition at initial capture using the residual scores from the linear regression of ln-transformed mass to body length. Males that were in better body condition at the time of their initial capture were more likely to remain near the den for longer periods, as indicated by the maximum interval between initial capture and last recapture (body condition versus maximum interval between captures: $n = 53$, $r = 0.28$, $P < 0.05$).

DISCUSSION

The broad outlines of the mating system of gartersnakes have been understood for a long time (e.g., Fitch, 1965; Gregory, 1974; Gregory and Stewart, 1975). Nonetheless, our radiotelemetry data provide the first quantitative information on actual movement patterns of these animals during the mating season. Our results broadly conform to those suggested by previous workers (e.g., Hawley and Aleksiuk, 1975, 1976; Sexton and Bramble, 1994) but with several surprises. For example, the highly male-biased sex ratio suggests that males remain near the den for long periods, whereas females disperse rapidly. In fact, individual males rarely (if ever) remain for the entire mating period, and females wait near the den for some days prior to dispersing. Similarly, casual observation suggests that mating activity is focused in the immediate vicinity of the den. In fact, these spectacular aggregations draw attention away from the fact that most mating actually occurs over a much wider area, at much lower snake densities. We now consider each of these results in turn.

Patterns of emergence and dispersal by the two sexes.—The "conventional wisdom" in this respect for squamate reptiles (e.g., Gregory, 1974; Olsson et al., 1999) is that (1) males emerge before females; and (2) males remain near the den throughout the mating period (to intercept emerging females and mate with them), whereas females disperse immediately after emerging. There is truth to both of these scenarios, but they are considerable oversimplifications. Our data suggest that the differences between males and females are quantitative rather than qualitative: (1) both males and females continue to emerge throughout the entire period; and (2) most males remain near the dens for only part of the mating period, and most females remain near the den for some days before dispersing.

The patterns of emergence and dispersal that we have documented are easily explicable in the light of our other data. First, we consider males. These animals engage in frantic activity throughout their time at the dens during the mating season and lose mass rapidly as a result (Fig. 5). Males in better body condition (more energy stores?) remained near the den longer than males in poor body condition. This high energy expenditure and consequent mass loss may explain why few if any individual males remained for the entire four-week mating period. Instead, some males left the den long before mating was finished (e.g., Fig. 2). Some of these males may have ceased reproducing and moved

to their summer ranges, whereas others may have continued courtship away from the den. Males continued to emerge throughout this period (pers. obs.), presumably because of strong selection for males to time their own emergence so as to encounter newly emerging females. The result is substantial turnover in the population of male snakes over the course of the mating season. These conclusions accord well with the results of earlier mark-recapture work (Gregory, 1974). Termination of courtship activity by male gartersnakes may also relate to a decline in their mating capacity. Males of this species do not produce sperm during the mating season and, thus, cannot replenish their supplies (e.g., Rossman et al., 1996). Also, males may be unable to produce large gelatinous mating plugs in repeated matings (Shine et al., 2000c). The wanderings of our telemetered males suggest that turnover is increased by occasional migration of males among dens, even when these sites are separated by several hundred meters. Similar movement by a male gartersnake between widely separated dens was reported by Larsen and Gregory (1989).

Might our radio-tracked male snakes have dispersed "prematurely" because of disturbance associated with transmitter implantation? We doubt that this is the case. First, the telemetered snakes showed no overt signs of discomfort (e.g., males courted frantically as soon as they were released), and their mobility was excellent. Second, paint-marked male animals also disappeared from the population very rapidly (unpubl. data). We thus suspect that there is a very high turnover of male snakes within the den population, with new snakes emerging and other snakes dispersing to their summer ranges.

What about female snakes? Like males, females emerge throughout the spring period. However, they do not then disperse immediately. Most females mate only once while they remain near the den, usually within a day of emerging (Shine et al., 2000c). Thus, their tendency to delay dispersing to summer feeding areas is not likely to be the result of waiting for additional copulations. Instead, our data on locomotor performance suggest that newly emerged females may be physiologically incapable of the rapid long-distance moves required to reach the summer feeding area, especially since they must cross open ground and run the gauntlet of avian predation during these moves. Many snakes near the den (including one of our telemetered females) were killed by predators. Thus, selection may favor a female delaying her long-distance move until she has fully

recovered her muscular ability after the long period of winter inactivity.

The overall result of these selective forces is that patterns of emergence and dispersal of male and female snakes are more similar to each other than might be suggested by published literature. Both sexes emerge throughout the mating period, remain near the den for days or weeks, and then disperse. The mean duration of their residency and its functional basis differ considerably, but these differences are quantitative rather than qualitative.

Does population size influence the mating system?—Do the massive numbers of snakes at the Manitoba dens introduce significant artifacts, such that these animals differ substantially from other *Thamnophis* populations in important attributes of the mating system? Our data militate against this hypothesis, because most courtship and mating occur in small, well-dispersed groups.

The dispersion of these groups reflects female movement patterns. Crucially, most females that emerge from the den move at least 30 m away from the den before they stop to rest. Some females mate before they complete this first move; indeed, some mate on the floor of the den, within minutes of emerging. However, many of our telemetered females mated at their resting sites in the clearings in aspen forest around the den. Because mating is delayed until they reach these sites, the snakes are relatively dispersed at this time. The degree of dispersion is enhanced by the fact that the females spread out in all compass directions (Fig. 3), rather than funneling into a narrow migration corridor. This latter behavior has been reported in other communally denning snakes (Viitanen, 1967; Gregory and Stewart, 1975), including other populations of *T. sirtalis* (Larsen, 1987). Many local people in the Chatfield area talk of such migration corridors (A. Johnson, pers. comm.). However, our data suggest that females disperse over a wide area, and, thus, most mating occurs in the context of small groups (Fig. 4). Plausibly, the snakes may concentrate into narrower migration corridors as they move farther away from the den (P. T. Gregory, pers. comm.).

Group sizes are also affected by the males' choices of groups to join. Males pause to court every potentially receptive female that they encounter but often leave courting groups in search of another female (pers. obs.). We do not know the criteria that male snakes use to decide whether to stay with a group or leave it, but the potential role of group size in this respect has important implications for male dispersion. If males selectively remained with larger groups, then we would see small numbers of large groups. However, larger group size does not facilitate courtship, and introduces the risk of suffocation beneath other snakes (Shine et al., 2000d). Thus, a male's best chance for obtaining a mating may lie with a small group, in which he has fewer rivals. On a mechanistic level, small groups may be most common because of the greater ease of detecting female pheromones when there are fewer males to obscure any cues emanating from the female's body.

The end result of these factors is that a high proportion of all activity occurs well away from the den. Thus, much of the courtship and mating occurs in relatively small, widely dispersed groups of snakes rather than in massive mating aggregations within the den. This result stands in strong contrast to many previous descriptions that have stressed the very large ''mating balls'' that occur within the den. Casual observation suggests that the den itself is the primary center of activity. As soon as one moves away from the den, the number of snakes fall rapidly (e.g., for courting groups, see Fig. 4). The likely resolution to this paradox is simple geometry. Imagine that 20% of all snakes remain within 20 m of the den, whereas the other 80% move away to a distance of between 20 m and 200 m. The area enclosed by the inner (20 m radius) circle is only 1% of that enclosed by the larger circle (200 m radius). Thus, the density of snakes per square meter will be 25 times higher in the small circle than in the larger one, despite the fact that 80% of all snakes are in the larger circle. Consequently an observer will be impressed by the extraordinary concentration of snakes close to the den and fail to realize that these animals constitute only a small proportion of the animals in the broader area.

Undoubtedly, the Manitoba situation differs in important ways from the situation experienced by gartersnakes in other areas. For example, the distances between dens and feeding grounds are greater than in warmer climates (e.g., Brown and Parker, 1976; Larsen, 1987). The stresses associated with overwintering may also be greater and may influence the duration of the female's postemergence resting phase prior to dispersal. Low temperatures may affect a snake's vulnerability to predation, and thus their patterns of habitat selection (unpubl. data). Despite these caveats, the overall suggestion from our study is that the mating system of gartersnakes at their large communal dens in Manitoba is more similar to the situation in other places (with smaller dens) than would seem

likely at first sight. The Manitoba dens are truly spectacular, but they are a less important focus of mating activity than would appear from casual observation.

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