

Behavioral shifts associated with reproduction in garter snakes

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Reproduction may involve profound modifications to behaviors such as feeding, antipredator tactics, and thermoregulation. Such shifts have generally been interpreted as direct consequences of reproduction but may instead be secondary effects of reproduction-associated changes in other traits such as habitat use. We quantified behaviors of red-sided garter snakes (*Thamnophis sirtalis parietalis*) courting and mating at a communal den, and also of postreproductive snakes dispersing from the same den. Snakes at the den actively courted, did not feed, tolerated close approach by humans, and did not retaliate (bite) when seized by us. Dispersing snakes did not court, fed, fled from our approach, and bit when seized. Snakes of both groups were then transferred to outdoor arenas and retested. Courtship vigor by males, and attractiveness of females, had declined but not disappeared for the dispersing snakes. Snakes of both groups ate readily, showing that reproduction-associated anorexia was a facultative response to lack of prey in the den. Body temperature regimes were also similar in the two groups of snakes. Overall, many of the characteristic behavioral changes associated with reproduction were responses to features of the den environment (e.g., presence of sexual partners, lack of food) rather than to reproduction per se. The shift in antipredator responses, however, may reflect a neural or endocrine “switch,” suggesting that the link between reproduction and other behaviors involves a diversity of proximate mechanisms. *Key words*: antipredator, courtship, feeding, *Thamnophis sirtalis parietalis*, thermoregulation. [*Behav Ecol* 14:251–256 (2003)]

Broadly, the adult life of any organism can be divided into reproductive and nonreproductive periods. Reproduction may not involve any major behavioral changes for some animals, notably for sessile aquatic taxa that simply liberate gametes into the surrounding environment (Ghiselin, 1974). For many others, however, reproduction entails substantial changes. These modifications most obviously involve behaviors directly associated with reproduction (e.g., mate-searching, courtship, male–male rivalry) but may extend to many other traits. For example, reproduction may be associated with a decline or cessation of feeding in some taxa (e.g., male elephant seals; Le Bouef, 1974) but an increase in others (e.g., birds feeding nestlings; Lack, 1968). Antipredator tactics may differ between reproductive and nonreproductive animals (Lack, 1968; Lima and Dill, 1990; Sinclair and Arcese, 1995). Thermoregulation may also be modified; for example, pregnancy may stimulate shifts in either the mean selected body temperature or the degree of precision with which temperature is regulated (Beuchat, 1986; Beuchat and Ellner, 1987; Gibson and Falls, 1979).

Why is reproduction associated with such shifts in “non-reproductive” behaviors? Intuition suggests a direct link, whereby some intrinsic mechanism within the animal switches off “inappropriate” behaviors during the reproductive period. For example, feeding may be incompatible with mate searching (especially in organisms such as ambush predators), and precise thermoregulation may be incompatible with effective courtship (Shine et al., 2000a). However, interpretation is complicated by the fact that reproductive animals often occur in different places, and at different times, than do nonreproductive animals. For example, consider behavioral differences between reproductive and nonreproductive ani-

mals in a seasonally migrating bird species that breeds in Siberia but spends the rest of the year in tropical Asia (De Schauensee, 1984). Differences in feeding rates, antipredator behaviors, thermoregulation, and so forth might reflect effects of season (weather) or of local habitats (e.g., abundance of predators, food supply, availability of shelter) rather than reproduction per se. Such effects could be significant even if the habitat difference between reproductive and nonreproductive activities involves tens of meters rather than thousands of kilometers, and the temporal separation weeks rather than months. Many habitats exhibit great spatial and temporal heterogeneity in aspects such as food supply, predator risk, and operative temperatures (Peterson et al., 1993; Sinclair and Arcese, 1995).

It is important to understand whether distinctive behaviors of reproductive animals are indeed direct consequences of reproduction, or correlated effects owing to spatial and temporal separation of reproductive and nonreproductive activities. For example, this distinction influences the interpretation of causal mechanisms underlying “costs of reproduction.” If such costs (reduction in energy stores owing to anorexia, etc.) are driven by features of the habitats in which reproduction occurs, then laboratory-based studies will fail to capture this phenomenon. On the other hand, laboratory work could efficiently clarify “hard-wired” behavioral shifts associated with reproductive activity.

To identify behavioral shifts associated with reproduction, we must compare reproductive versus nonreproductive organisms. There are several ways to conduct such comparisons, but most introduce confounding factors. Populations with less-than-annual reproduction offer particular opportunities, because we can compare reproductive and nonreproductive individuals at the same time and in the same place (Bonnet et al., 1999). However, if reproductive frequency depends on other factors such as disease or parasite load, then these comparisons also will be confounded. Experimental initiation or cessation of reproduction (e.g., by hormonal

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manipulation) avoids this problem but introduces potential side-effects of the procedures themselves.

The simplest comparison is between the same individuals during successive reproductive and nonreproductive phases. To avoid spatial and temporal confounding, however, we need a rapid and clearly defined onset or cessation of reproductive activities. Garter snakes in central Canada fit this criterion. Courtship and mating are largely confined to a period of a few weeks in early spring, after which the snakes disperse to their summer ranges (Gregory, 1974, 1977; Gregory and Stewart, 1975). During the mating season, the snakes engage in frantic courtship, do not feed, virtually ignore predators, and forego precise thermoregulation (Shine et al., 2000c,e, 2001a). All of these behaviors differ from those of nonreproductive individuals of the same species later in the season (Fitch, 1965; Passek and Gillingham, 1997; Shine et al., 2000a). We can thus compare snakes in the den (the center of mating activity) to snakes that have commenced dispersal. Because both reproductive and nonreproductive animals are available at the same time and within a few hundred meters of each other, we can directly compare their behaviors and quantify their responses to stimuli such as food and predators. Additionally, by transferring snakes from both groups to a "common garden" and reexamining their behaviors, we can clarify the degree to which reproduction-associated shifts are hard-wired versus facultative.

METHODS

Study species

Red-sided garter snakes (*Thamnophis sirtalis parietalis*) are small nonvenomous colubrid snakes, a northeastern subspecies of a taxon (the common garter snake) that is widely distributed through North America (Rossman et al., 1996). In the Interlake region of central Manitoba, low winter temperatures and a scarcity of suitable hibernacula concentrate the snakes into large communal dens (Gregory, 1974; Mason, 1993). Mating occurs close to the den, immediately after the snakes emerge from their 8-month hibernation period (Gregory, 1974). Radio-tracked female snakes generally mate within 48 h of emergence and disperse from the den within a few days (Shine et al., 2001a). In contrast, males remain for about 2 weeks before dispersal (Shine et al., 2001a). Snakes may travel more than 15 km away from the den to their summer ranges (Gregory and Stewart, 1975; Larsen, 1987).

Previous work documents several differences between reproductive and nonreproductive garter snakes. Most obviously, males court vigorously during the mating season in spring but not during summer or autumn (Whittier et al., 1985). Females attract intense courtship as soon as they emerge from hibernation, but pheromones in copulatory fluids reduce the intensity of courtship to a female after she mates (Shine et al., 2000f). Longer-term, there is a decline in attractiveness of copulated females, possibly reflecting shifts in skin lipids (Mason, 1993; Shine et al., 2000f). Garter snakes also do not feed during the courtship period, but take worms and frogs after they begin to disperse (Fitch, 1965; Hart, 1979). Antipredator responses to humans are similar to those directed to natural predators (Burger, 1998; Shine et al., 2000e). Biting is recorded only rarely when den snakes are handled but may be frequent in other seasons (Rossman et al., 1996). Courting male garter snakes forego precise thermoregulation, whereas snakes studied later in the season exhibit more stable thermal preferences (Shine et al., 2000a).

Study area

In May 2001, we worked at a communal den containing approximately 10,000 garter snakes 1.5 km north of the town of Inwood, 250 m east of Highway 17 in central southern Manitoba (50° 31.58' N, 97° 29.71' W). This den has been used for other studies, providing considerable background data on snake behavior (Shine et al., 2000c). To ensure consistency of habitats in the collection sites, our "den" samples came from a dirt road immediately adjacent to the main den area (a rock slope honeycombed with holes from which the snakes emerge). Our "dispersing" sample was taken beside the highway 250 m west of the den. Snakes in this area were obviously leaving the den; they were all solitary, and all moved across the road in the same direction (away from the den). We quantified behaviors both in the field (when collecting snakes) and also after transferring them to outdoor open-topped nylon areas (1 × 1 × 1 m) set up beside our field laboratory 30 km away. Each snake was used only once, so that in total, our results are based on data from 354 individual animals.

Reproduction

To quantify courtship vigor in arena trials, we marked snakes for individual recognition by painting numbers on their heads. We placed 12 "den" males into one arena and 12 "dispersing" males into another. To provide a standardized stimulus, we wished to eliminate cues such as female movement (which might be modified by male behavior and, thus, influence subsequent courtship). Thus, we used recently dead female snakes. We collected four dead or dying females from the den after they had been attacked by crows; all had been dead for less than 24 h when used in the behavioral trials. Each female was suspended by the tail with fishing line from a 1.5-m rod, and deposited on the ground inside an arena with her midbody 5 cm in front of the head of a male. After a 10-s delay to allow the male to approach, we recorded whether he exhibited active courtship within the next 30 s (i.e., aligned with the female's body and performed caudocephalic waves; Whittier et al., 1985). All trials were conducted on the same day.

The attractiveness of 12 live female snakes (six from the den, six dispersers) was evaluated by placing individually numbered females into each of the arenas above. The females were added one at a time in random order. We then scored the responses of the first three males to encounter each female. She was then removed and another female added, for which we scored the responses of another three males. Thus, this experiment used a total of 12 females and 72 males. Because female body size affects attractiveness in this population (Shine et al. 2001b), we selected equally sized den and dispersing females for these trials.

Feeding

After the courtship trials concluded (above), we removed all snakes and replaced them with equal numbers of new animals collected from the field less than 24 h earlier. We threaded two live garden worms onto a safety pin attached to a fishing line and dangled it 5 cm in front of snakes' heads in the arenas (as above). We recorded whether or not the snake seized the lure within 30 s, and how long before this occurred.

Antipredator responses

We selected a snake in an open flat area at least 3 m away from us, and walked slowly toward it. If it fled, we pursued it. We

then seized the snake by the midbody, and held it for 10 sec. We recorded each snake's approach distance (distance from us when it fled), and whether or not it bit us when held. We then recorded the animal's body temperature (by cloacal insertion of an electronic thermal probe, Comark Ltd, Swallowfields, Herts, UK), its sex, and its snout-vent length. All observations were made on clear, sunny days when air temperatures were more than 20°C.

Thermoregulation

We attached miniature thermal data-loggers to the dorsal midbodies of four snakes in each arena, with two arenas per group (i.e., total of eight den females, eight den males, eight dispersing females, eight dispersing males). These small circular loggers (Thermochron ibutton, Dallas Semiconductor, Dallas, Texas, USA; diameter, 15 mm; height, 6 mm; mass, 3.3 g) were attached to the snake's body with superglue (Loctite 406, Loctite Australia, Caringbah, NSW, Australia) and then covered with adhesive tape. Because the thermistor within each unit was applied closely to the snake's dorsal surface, the resultant temperature reading closely approximated the snake's internal temperature (in calibration trials: $n = 27$, $r = .95$, slope = 0.98, $p < .0001$; data not shown). Temperatures were recorded every 4 min over the next 5 days.

Analyses

Data were analyzed using the programs Stview 5 and SuperANOVA 1.1 on a Macintosh G4 computer. Assumptions of statistical tests were evaluated before analysis, and data transformed when necessary.

RESULTS

Morphology

Females were on average larger than males, among both den snakes and dispersing snakes. In both sexes, the dispersing animals were on average smaller than those collected in the den (Figure 1; see statistical analysis in caption). We evaluated body condition (mass relative to length) for snakes in the two samples by using a heterogeneity of slopes test (with sex and location as factors, \ln SVL as the covariate, and \ln mass as the dependent variable). This revealed a significant interaction term between sex and location ($F_{1,82} = 7.00$, $p < .01$). We thus conducted further ANCOVAs separately for the two sexes. Females in the two locations were in similar body condition (slopes: $F_{1,31} = 0.07$, $p = .80$; intercepts: $F_{1,32} = 0.36$, $p = .36$), but dispersing males were thinner than den males (slopes: $F_{1,31} = 0.74$, $p = .39$; intercepts: $F_{1,32} = 10.27$, $p < .003$).

Reproductive behavior

When placed in an outdoor arena and presented with a recently killed female, both den males and dispersing males showed intense courtship. However, den males were slightly more vigorous (12 of 12 males aligned with the female's body, versus nine of 12 dispersing males; log-likelihood ratio table from logistic regression with "alignment or not" as the dependent variable: $\chi^2 = 4.59$, 1 df, $p < .033$).

Trials with live females did not reveal any such difference in courtship vigor between den and dispersing males, but showed that dispersing females attracted less courtship than did den females (Figure 2). We used ANOVA to test the significance of this pattern, with the dependent variable being the proportion of males (out of three tested per female) that

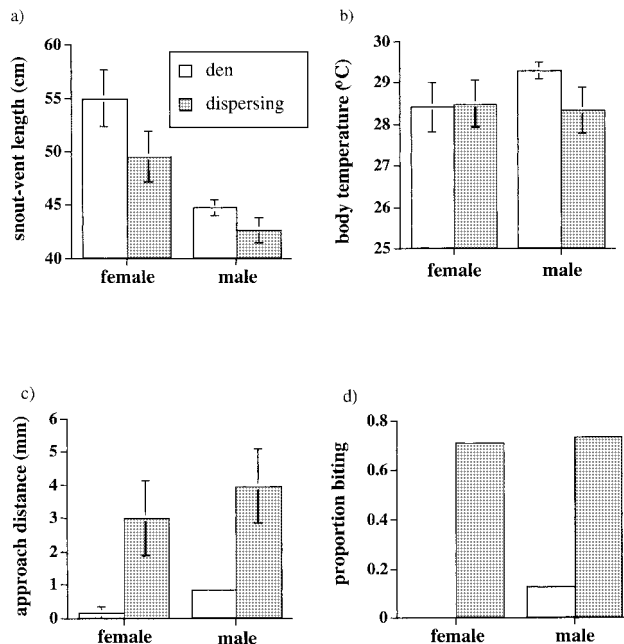


Figure 1

Attributes and behaviors of garter snakes collected either at a communal den, or 250 m from the den as the snakes dispersed. (a) Mean snout-vent length was greater for females than males, and was greater at the den than for dispersing animals (ANOVA with sex and location as factors; main effect of sex: $F_{1,101} = 33.82$, $p < .0001$; effect of location: $F_{1,101} = 6.58$, $p < .02$; interaction: $F_{1,101} = 1.26$, $p = .26$). (b) Mean body temperature was similar for both sexes at both sites (two-factor ANOVA, all $p > 0.25$). (c) Mean approach distance was greater for dispersing snakes than for den snakes (ANOVA $F_{1,64} = 11.86$, $p < .001$) but did not differ between sexes ($F_{1,64} = 0.91$, $p = .34$; interaction: $F_{1,64} = 0.03$, $p = .87$). (d) Snakes at the den rarely bit when seized, whereas dispersing snakes typically retaliated in this way (see text for statistical analysis). Graphs show mean values and associated standard errors.

aligned with a female during the trial. The analysis did not yield a significant interaction term ($p = .36$), simplifying interpretation of main effects. Den females attracted more courtship than did dispersing females ($F_{1,20} = 51.86$, $p < .0001$), but den and dispersing males were equally amorous ($F_{1,20} = 0.98$, $p = .75$; see Figure 2).

Feeding

Snakes in the arenas readily seized worms (mean latency to attack, 7.6 s; range, 1–29 s). Five of 11 den females fed within 30 s, as did three of eight dispersing females, 10 of 12 den males, and 11 of 12 dispersing males. Logistic regression with "feed or not" as the dependent variable shows that the difference between sexes was statistically significant (log-likelihood ratio table: $\chi^2 = 6.29$, 1 df, $p < .013$) but that between den and dispersing snakes was not ($\chi^2 = 0.93$, 1 df, $p = .34$). Because we were surprised by this result, we repeated the study with free-ranging snakes at the den itself (in case capture and handling had modified feeding responses). Again, snakes fed readily, even when they were active participants in mating balls. For example, 28 of 52 males engaged in active courtship seized the worms less than 10 s after they were offered. One female in the midst of a large mating ball (covered by more than 50 males) also seized the worm immediately; we were unable to locate other females to test.

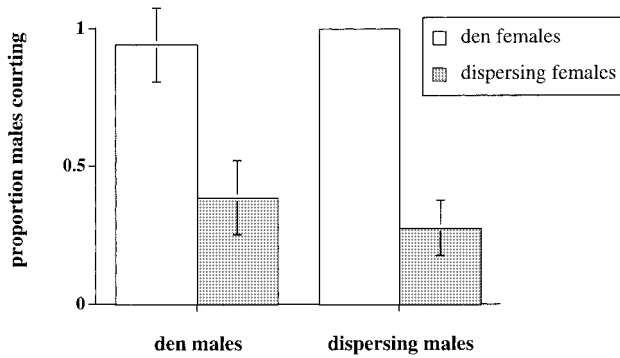


Figure 2
Effects of site of collection of garter snakes (at a communal den versus 250 m away as the snakes dispersed from the den) on the intensity of courtship exhibited by (and directed to) these animals. Data are shown for courtship in outdoor arenas by males from both locations, to both groups of females. The histograms show the proportion of males (out of three tested per female) that displayed vigorous courtship (body alignment and caudocephalic waving). See text for statistical analysis of these data. Graphs show mean values and associated standard errors.

Antipredator responses

Snakes in the den ($N = 47$) tolerated our close approach and rarely bit when handled. In strong contrast, dispersing snakes ($N = 21$) often fled from us when we were several meters away and bit vigorously when seized (Figure 1). This behavioral shift cannot be attributed to differences in mean body temperatures or body sizes, which were minor (Figure 1). Also, logistic regression with "bite or not" as the dependent variable shows that whether or not a snake bit during capture was not affected by its sex (log-likelihood ratio test: $\chi^2 = 0.85$, 1 df, $p = .36$), its snout-vent length ($\chi^2 = 0.79$, 1 df, $p = .37$), or its body temperature ($\chi^2 = 0.17$, 1 df, $p = .68$). However, bites were more likely from dispersing snakes than from den snakes ($\chi^2 = 8.02$, 1 df, $p < .005$), and especially from animals that fled at greater distances ($\chi^2 = 4.89$, 1 df, $p < .03$). Because capture and handling can substantially modify antipredator responses in snakes (see Fitch, 1975; Platt, 1969), we did not conduct any further tests on these snakes at later times.

Thermoregulation

The miniature data-loggers attached to snakes in arenas provided a massive data set on body temperatures (more than 48,000 data points from 32 snakes at 4-min intervals over 5 days). To summarize general patterns, we calculated hourly mean temperatures for each snake and subjected them to repeated-measures ANOVA with sex and location (den versus dispersing) as factors. We conducted analyses for the period 0700–1700 h separately for data from 2 days when conditions were clear and sunny, allowing effective behavioral thermoregulation. On neither day did the den and dispersing snakes differ from each other in mean body temperatures ($F_{1,28} = 0.14$, $p = .72$; $F_{1,28} = 2.02$, $p = .17$). Overall, body temperatures of all groups of snakes showed very similar diel cycles (Figure 3).

DISCUSSION

Our two samples of snakes (den and dispersing) were taken only 250 m apart, and all of these snakes would have been together at the den only a day or so beforehand (radio-tracked snakes leaving the den usually travel more than 300 m

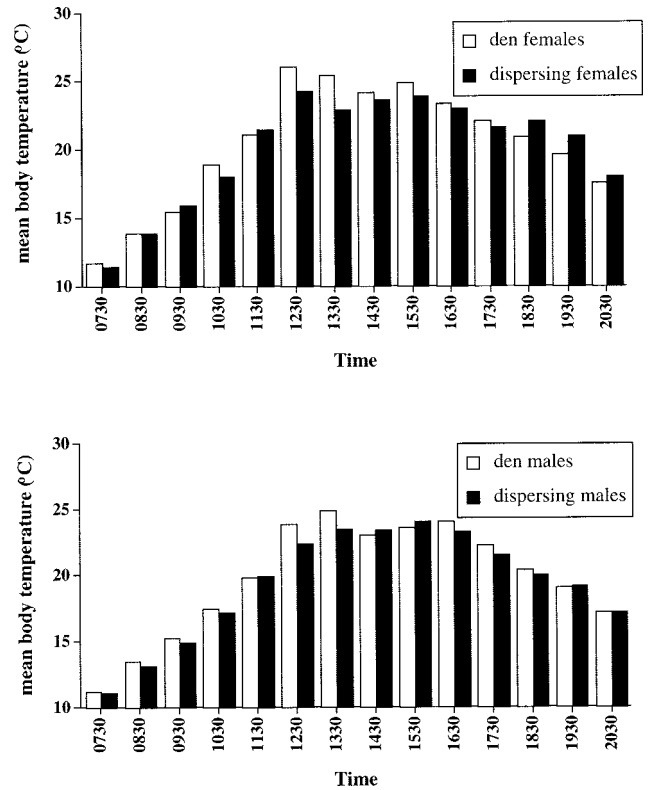


Figure 3
Mean hourly body temperatures of garter snakes in outdoor arenas during daylight hours on a clear warm day (17 May 2001). The snakes were collected either at a communal den, or 300 m from the den as the snakes dispersed. Histograms show mean values (based on data recorded every 4 min) for each group. See text for statistical analysis of these data.

within the first day; Shine et al., 2001a). Nonetheless, an array of behavioral traits differed between snakes that had left the den compared to those remaining behind. When we encountered them in the field, the dispersing snakes had apparently ceased reproductive behaviors (no animals were seen courting) and had commenced feeding (most dispersing snakes contained prey items or defecated at capture, whereas we never recorded either food or feces from den snakes). The dispersing snakes also fled from our approach and retaliated if attacked, whereas these behaviors were rare in animals still at the den. Significant morphological differences were also apparent, with dispersing snakes smaller and (in males only) thinner-bodied. However, thermal biology was apparently unaffected by dispersal from the den (Figure 1).

The morphological differences between den snakes and dispersing snakes are consistent with previous work showing that males lose mass rapidly during the courtship season (Shine et al., 2000b), and hence, we might expect smaller thinner males to be the first to leave the den. Departure by smaller females is less easily explained but may reflect escape from sexual conflict (intense and sustained courtship even to juvenile females; Shine et al., 2000d). Shifts in behavior are more complex and may reflect multiple causes:

Courtship by males

The males collected while dispersing were those that had "decided" to abandon the site where most courtship and mating occur (the den), and hence, we expected that they might show little or no courtship when presented with

a female. In fact, these males were only slightly less vigorous in courtship than were den males. The lower-body condition of these males suggests that they may have been running out of energy reserves, to the point that courtship in the den (where male–male rivalry is intense) was not worthwhile. However, dispersing snakes occur at much lower densities, and hence, rivalry will be much less intense. Arena trials have shown that male garter snakes adjust their intensity of courtship to the numbers and body sizes of competing males (Shine et al., 2000c). Thus, it may be worthwhile for a dispersing male to court any “attractive” (reproductively active) female that he encounters.

Female attractiveness

The lower numbers of males courting dispersing females, even in arena trials, fits well with the conclusion that postmating shifts in the skin lipids of a female signal that she is unreceptive to further courtship (Mason, 1993; Shine et al., 2000f). Being subjected to courtship is unlikely to benefit such a female and may attract predators to her; thus, a decline in sexual signals may enhance her fitness.

Feeding

In many snake species, both sexes cease feeding during the reproductive season (see Madsen and Shine, 2000; Ross, 1978; Shine, 1980). We were surprised to find that this was a facultative response in our garter snakes: Even when actively involved in courtship, the snakes enthusiastically accepted prey items. Presumably, there is little real conflict between courtship and feeding within this system, because prey are virtually absent from the area of the den (which is rocky and contains thousands of active snakes). Swallowing a worm required less than 2 min in our trials (personal observation), so any snake that encountered a prey item might well benefit from consuming it. The greater willingness of males to feed may reflect their higher energy expenditure in courtship and consequent lower energy reserves (Aleksiuk and Stewart, 1971).

Antipredator behavior

Having handled many tens of thousands of these snakes at dens over many years without being bitten, we were astonished to find the same animals behaving ferociously as soon as they left the den. Proximate factors such as body temperature and distance from cover can modify antipredator tactics in snakes (Duvall et al., 1985; Goode and Duvall, 1988; Passek and Gillingham, 1997) but cannot be invoked in this case because these factors were held constant. The proximity of other snakes might also affect optimal antipredator tactics, although we saw no pattern within the den in this respect (i.e., isolated animals were no more likely to flee or bite than were animals in aggregations; personal observation). Thus, the dramatic shift in approach distances and retaliatory behavior may reflect a genuine “switch” in some neural or endocrine pathway. In keeping with this interpretation, previous studies have documented effects of sex and reproductive status (gravid versus not) on antipredator responses of snakes (Duvall et al., 1985; Shine et al., 2000e).

Thermoregulation

Our data on free-ranging snakes did not reveal any differences in mean body temperatures as a function of a snake’s sex or its location (Figure 1). The same was true after opportunities for behavioral thermoregulation were standardized in outdoor

arenas (Figure 3). Similarly, previous field studies have detected only minor sex differences in temperature relations of garter snakes at the den (Shine and Mason, 2001). None of the snakes in our study regulated their temperatures with the same level of precision as has been reported for this (and related) species later in the year (Gibson and Falls, 1979; Peterson, 1987; Peterson et al., 1993). Careful thermoregulation may be incompatible with the need to travel rapidly through densely shaded aspen groves. Previous work showed that male garter snakes do not regulate their temperatures precisely during the mating season (Shine et al., 2000a), and our study extends this conclusion to both sexes during their initial postmating dispersal.

In summary, some of the behavioral shifts associated with dispersal from the den (and hence, from reproductive activity) are facultative responses to environmental differences between the den and the surrounding prairie. Most obviously, the lack of feeding by reproductive snakes is owing to a cessation of foraging behavior and/or lack of encounter with prey items, rather than by some intrinsic anorexia. Similarly, the lack of courtship by dispersing males reflects a lack of stimuli to elicit this behavior rather than a hard-wired celibacy.

In contrast, other differences between den and dispersing snakes are hard-wired rather than facultative and may involve neural or endocrine switches. The dramatic shift in antipredator tactics of dispersing snakes may fall into this category. That is, the snake’s behavior shifts not because it finds itself in a different habitat, but because of internal physiological states (dispersal mode).

The annual cycle of a red-sided garter snake can be viewed in terms of a succession of alternative physiological states. For example, an adult male snake will pass through at least six phases each year: hibernation, “she-maleness” (female mimicry) for a day or two immediately after emergence, “he-maleness” (active courtship and mating at the den), dispersal, feeding at the summer range, and dispersal back to the den in autumn (see Shine et al., 2000b, 2001a). For an adult female, the phases will be: hibernation, mating at the den immediately after emergence, dispersal, feeding at the summer range, pregnancy, and dispersal back to the den in autumn. The physiology and behavior of the snakes will differ substantially among many of these phases; for example, both pregnancy (for females) and courtship (for males) are associated with a decline in food intake and a modification of thermoregulatory precision (Charland and Gregory, 1990; Shine et al., 2000a).

Nonetheless, the proximate mechanisms that generate such effects may be diverse. For example, anorexia of gravid female snakes may be obligate in some species but facultative in others (Ross, 1978), and indeed, this aspect may differ among individuals even within a single population (personal observation). Likewise, anorexia in mate-searching males is widespread but not universal among snakes (Shine, 1977). Even where food intake is reduced during reproductive bouts, this effect may be either obligate or facultative. Undoubtedly, some of the distinctive behavioral shifts that occur as a snake moves through successive phases of its annual cycle will rely upon physiological “switches,” but others will reflect facultative responses to local conditions. Teasing apart this array of causal mechanisms remains a substantial challenge.

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