

---

# Conflicts between Courtship and Thermoregulation: The Thermal Ecology of Amorous Male Garter Snakes (*Thamnophis sirtalis parietalis*, Colubridae)

R. Shine<sup>1,\*</sup>

P. S. Harlow<sup>1</sup>

M. J. Elphick<sup>1</sup>

M. M. Olsson<sup>1</sup>

R. T. Mason<sup>2</sup>

<sup>1</sup>School of Biological Sciences A08, University of Sydney, New South Wales 2006, Australia; <sup>2</sup>Zoology Department, Oregon State University, Cordley Hall 3029, Corvallis, Oregon 97331-2914

Accepted 4/28/00

---

## ABSTRACT

Thermoregulatory behavior is an important component of daily activities for many reptiles, especially for small heliothermic (sun-basking) species that inhabit cold climates. However, the relative costs and benefits of thermoregulation depend on numerous factors, such that reptiles may sometimes accord a low priority to precise control of body temperatures. We observed and radio tracked garter snakes (*Thamnophis sirtalis parietalis*) in central Manitoba during the mating season (spring). Previous studies on this species have documented precise behavioral regulation of body temperatures during summer. In contrast, the courting snakes that we studied in springtime spent little time in overt thermoregulatory behavior. Body temperatures were extremely variable (both in outdoor enclosures and in the field) despite abundant opportunities for more precise thermal control. These small elongate reptiles cool so quickly (relative to the time periods needed for effective courtship) that any benefit to higher body temperatures would be transitory at best. Experiments show that hotter males are no better at obtaining matings or at detecting predators. Thus, male garter snakes concentrate on courtship rather than on basking. In the face of conflicting priorities, reptiles may often forgo precise thermoregulation because its benefits are too low, and its costs too high, compared with alternative behaviors.

---

\*To whom correspondence should be addressed; e-mail: rics@bio.usyd.edu.au.

---

## Introduction

Reptilian thermoregulation has attracted intense scientific interest. Many authors have emphasized the importance of behavioral thermoregulation in the day-to-day life of reptiles (e.g., Cowles and Bogert 1944; Huey and Slatkin 1976; Hertz et al. 1993; Peterson et al. 1993). Studies on this topic have documented many examples of precise thermoregulation and have elucidated the ways in which thermal factors may influence a reptile's life. For example, unfavorable thermal microenvironments may constrain the times and places that an animal is active or the kinds of retreat sites that it selects for periods of inactivity (Huey et al. 1989). Body temperatures may affect many aspects of organismal performance (e.g., locomotion, digestion, strike speed), thus providing strong advantages for precise temperature regulation (Heckrotte 1967; Stevenson et al. 1985).

Nonetheless, we still have too little information for an overall evaluation of the importance of thermoregulation in the day-to-day lives of reptiles. It is clear that thermoregulation often is important, but it is equally clear (both from theory and data) that sometimes it may play only a trivial role. There are two main reasons why behavioral thermoregulation may be unimportant for some reptiles, at some times and in some places. Either the costs of precise temperature regulation may exceed the benefits (Huey and Slatkin 1976) or else a benign ambient environment makes "preferred" temperatures so easy to attain that regulating temperature imposes only trivial constraints on the organism (Huey 1974; Shine and Madsen 1996).

In this article, we describe studies on the thermal biology of red-sided garter snakes during their spring mating season in Manitoba. Our study species is a small diurnally active heliotherm that has served as a model organism for previous studies on reptilian thermoregulation. Individuals of this species typically regulate their temperature precisely (to ~30°C) over much of the year (e.g., Stewart 1965; Peterson et al. 1993). This thermal stability is achieved by strongly nonrandom temperature selection. Because spring in Manitoba is severely cold, we might expect that behavioral thermoregulation will be important in these animals. Nonetheless, a male garter snake also must engage in vigorous courtship during the brief (1 mo) mating

season, thus raising a potential conflict in terms of time allocation.

To evaluate the role of thermoregulation in the biology of male garter snakes at this time of year, we need to answer the following questions: (1) What thermal opportunities are available to the snakes, and how do they use them? To answer this question, we need data on the body temperatures potentially attainable by the animals, as well as those they actually exhibit. If basking opportunities are limited, snakes may display low and variable temperatures despite intense thermoregulatory effort. Conversely, a benign thermal environment may result in high and constant body temperatures without overt thermoregulation. (2) To what degree is active thermoregulation compatible with courtship? The two activities may be incompatible (thus enforcing a conflict) if mating occurs in a habitat where basking is impossible, or requires behaviors that are not consistent with thermoregulation. (3) Can the snakes resolve any such conflict by temporal partitioning of activities? That is, the snake could bask to achieve high temperatures, then move to other places (or behave in other ways) for courtship. The feasibility of this "solution" will depend on rates of heating and cooling. If the snakes have too little thermal inertia, any increased temperature through basking will be rapidly lost as they move to cooler habitats. (4) Do elevated body temperatures enhance a male's ability in courtship or male-male rivalry? Although higher temperatures enhance some aspects of locomotor performance in snakes, other behaviors are relatively unaffected by body temperature (e.g., Heckrotte 1967; Huey and Slatkin 1976; Stevenson et al. 1985; Whitaker et al. 2000). If basking does not enhance male mating success, we might expect male garter snakes to forgo precise thermoregulation during the mating season.

## Material and Methods

### *Species and Study Area*

Red-sided garter snakes (*Thamnophis sirtalis parietalis*) are small (adult males average 45-cm snout-vent length [SVL] and 35 g; females average 55-cm SVL and 75 g), nonvenomous snakes. This species has a very broad geographic distribution in North America (e.g., Rossman et al. 1996). We studied these snakes at large communal dens in central Manitoba, near the towns of Chatfield (50°45'N, 97°35'W) and Inwood (50°35'N, 97°34'W). Thousands of these snakes overwinter in each of the dens, emerging in spring to mate and then disperse long distances to their summer feeding ranges (Gregory 1974; Gregory and Stewart 1975; Larson 1987). Courtship and mating occur in the den itself, as females emerge, or in open grassy areas adjacent to the den. At this time the snakes form "mating balls," consisting of one female plus one or more males (e.g., Hawley and Aleksyuk 1975; Whittier et al. 1985). We gathered data on this system throughout May of 1997, 1998, and 1999.

### *Monitoring Environmental and Operative Temperatures*

We obtained records of daily maximum and minimum temperatures from Lundar, 20 km west of Chatfield (Environment Canada). We also used small field-portable data loggers (Hobotemp, Onset Computer, Meadowbrook, Pa.) to record environmental temperatures (at 10-min intervals) in and near the den. We placed these probes (1.5-mm diameter) inside hollow, thin-walled metal cylinders (10 × 100 mm, painted black to mimic the thermal reflectivity of the garter snakes; Peterson et al. 1993). These tubes acted as physical models to determine operational temperatures that a basking snake would attain if it remained indefinitely in the same position as the model, under the same insolation regime (Peterson et al. 1993). These models thus provide an indication of the temperatures that a snake could attain if it took advantage of the available basking opportunities. Models were placed in two positions: (i) on the floor of the den and (ii) on adjacent grassland. Two models were placed at each of these positions: one where it would receive maximal exposure to the sun and one in a shaded location. All models were oriented north-south.

### *Heating and Cooling Rates of Garter Snakes*

To quantify rates of heat exchange, we monitored cloacal temperatures of snakes after transferring them from cold to warm conditions and then vice versa. Trials for males and females were conducted separately by using six animals of each size group (small [15–32 g] and large [34–52 g] for males; small [12–32 g], medium [35–52 g], and large [54–164 g] for females). For heating trials, cold snakes (cloacal temperature ~15°C) were placed in a large plastic tub (100 × 50 × 40 cm) with a 60-W incandescent lightbulb suspended 20 cm above the snakes. Temperatures were recorded at 10-min intervals for 30 min, after which time the animals were returned to a cold area and monitored at 10-min intervals as they cooled.

### *Selected Body Temperatures*

We attempted to measure the snakes' "preferred" range of temperatures in the absence of any confounding factors that might be present in the field (e.g., where shelter sites offer protection from predators as well as lower temperatures). To do this, 20 snakes (10 males, 10 unmated females) were placed individually in open-topped outdoor nylon arenas (each measuring 1.0 × 1.0 m and 0.8 m high) at 1000 hours on May 29, 1998. Part of each arena was in full sun, and the rest was shaded by the walls of the arena. The cloacal temperatures of these snakes were recorded every 15 min from 1050 to 1235 hours. The weather on this day was fine and sunny, with no clouds and a maximum air temperature of 14.1°C. Copper models placed within the sunny part of the enclosures recorded operative temperatures of >32°C from 1000 to 1300 hours, whereas mod-

els in the shaded sections remained  $<22^{\circ}\text{C}$  throughout the day. Thus, the snakes in these arenas had ample opportunity to thermoregulate precisely by shuttling between sun and shade.

#### *Radiotelemetry*

Miniature temperature-sensitive radiotransmitters (Holohil model BD-2GT, 1.29 g; Tittley model LTM,  $<0.4$  g) were calibrated against a certified thermometer ( $2^{\circ}\text{C}$  steps) and then surgically implanted in 33 male and 13 female garter snakes under Brevital sodium anesthesia. The snakes were collected the day before the surgery and released the day afterward. The transmitters weighed  $<2\%$  of snake body mass in all cases. The units were implanted in the peritoneal cavity, with the whip antenna resting posteriorly beneath the skin (Reinert and Cundall 1982). The snakes showed no obvious ill effects from the surgery; males recommenced courtship  $<30$  s after their release back at the den. Transmitter signals were received with an automatic monitoring system (Televilt model RX900) set to record pulse intervals every 30 min.

#### *Field Sampling of Temperatures from Nontelemetered Snakes*

To characterize body temperatures of male snakes that were actively engaged in mate searching, courtship, or mating, we collected data on sizes and temperatures of snakes in and near the den. Temperatures were taken with quick-registering cloacal thermometers. Whenever we found a copulating pair, we immediately recorded cloacal temperatures of both partners, as well as temperatures of two other adjacent males (one courting animal and one solitary [mate-searching] individual) plus ground and air (at 1 m aboveground) temperatures. These data could usually be gathered within 30 s of capturing the snakes.

#### *Effect of Body Temperature on Detection of Predators*

When we approached mating balls closely, some of the males would notice our presence and rapidly flee the group. Others would remain oblivious and continue to court. To test the hypothesis that warmer snakes might be more likely to detect our approach, we approached a group quietly and then passed our open hands directly above the group at a height of 20 cm. This procedure was designed to mimic the opening wings of a crow, a common predator of snakes in this area (Shine et al. 2000a; R. Shine and R. T. Mason, unpublished data). We then captured the snakes that fled, as well as those that remained and gathered thermal data separately (as described earlier) for each of these groups.

#### *Effect of Body Temperature on Male Mating Success*

In the field, we took temperatures of snakes that were mating compared with those that were either courting or mate search-

ing (see earlier description). If higher temperatures enhanced mating success, we would expect to see that mating males were (on average) hotter than unmated males monitored at the same time. However, if copulating males cool down rapidly (because the female is generally cooler than her partner; R. Shine, unpublished data), then we might see the reverse pattern, with mating males cooler than unmated animals.

We also conducted two sets of trials by using outdoor arenas (as described in "Selected Body Temperatures"). For the first set of trials, we allowed two males to court a single female and measured their cloacal temperatures as soon as copulation commenced. If higher temperatures enhance a male's ability to court, we would expect that hotter males would achieve copulation sooner.

In the second set of trials, we directly tested the hypothesis that basking before courtship will enhance a male's chances of mating. We used two same-sized males for these trials, as earlier. Both males were kept in bags overnight in a basement, where they cooled to  $5^{\circ}\text{C}$ . One snake was kept in this condition, whereas the other one was taken out of its bag and allowed to thermoregulate in an open arena until it had attained a body temperature of  $>20^{\circ}\text{C}$ . The two males, plus an unmated female, were then placed together in the test arena, and we recorded which male obtained the mating.

## **Results**

### *Thermal Environment*

In Manitoba, May is a period of rapid thermal transition. Ambient temperatures thus vary substantially from day to day. Mean maximum air temperature is  $14.3^{\circ}\text{C}$  for May 1 and  $22.6^{\circ}\text{C}$  for May 31 (respective minima  $0.0^{\circ}$  and  $7.9^{\circ}\text{C}$ ; weather data from Lundar: Environment Canada). However, temperatures vary considerably both within and between years. For example, May of 1997 was atypically cold (minima averaged  $1.5^{\circ}\text{C}$  and maxima averaged  $14.3^{\circ}\text{C}$ ), whereas May of 1998 was unusually warm (minima averaged  $5.0^{\circ}\text{C}$  and maxima averaged  $18.8^{\circ}\text{C}$ ).

We used thermal data loggers to translate these ambient temperatures into equilibrium body temperatures potentially available to garter snakes. Minima (from deep shade probes) were relatively stable, but maxima varied considerably from hour to hour (Fig. 1). Spatial variation was also significant. In particular, the steep walls of the den limited sun exposure to the den floor so that shaded crevices remained much cooler than shaded areas in the grassland above the den (Fig. 1). However, the rocky walls of the den reflected substantial heat during the day, so that operative models in "basking" positions inside the den attained higher temperatures than did similar models placed in the grassland adjacent to the den (Fig. 1).

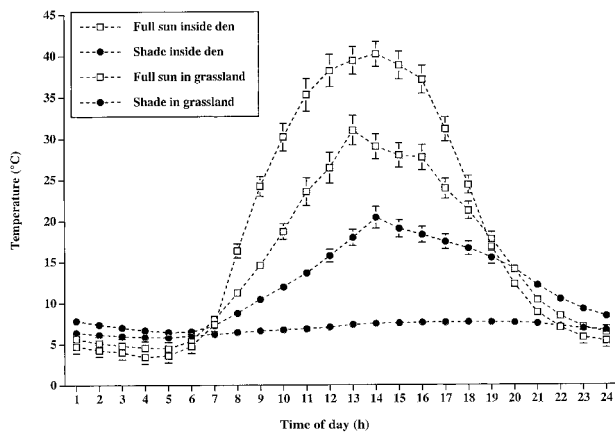


Figure 1. Measures of the ambient thermal environment in Manitoba in May based on 14 d of data. Temperatures were recorded from portable data loggers with their probes inside hollow copper models. These probes were placed in shaded and unshaded locations both on the floor of the den and in adjacent grassland. Note the high level of spatial and temporal variation in ambient (operative) temperatures, especially for models exposed to solar radiation. Figure shows mean values  $\pm$  2 SEs.

#### Heating and Cooling Rates of Garter Snakes

Both sexes heated and cooled very rapidly. Snakes allowed to bask gained a mean of  $5.5^{\circ}$ – $8.3^{\circ}\text{C}$  within the first 10 min, with only minor effects of body size. Cooling rates were similar in magnitude (means per size/sex group of  $2.4^{\circ}$ – $8.7^{\circ}\text{C}$  in the first 10 min) but more sensitive to body size. Repeated-measures ANOVA on data for females showed that they cooled more slowly than they heated ( $F_{1,202} = 126.1$ ,  $P < 0.0001$ ) but with no significant main effect of body size or interactions involving size (all  $P > 0.22$ ). In contrast, males heated at about the same rate as they cooled ( $F_{1,86} = 0.49$ ,  $P = 0.49$ ), with only trivial effects of body size.

#### Overt Thermoregulatory Behavior

On cold or rainy days, few snakes were active. On sunny days, snakes emerged from the den and from under grass around 0700 hours. Recently emerged snakes flattened their bodies in full sunlight, and some climbed onto a low fence surrounding the den, such that they were exposed to sunlight slightly earlier than if they had remained on the ground. However, these behaviors were transitory ( $<30$  min, depending on weather), and we saw little evidence of basking for most of the day (1000–2000 hours). As dusk approached, many of the snakes gathered into large piles on and around large exposed boulders in the grassy areas near the den. Eventually, the animals moved back down below the surface into holes and under grass clumps. Thus, overt thermoregulatory behaviors such as flattening and ori-

entation to the sun's rays were frequently seen early in the morning but rarely seen at any other time of day.

#### Selected Temperatures

Snakes in outdoor arenas on a day with ideal weather conditions, nonetheless, displayed little overt thermoregulation. Body temperatures varied considerably among individuals and with time for any given individual. Mean body temperatures were similar in the two sexes ( $\bar{X} = 24.2^{\circ}\text{C}$  for females,  $25.6^{\circ}\text{C}$  for males;  $F_{1,18} = 0.63$ ,  $P = 0.44$ ) but ranged from  $22.2^{\circ}$  to  $29.5^{\circ}\text{C}$  for individual males and from  $18.0^{\circ}$  to  $31.0^{\circ}\text{C}$  for individual females (Fig. 2). During the period of the day when snakes could have selected whatever temperature they wanted within this range simply by moving  $<1$  m into sun or shade, most snakes did not do so. Thus, for example, the average range of

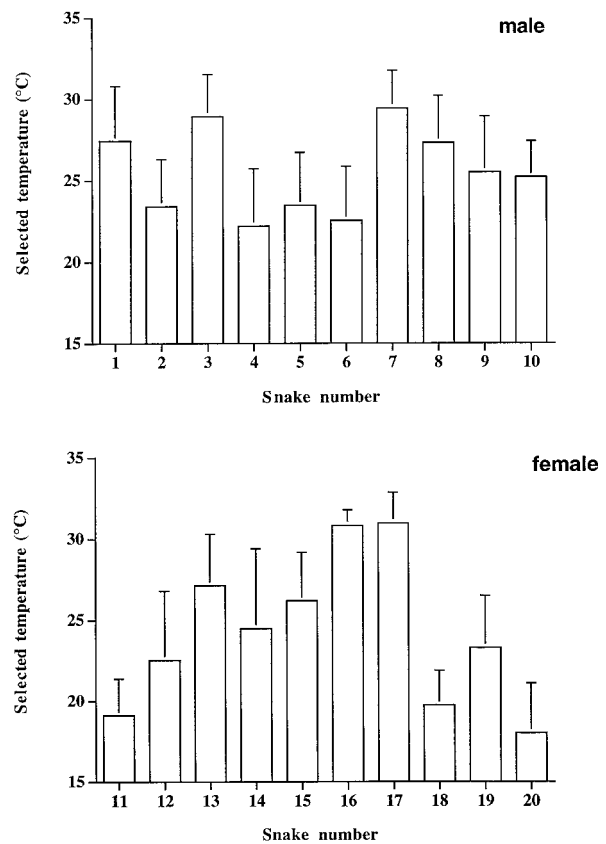


Figure 2. Selected body temperatures of male and female garter snakes in individual outdoor arenas on May 29, 1998. Figure shows mean values (and two associated SEs) for each snake based on records of cloacal temperatures taken every 15 min over the period 1050–1235 hours. Operative temperatures of  $<22^{\circ}$  to  $>32^{\circ}\text{C}$  were available throughout this period based on temperatures inside copper models placed in shaded and unshaded areas of the arenas.

body temperatures recorded from the eight readings for each individual was 12.5°C for males and 12.0°C for females.

#### Patterns of Body-Temperature Variation in Free-Ranging Snakes

Mean hourly body temperatures of the radio tracked snakes varied from 2.0° to 32.8°C with strong diurnal variation (Fig. 3). Overall, females averaged higher temperatures than did males (overall means  $\pm$  SD of 26.9  $\pm$  2.5°C for females, 22.9  $\pm$  4.9°C for males; effect of sex,  $F_{1,114} = 4.63$ ,  $P < 0.04$ ). Mean hourly temperatures over the activity period (1000–2000 hours) ranged from 24.5° to 28.1°C for females and from 19.9° to 25.3°C for males. When snake temperatures are compared with model temperatures over the same time period, it is clear that snakes had abundant opportunities to select a narrow range of temperatures over most of the day (Fig. 3).

Cloacal temperatures of males from courting groups also provide useful information on sources of thermal variation. The mean body temperatures of snakes in these groups varied considerably, but there was little variation among snakes within a single group (mean thermal range within groups  $< 3.0^\circ\text{C}$  vs. the range among groups of  $> 18.0^\circ\text{C}$ ; see Fig. 4). Body temperatures were higher in larger groups (see Fig. 5). These larger groups generally occurred in midafternoon, the warmest part of the day (see Fig. 5).

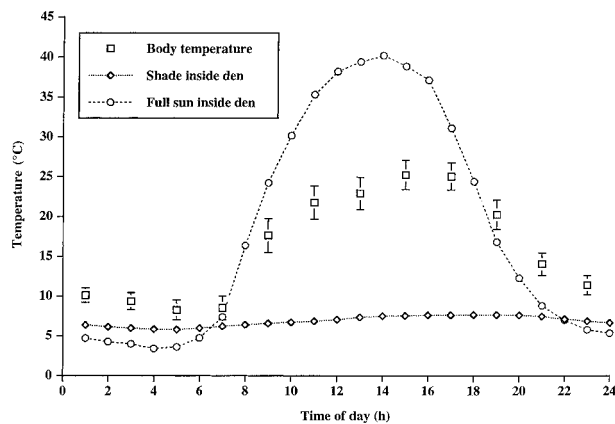


Figure 3. Body temperatures of radio tracked garter snakes and operative temperatures from physical models, as a function of the time of day that the data were recorded. Figure shows mean values  $\pm$  2 SEs for snake temperatures; these means are themselves based on one mean value per radio tracked snake per hour. The number of snakes represented in each hour ranged from 18 to 27. Values for ambient temperatures are taken from Figure 1. Note that a wide range of operative temperatures was available throughout most of the day, but the snakes rarely selected high or constant temperatures.

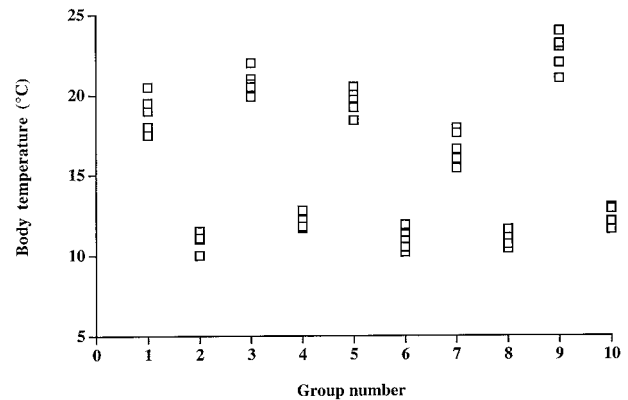


Figure 4. Variation in body temperatures among and within mating balls of red-sided garter snakes based on cloacal temperature readings. Note that groups varied substantially in mean temperatures but that there was generally little variation among males within a single group.

#### Influence of Body Temperature on Predator Detection

When startled by our sudden approach, an average of 69% (SD = 26.4%) of males remained courting the female, whereas the others fled. The proportion of males that fled from our approach was higher in groups with higher average body temperatures (R. Shine et al., unpublished data). However, there was no trend for warmer animals within each group to be more likely to flee. We analyzed these data by using a two-factor ANOVA, with the factors being group number and snake response. Groups differed significantly in mean body temperature ( $F_{37,177} = 30.42$ ,  $P < 0.001$ ) but not mean body size ( $F_{37,177} = 1.25$ ,  $P = 0.17$ ). Within each group, males that stayed did not differ from those that fled in terms of either mean body temperature ( $F_{1,177} = 0.28$ ,  $P = 0.60$ ) or mean body size (for SVL,  $F_{1,177} = 0.06$ ,  $P = 0.81$ ).

#### Influence of Body Temperature on Mating Success

Figure 6 provides data on the frequency distributions of temperatures measured in the field at the times that we found mating pairs. These data show that (i) matings occurred over a surprisingly wide range of ambient temperatures and snake body temperatures, (ii) males achieved matings even at body temperatures  $< 10^\circ\text{C}$ , and (iii) the body temperatures of mating males were no higher than those of unmated males (courting or mate-searching animals) measured at the same time. A one-factor ANOVA comparing temperatures of these simultaneously measured categories revealed highly significant differences among groups ( $F_{5,558} = 60.56$ ,  $P < 0.0001$ ). Post hoc (Fisher's protected least significant difference) tests show that air temperatures were lower than ground temperatures, which in turn were lower than the body temperatures of copulating snakes (both males and females). These copulating animals in turn

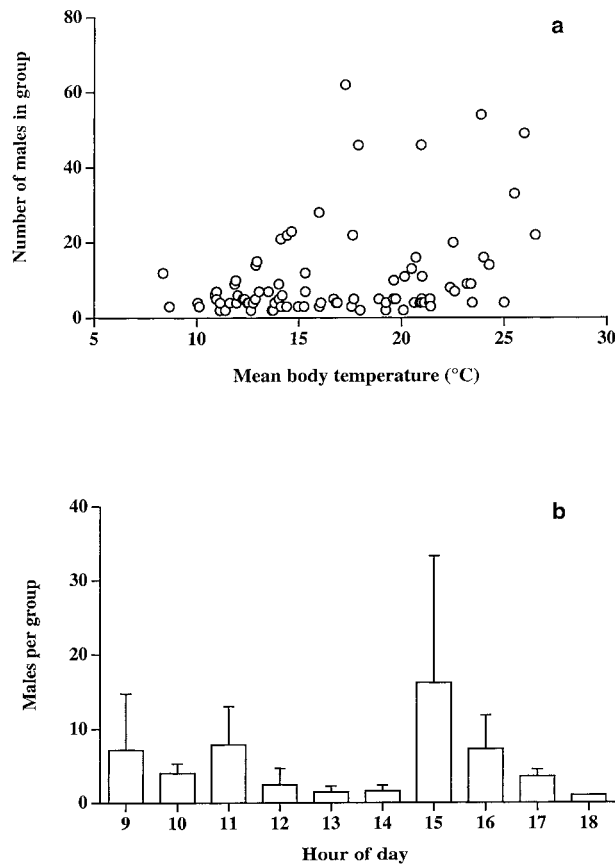


Figure 5. The size of garter snake mating balls (number of males per group) is correlated with mean body temperature of the snakes in those groups (mean temperature vs. group size [a],  $n = 87$  groups,  $r = 0.33$ ,  $P < 0.002$ ). Because body temperatures varied through the course of the day (see Fig. 3), this trend was also reflected in a tendency for groups to be larger in midafternoon than at other times (one-factor ANOVA, with hour of the day as the factor and number of males per group [b] as the dependent variable:  $F_{9,268} = 3.31$ ,  $P < 0.001$ ). In panel b, error bars show 2 SEs on either side of the mean. Sample sizes (groups per h) are as follows: 6, 99, 30, 15, 28, 17, 5, 28, 48, and 2.

were significantly cooler than either mate-searching or courting males. Thus, copulating males were actually cooler, not warmer, than their unsuccessful rivals.

In arena trials with two males per female, the duration of courtship that was required to achieve copulation was not significantly linked to mean body temperature of the copulating male (regression of courtship duration against mean male body temperature at coitus:  $n = 14$ ,  $r = -0.20$ ,  $P = 0.50$ ). This result suggests that hotter males are no more effective at courtship.

The most direct evidence on the influence of male temperature on mating success comes from experimental trials in which we added one hot male and one cold male to an arena

containing a receptive female. Matings were achieved after an average of 31 min (range = 5–65 min), with no clear advantage to the hot male (13 matings) over his colder rival (10 matings;  $\chi^2 = 0.39$ ,  $df = 1$ ,  $P = 0.60$ ). The thermal difference between the two males had disappeared or reversed in many of these trials before copulation occurred. Thus, basking before the commencement of courtship did not enhance a male's mating success.

## Discussion

Previous studies on *Thamnophis sirtalis* provide abundant evidence that these animals sometimes use behavioral means to regulate their body temperatures quite precisely. For example, >40% of snakes studied by Stewart (1965) had body temperatures between 29° and 31°C in the field as well as in the laboratory. Similarly, >80% of Fitch's (1965) captive snakes exhibited body temperatures of 27°–33°C. In a general review of six studies on *T. sirtalis* thermal biology, Lillywhite (1987) summarized mean selected temperatures of this species as 26°–30°C. In contrast, our data suggest that thermoregulation is not a particularly important factor in the day-to-day life of

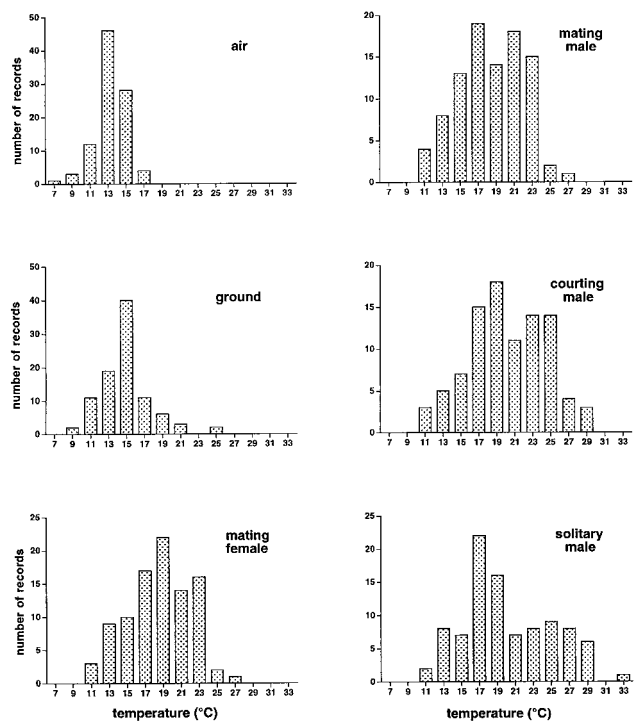


Figure 6. Frequency distributions of temperatures measured in the field at the times that we found copulating garter snakes. Data are provided for ambient temperatures (ground, and air at 1-m height), the cloacal temperatures of copulating males and females, and the cloacal temperatures of courting and mate-searching males measured at the same time. See text for statistical results.

a male garter snake in Manitoba during the mating season. This conclusion rests on three main results: (1) The snakes spend little time in overt thermoregulatory behavior, at least during the time of day when they are engaged in reproductive activities. (2) The snakes do not maintain relatively high, constant temperatures even when ambient conditions allow them to do so. (3) Body temperature has little effect on the snake's ability to do ecologically relevant behaviors (mating success, predator avoidance).

It would be nonsensical to suggest that thermal factors are irrelevant to the garter snake's ecology: ambient temperatures in this severely cold region have many impacts on these small ectotherms. For example, low nighttime temperatures enforce retreat to sheltered sites and favor (brief) periods of thermoregulatory behavior (flattening, basking, etc.) each morning. Thermal factors also modify the snakes' behavior, including their antipredator tactics (bluff rather than escape; Fitch 1965; Passek and Gillingham 1997; Shine et al. 2000a), which hemipenis the male uses during copulation (Shine et al. 2000b), and the size of mating balls (Fig. 5). Nonetheless, thermoregulatory behavior occurs less often and less overtly than we might expect from previous studies of small diurnal heliotherms in similar climates. We had initially expected that the male snakes would shuttle between sun and shade and participate in mating balls only when they had attained close to some optimal temperature. This prediction was strongly falsified.

Although many species of reptiles may sometimes accord a low priority to overt thermoregulation, the reasons for this situation appear to be different in our garter snakes than in previously studied systems. Reptiles may refrain from basking if suitable basking sites are scarce, costly to reach, or risky to use (e.g., Huey 1982; Rummery et al. 1995), or if high stable temperatures are easily maintained without basking (e.g., Shine and Madsen 1996). In the Manitoba snakes, however, none of these conditions apply. Instead, higher body temperatures are relatively easy to obtain (at least in suitable weather) but confer little benefit to a male garter snake. Courtship requires a considerable period of time in close contact with cold ground and (usually) many other rival snakes, and these small snakes heat and cool so rapidly that an initially high temperature would soon be lost. Thus, higher body temperatures have little or no impact on the snake's ability to obtain matings or (given their single-minded concentration on courtship) to detect our approach.

Previous work has emphasized the thermal dependency of several measures of organismal performance, including the speeds of crawling or striking, rate of tongue flicking, and digestive rate (e.g., Stevenson et al. 1985). However, the degree to which performance depends on temperature varies considerably among different types of performance measures (e.g., Heckrotte 1967; Huey 1982; Stevenson et al. 1985; Whitaker et al. 2000). Plausibly, mating performance may have more to do with strength than with speed, and force production is generally

less thermally sensitive than is timing (Bennett 1990). One unique advantage of our study system is that it allows us to quantify the effects of thermoregulation on an important fitness component (mating success). Previous studies on reptilian thermoregulation have necessarily relied on performance measures that bear much less directly on organismal fitness. Selection for successful performance in traits such as mating ability may have been so strong that it has reduced the variance in performance attributable to local conditions (such as temperature). In keeping with this suggestion, successful copulation occurred at body temperatures as low as 10°C (Fig. 6; see also Hawley and Aleksuk 1975; contra Gartska et al. 1982).

The lack of any strong link between a male's body temperature and his ability to obtain a mating may explain why (at an ultimate level) males do not engage in overt thermoregulation during most of the day. Our data suggest that a male does not obtain any mating advantage by being warmer than his rival. Indeed, the best strategy for a reproductive male may be to obtain the optimal position for copulation, with his tail base immediately adjacent to the female's and to allow his rival to bring the female to receptivity through vigorous courtship, rather than doing so himself. Courtship requires considerable movement (e.g., chin rubbing, caudocephalic waves; Whittier et al. 1985), potentially reducing the male's ability to maintain his tail base in the correct position, especially given the frequent "tail-wrestling" battles among rival males (Shine et al. 2000c). More generally, a male that obtained a suitable position beside a receptive female would be likely to lose rather than gain in probable reproductive success if he left the mating ball to thermoregulate.

Hotter versus colder males within a given mating ball also did not differ for the other performance measure that we assessed: the ability of actively courting males to detect and respond to our approach. This measure can be criticized on the grounds of its artificiality, but we have shown elsewhere that the response of the snakes to people is similar to their response to a more natural stimulus (a plastic crow; Shine et al. 2000a). Hotter snakes can crawl away more rapidly (Heckrotte 1967; Stevenson et al. 1985), but for many reptiles confronted by avian predators, the most important determinant of vulnerability may lie in their ability to detect, rather than to evade, the predator (Schwarzkopf and Shine 1992).

Reptiles may often be faced with conflicts among various activities such as mating, predator avoidance, and thermoregulation because these alternative activities often require different behaviors. The conflict between mating success and thermoregulatory precision that we have explored in the Manitoba snakes is only one such trade-off (e.g., Peterson et al. 1993). For example, snow may constitute the only nearby water source for the Manitoba snakes in dry weather, and we have seen snakes drinking from snowdrifts. This behavior must constrain maintenance of high body temperatures, but the hydric benefit presumably outweighs the thermal disadvantage. Similar com-

promises may be widespread. In selecting retreat sites, velvet geckos (*Oedura lesueurii*) accord a lower priority to thermal concerns than to the avoidance of predators or conspecifics (Downes and Shine 1998). Hence, although much herpetological research has stressed the importance of behavioral thermoregulation, recent studies (including this one) suggest a slightly different focus.

Thermoregulation is indeed important but is only one of several factors that a reptile must take into account in its behavioral decisions. These factors interact in complex ways. For example, body size may influence thermoregulatory precision if smaller garter snakes (because they are more vulnerable to predators) spend more time hidden under shelter (Gregory 1984). Similarly, snakes may bask more often if they have recently fed or are about to shed (Gibson et al. 1989). The influence of reproduction on thermoregulation is particularly complex. For some animals at some stages of the season, costs and benefits associated with reproduction may favor extreme stenothermy and very active thermoregulation. This may be true, for example, of gravid female garter snakes because high and constant temperatures accelerate embryogenesis and may optimize offspring phenotypes (Fitch 1965; Stewart 1965; Gregory 1984; Charland and Gregory 1990; Peterson et al. 1993). In contrast, other garter snakes at other times of year may give much less priority to thermal biology. Seasonal variation in garter snake body temperature regimes has been revealed by previous studies (e.g., Gibson and Falls 1979; Peterson et al. 1993). Undoubtedly, some of this difference reflects externally imposed constraints: snakes may be unable to attain high constant temperatures because of insufficient insolation under some conditions (Gibson and Falls 1979; Rosen 1991). However, our data from physical models show that this cannot be the complete answer. Thermal opportunities are available but are not exploited to the full: snakes remain cool because they choose not to bask, not because of a lack of basking opportunities (see Fig. 3). The unseasonably hot conditions in May 1998 (when we gathered the telemetry data) were fortuitous in this respect, because they enabled us to examine thermoregulation by courting snakes under conditions when high body temperatures were achievable. In cooler years, it would be difficult to test the alternative hypothesis that courting snakes remain cool simply because of limited basking opportunities.

Thus, even in systems that seem ideally suited to a central importance for thermoregulation, reptiles may forgo precise temperature control. Overall, male garter snakes may be less determined and precise thermoregulators than are conspecific females (Gibson and Falls 1979). Our data suggest that this effect is particularly pronounced during the mating season. Because behavioral thermoregulation imposes a substantial cost to mating opportunities, with little compensating benefit, males do not thermoregulate carefully at this time of year.

### Acknowledgments

We thank Dave Roberts (Manitoba Department of Natural Resources) for logistical support and the residents of Chatfield (especially Al and Gerry Johnson) for help and encouragement. D. O'Connor, R. Nesbitt, K. Vanning, M. LeMaster, and several Earthwatch volunteers assisted with data collection. We thank Thomas Madsen and David O'Connor for comments on the manuscript. Financial support was provided by the Australian Research Council (to R.S.), by a National Science Foundation National Young Investigator Award (IBN-9357245), and by the Whitehall Foundation (W95-04) to R.T.M. Research was conducted under the authority of Oregon State University Institutional Animal Care and Use Committee Protocol LAR-1848B. All research was conducted in accord with the U.S. Public Health Service Policy on Humane Care and Use of Laboratory Animals and the National Institutes of Health Guide to the Care and Use of Laboratory Animals.

### Literature Cited

- Bennett A.F. 1990. Thermal dependence of locomotor capacity. *Am J Physiol* 259:R253–R258.
- Charland M.B. and P.T. Gregory. 1990. The influence of female reproductive status on thermoregulation in a viviparous snake, *Crotalus viridis*. *Copeia* 1990:1059–1068.
- Cowles R.B. and C.M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull Am Mus Nat Hist* 82:265–296.
- Downes S. and R. Shine. 1998. Heat, safety or solitude? using habitat selection experiments to identify a lizard's priorities. *Anim Behav* 55:1387–1396.
- Fitch H.S. 1965. An ecological study of the garter snake, *Thamnophis sirtalis*. *Univ Kans Publ Mus Nat Hist* 15:493–564.
- Gartska W.R., B. Camazine, and D. Crews. 1982. Interactions of behaviour and physiology during the annual reproductive cycle of the red-sided garter snake (*Thamnophis sirtalis parietalis*). *Herpetologica* 38:104–123.
- Gibson A.R., D.A. Smucny, and J. Kollar. 1989. The effects of feeding and ecdysis on temperature selection by young garter snakes in a simple thermal mosaic. *Can J Zool* 67:19–23.
- Gibson R. and J.B. Falls. 1979. Thermal biology of the common garter snake *Thamnophis sirtalis* (L.). 1. Temporal variation, environmental effects and sex differences. *Oecologia* 43: 79–97.
- Gregory P.T. 1974. Patterns of spring emergence of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake region of Manitoba. *Can J Zool* 52:1063–1069.
- . 1984. Correlations between body temperature and environmental factors and their variations with activity in garter snakes (*Thamnophis*). *Can J Zool* 62:2244–2249.
- Gregory P.T. and K.W. Stewart. 1975. Long-distance dispersal and feeding strategy of the red-sided garter snake (*Tham-*



- nophis sirtalis parietalis*) in the Interlake of Manitoba. *Can J Zool* 53:238–245.
- Hawley A.W.L. and M. Aleksiuik. 1975. Thermal regulation of spring mating behavior in the red-sided garter snake (*Thamnophis sirtalis parietalis*). *Can J Zool* 53:768–776.
- Heckrotte C. 1967. Relations of body temperature, size, and crawling speed of the common garter snake, *Thamnophis sirtalis*. *Copeia* 1967:759–763.
- Hertz P.E., R.B. Huey, and R.D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *Am Nat* 142:796–818.
- Huey R.B. 1974. Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184:1001–1003.
- . 1982. Temperature, physiology and the ecology of reptiles. Pp. 25–91 in C. Gans and F.H. Pough, eds. *Biology of the Reptilia*. Vol. 12. Academic Press, London.
- Huey R.B., C.R. Peterson, S.J. Arnold, and W.P. Porter. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70:931–944.
- Huey R.B. and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. *Q Rev Biol* 51:363–384.
- Larson K. 1987. Movements and behavior of migratory garter snakes, *Thamnophis sirtalis*. *Can J Zool* 65:2241–2247.
- Lillywhite H.B. 1987. Temperature, energetics and physiological ecology. Pp. 422–477 in R.A. Seigel, J.T. Collins, and S.S. Novak, eds. *Snakes: Ecology and Evolutionary Biology*. Macmillan, New York.
- Passek K.M. and J.G. Gillingham. 1997. Thermal influence on defensive behaviours of the eastern garter snake, *Thamnophis sirtalis*. *Anim Behav* 54:629–633.
- Peterson C.R., A.R. Gibson, and M.E. Dorcas. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. Pp. 241–314 in R.A. Seigel and J.T. Collins, eds. *Snakes: Ecology and Behavior*. McGraw-Hill, New York.
- Reinert H.K. and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702–705.
- Rosen P.C. 1991. Comparative field study of thermal preferences in garter snakes (*Thamnophis*). *J Herpetol* 25:301–312.
- Rossman D.A., N.B. Ford, and R.A. Seigel. 1996. *The Garter Snakes: Evolution and Ecology*. University of Oklahoma Press, Norman.
- Rummery C., R. Shine, D.L. Houston, and M.B. Thompson. 1995. Thermal biology of the Australian forest dragon, *Hypsilurus spinipes* (Agamidae). *Copeia* 1995:818–827.
- Schwarzkopf L. and R. Shine. 1992. Costs of reproduction in lizards: escape tactics and vulnerability to predation. *Behav Ecol Sociobiol* 31:17–25.
- Shine R. and T. Madsen. 1996. Is thermoregulation unimportant for most reptiles? an example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiol Zool* 69:252–269.
- Shine R., M.M. Olsson, M.P. Lemaster, I.T. Moore, and R.T. Mason. 2000a. Effects of sex, body size, temperature and location on the antipredator tactics of free-ranging garter snakes (*Thamnophis sirtalis*, Colubridae). *Behav Ecol* 11:239–245.
- Shine R., M.M. Olsson, I.T. Moore, M.P. LeMaster, and R.T. Mason. 2000b. Are snakes right-handed? asymmetry in hemipenis size and usage in garter snakes (*Thamnophis sirtalis*). *Behav Ecol* 11:411–415.
- . 2000c. Body size enhances mating success in male gartersnakes. *Anim Behav* 59:F4–F11.
- Stevenson R.D., C.R. Peterson, and J.S. Tsuji. 1985. The thermal dependence of locomotion, tongue-flicking, digestion and oxygen consumption in the wandering garter snake. *Physiol Zool* 58:46–57.
- Stewart G.R. 1965. Thermal ecology of the garter snakes *Thamnophis sirtalis concinnus* (Hallowell) and *Thamnophis ordinoides* (Baird and Girard). *Herpetologica* 21:81–102.
- Whitaker P., K. Ellis, and R. Shine. 2000. The defensive strike of the eastern brownsnake (*Pseudonaja textilis*, Elapidae). *Funct Ecol* 14:25–31.
- Whittier J.M., R.T. Mason, and D. Crews. 1985. Mating in the red-sided gartersnake, *Thamnophis sirtalis parietalis*: differential effects on male and female sexual behavior. *Behav Ecol Sociobiol* 16:257–261.