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Seasonal anorexia in the male red-sided garter snake, *Thamnophis sirtalis parietalis*

Abstract Many animals show seasonal shifts in behaviors that coincide with breeding, migration, or hibernation. These behavioral shifts provide ideal opportunities to study the regulation of behavior. The red-sided garter snake (*Thamnophis sirtalis parietalis*) spends 8 months of the year inactive in underground hibernacula, 1 month breeding, and 3 months feeding to build up enough energy stores to survive the following winter. Although they emerge from 8 months of hibernation with severely depleted energy reserves, they do not feed until weeks later, after the breeding season. We tested the hypothesis that this lack of feeding during the breeding season is due to a shift in behavior rather than the distribution of food and potential mates. Male garter snakes were given a series of choices between pursuing a breeding or feeding opportunity. The proportion of tests in which males selected feeding over breeding gradually increased throughout the study period, reaching almost 100% in the final tests. Males also were given opportunities to feed and court at the beginning and end of the study. Males initially refused food and courted females, but when retested at the end of the study they fed and did not court females. Thus aphagia during the breeding season is due at least in part to an endogenous shift in behavior.

Keywords Anorexia · Aphagia · Courtship · Feeding · *Thamnophis sirtalis parietalis*

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Introduction

Many animals experience seasonal shifts in behavior. For example, migration, hibernation, and breeding seasons represent seasonal shifts in locomotion, dormancy, and mating, respectively. Seasonal changes in behavior such as these are extreme, easy to observe, and may provide insight into other, more subtly variable behaviors.

One common shift in behavior is an inverse relationship between breeding and feeding. Not infrequently, both sexes forego feeding entirely during the reproductive season (Mrosovsky and Sherry 1980; Shine 1980; Bonnet and Naulleau 1996). Aphagia (a lack of feeding—regardless of its cause) during the breeding season may severely deplete energy reserves, and indeed, the ability to maintain high levels of reproductive activity in the absence of feeding has been identified as a major target of sexual selection (Bartholomew 1970; Andersson 1994). For example, a dominant male elephant seal (*Mirounga angustirostris*) must remain on his defended beach to maintain control of receptive females throughout the entire mating period before returning to the ocean to feed (Bartholomew 1970; Deutsch et al. 1990). Breeding male emperor penguins (*Aptenodytes forsteri*) walk up to 120 km to the breeding grounds and remain there without feeding for 115 days (Le Maho 1977).

The causal basis for such aphagia is complex. At least two different kinds of mechanisms can generate aphagia in reproductive animals: either an intrinsic mechanism (i.e. anorexia, a loss of appetite, Mrosovsky and Sherry 1980); or an extrinsic mechanism (i.e. reproduction induces animals to spend their time in habitats where they do not encounter food).

The red-sided garter snake, *Thamnophis sirtalis parietalis*, is an example of an animal with dramatic seasonal shifts in behavior. In the northern part of their range, they are constrained to hibernate underground for 8 months of the year (Gregory 1977). In late April and early May, they emerge and begin their 4-week breeding season. At the conclusion of the breeding season, they migrate to marshes up to 17.7 km away (Gregory and Stewart 1975).

Upon reaching the marshes, they must feed sufficiently in 3 months to survive the subsequent 9 months of aphagia, including another energetically costly breeding season.

When males emerge from hibernation, they immediately begin energetically costly courtship (Shine et al. 2004). However, courting males at the dens are never found with food in their stomachs (Aleksiuk and Stewart 1971; Gregory and Stewart 1975; Crews et al. 1987). It is unclear whether the lack of stomach contents at the dens reflects an absence of food there, or a refusal to take food even if available (anorexia). Prey items appear to be scarce or absent at the den sites (Aleksiuk and Stewart 1971; Gregory and Stewart 1975; Crews et al. 1987), and a related natricine snake, the northern water snake (*Nerodia sipedon*), does take food during the breeding season when it is available (Brown and Weatherhead 1999; Weatherhead et al. 2002). However, male red-sided garter snakes have been reported to refuse food during the breeding season (Aleksiuk and Gregory 1974; Crews et al. 1987; but see Shine et al. 2002). During the 4 weeks after emergence, they eventually stop courting females and migrate to their summer feeding grounds (Gregory and Stewart 1975; Shine et al. 2001).

The switch from breeding to feeding in the garter snake offers a robust model system for the study of the regulation of behavior. This system is unique because we can quantify and compare the extent of an animal's interest in feeding versus reproducing. Snakes of both sexes use chemical trails to locate prey items such as earthworms (Halpern and Martínez-Marcos 2003), and males use chemical trails to locate potential mates (e.g., see Mason et al. 1989; Mason et al. 1990; LeMaster and Mason 2001). Hence, it is possible to examine and compare the responses of male garter snakes to trails of both mating partners and prey items. This system thus allows a direct comparison between a male's interest in mating and feeding, because we can provide each test subject with a choice between the two types of trails and see which one he chooses to follow. We can also examine courting and feeding responses more directly, by exposing males to females and to prey and scoring their responses at different times within the breeding season. Finally, this system is ideal because the presence of human observers does not deter the snakes from mating or feeding and simple, unequivocal bioassays are available to quantify these behaviors (Kubie and Halpern 1975; Halpern et al. 1986; Mason et al. 1989; Mason et al. 1990; LeMaster and Mason 2002).

Using these bioassays, we sought to characterize the behavioral shift from courtship to feeding, and to determine whether these behaviors are mutually exclusive simply due to their spatial arrangement in the field or to an intrinsic limitation in male behavior. This study takes advantage of the easily quantified behaviors exhibited by a species that not only offers a model for insight into seasonal shifts in behavior, but also the cues that may guide these changes.

Methods

We collected garter snakes from a hibernaculum near Inwood, Manitoba, Canada (50°31.6′N, 97°29.7′W) at the beginning of the breeding season. Twenty males and 40 females were collected on 11 May 2002, and 24 males and 40 females were collected on 9 May 2003. (For the sake of brevity, dates will be referred to by number, with these collection days defined as day 0 within each year.) Snakes were kept at ambient temperatures in nylon outdoor arenas (1×1×1 m) during the day and in cloth bags at night (LeMaster and Mason 2002). Each day during the experiment all males were given simultaneous access to three unmated females randomly selected from the pool of 40 to simulate the sex ratio experienced at the den (Gregory 1984; Shine et al. 2001). The females' cloacae were taped closed while in the arena so the males could court the females but not mate with them. Males were not fed during the course of the experiment, as males in the wild do not feed during most of the time period we tested (Crews et al. 1987). This also allowed us to exclude the confounding factor of recent male feeding history. We performed four experiments to characterize male behaviors in response to cues from prey and females over the course of the breeding season. Experiment 1 was performed in 2002, experiment 2 in 2003 and experiments 3 and 4 in both 2002 and 2003. After the conclusion of these experiments, all snakes were fed worms and fish ad libitum twice a week then released at the point of capture after they had regained their initial body mass.

Experiment 1: do male preferences for following the trail of a live female versus that of a worm change over time?

Our first experiment investigated whether male garter snakes' preferences shifted from mating to feeding over time. We gave a group of 20 males the choice between following the trail of an earthworm or that of a female. Although the diet of *Thamnophis sirtalis* varies throughout its range, they commonly eat earthworms, and in some parts of their range worms constitute the majority of their diet (Rossman et al. 1996). Worms are also eaten by *T. s. parietalis* at our study site in the Interlake region of Manitoba (Gregory 1974).

We tested male trailing preferences using a Y-maze. The maze was constructed of wood and consisted of a base arm (45×13.5 cm) and two diverging arms (100×13.5 cm) at a 135° angle to the base arm. Each arm had two rows of pegs (6 cm tall) to provide push points for the snake. The rows were 6.5 cm apart, and the pegs within each row were separated by 7.3 cm. The surface of the maze was covered with butcher paper and the pegs were covered with sections of plastic drinking straws, all of which were replaced after each trial to remove any chemical cues from the preceding trial. The maze was elevated 90 cm off the floor to discourage subjects from leaving the maze. It was built without walls because garter snakes are strongly thigmotaxic (Ford 1986; Costanzo 1989).

We made trails on the paper by holding a randomly chosen stimulus female snake at the neck and just above the cloaca, and wiping its ventral surface up one side of the base arm and across to the opposite arm of the Y-maze. The female was randomly selected from the pool of 40 females, with replacement. To the other arm, we applied the trail of a worm by dragging a large earthworm along the paper. Assignment of the trails to the arms was randomized by coin flip. The trails crossed at the junction of the arms so that the subject snake encountered each trail before proceeding up an arm.

We began each trial by randomly selecting a male and placing it into an opaque box (31×18×9 cm) at the start of the Y-maze. Test males were allowed to leave the box of their own accord through a small hole. The male typically proceeded up the base arm of the maze and down the left or right arm. Trials were not scored when the male failed to show a pronounced trail contact response (Brown and MacLean 1983). For a trial to be scored, the snake's entire head had to pass a mark 30 cm up either of the arms. All decisions on whether to score a trial were made by a second observer who was blind to the treatments.

Before any trials began, we tested for a bias in the Y-maze by offering ten males the choice between two blank arms. Trail contact responses were not required because no trails were present.

Male preferences were tested once every 8–11 days from day 1 to day 48. For each male, we computed a logistic regression of whether the male followed the female (0) or the worm (1) as a function of time. A positive slope indicated a trend from choosing the female to choosing the worm, and a negative slope indicated the reverse. A slope of zero indicated no net change in preference over time. The slopes from all males' regressions were analyzed using a two-tailed Wilcoxon signed-rank test to determine whether they were significantly positive or negative. We also analyzed the decisions of all males over time in a single, composite logistic regression, with and without terms for individuals. We compared these regressions with F-tests and assessed the significance of individual terms with Wald tests (analogous to t-tests, Sokal and Rohlf 1995).

To determine whether the amount of mass lost affected the change in trail followed, all individuals were weighed to the nearest 0.1 g on day 1 and day 20. The percent of mass lost between these 2 days was used as an index of mass loss. Mass loss was added as a continuous covariate in the logistic regressions, and the fit was compared with an F-test. Descriptive statistics are given as mean±SE. All statistical analyses were performed using S-Plus version 6.1 (Insightful Corporation 2002).

Experiment 2: do male preferences for following a trail of female pheromones versus a worm trail change over time?

Our second experiment examined whether a shift in trails followed on the Y-maze through the season (experiment 1) could be accounted for by shifts in the attractiveness of the females, rather than a change in male priorities. In experiment 1, female sexual attractiveness pheromones could have changed over time. Any shift in male behavior may have been a result of changes in the stimulus itself, rather than changes in response to the stimulus. Here we used identical stimuli throughout the experiment to control for this possibility. With the exception of the differences noted below, methods were identical to those in experiment 1.

Twenty-four males were again given a choice between following female and worm trails on a Y-maze. In this experiment, female trails were laid using extracted female sexual attractiveness pheromones (Mason et al. 1990; LeMaster and Mason 2003). Female extract was prepared by soaking 31 females in 1 l 100% hexane for 12 h to remove all skin lipids. All females were found recently killed or fatally wounded by crows at the den. Fatally wounded females were euthanized with an overdose of sodium brevital. Care was taken to keep the heads and cloacae out of the hexane to avoid contamination by body fluids. Hexane was then allowed to evaporate until 48 ml of skin lipids in hexane remained. Approximately 0.4 female equivalents of skin lipids in hexane were applied to the Y-maze with a single stroke of a fine paintbrush and the hexane was allowed to evaporate from the paper before the trial began. Lipids in hexane extract were stored at −10°C for the duration of the experiment. Male preferences were tested three times, once every 10 days from day 4 to day 24. In this experiment, we estimated mass loss using measurements from days 1 and 24.

Experiment 3: does feeding behavior change over time?

Our third experiment investigated whether there was a change in males' appetites during the breeding season, without the immediate alternative of courtship. A single large earthworm was placed in a 19-l container. A male snake from experiment 1 or 2 was then added to the container, with its head directed at the worm. The snake was allowed up to 300 s to attack the worm, and latency to attack the worm was recorded. The proportion of snakes attacking the worm was compared between days 4 and 40 in 2002, and days 9 and 24 in 2003. Presence of feeding behavior and latency to attack were compared between dates using a Wilcoxon signed-rank test.

Experiment 4: does courtship behavior change over time?

Our fourth experiment investigated whether males' interest in courting females changed during the breeding season, without the immediate alternative of feeding. All males from experiments 1 and 2 were given simultaneous access to six females. Males were removed from the group when they exhibited courtship behavior, and were given up to 2 h to do so. Willingness to court was tested on days 1 and 60 in 2002 and on days 3 and 24 in 2003. Presence of courtship behavior for each male was compared between dates within each year using a Wilcoxon signed-rank test.

Results

Experiment 1: do male preferences for following the trail of a live female versus that of a worm change over time?

There was no bias in the Y-maze. When there were no chemical cues on either arm, six males went left and four went right (binomial test, $P=0.75$).

Over time, males switched from following the female trail to following the worm trail (Fig. 1). Slopes of individual logistic regressions were significantly positive (two-tailed Wilcoxon signed-rank test, $Z=3.35$, $P<0.001$).

Time significantly affected the choice when data from all males were combined in a logistic regression (Wald test, $Z=4.54$, $P<0.001$). However, there were significant differences between individuals in the switch from following one trail to following the other. Allowing for individual difference in slope and intercept of a logistic regression of choice on time significantly increased the fit over a model that did not allow for individual differences ($F=84.84$, $df=38$; $P<0.001$). After allowing for individual differences in response, time still adds significantly to the model ($F=79.85$, $df=20$, $P<0.001$).

Mass loss did not affect the trail chosen by the male. Allowing mass loss, rather than the individual, to affect the intercept and slope of a logistic regression of choice on time did not increase the fit over a model that included only time ($F=0.69$, $df=2$, $P=0.70$). Mass loss was not af-
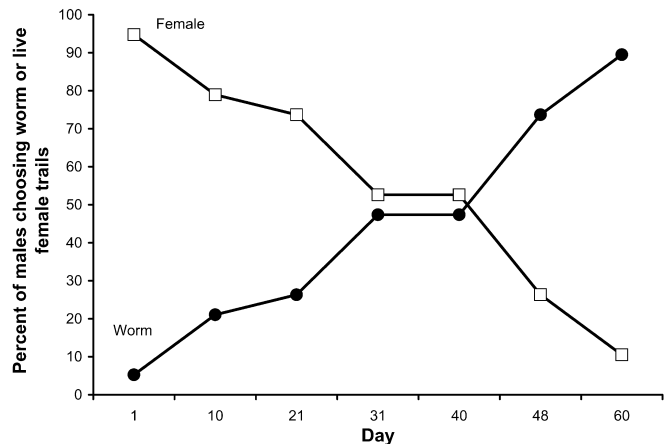

Fig. 1 Percentage of males choosing worms or live female trails over time. Data from all males are combined for clarity
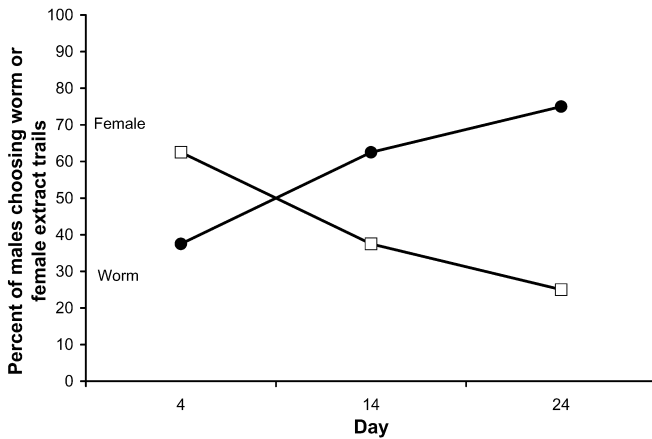
Fig. 2 Percentage of males choosing worms or extracted female pheromone trails over time. Data from all males are combined for clarity

fected by whether the male ate a worm in the first feeding trial (two-tailed Wilcoxon rank sum test, $Z=-0.48$, $P=0.63$). On average, males lost 2.8 ± 0.23 g between days 1 and 20. This was $10.4\pm0.63\%$ of their body mass.

Experiment 2: do male preferences for following a trail of female pheromones versus a worm trail change over time?

There was no bias in the Y-maze. When there were no chemical cues on either arm, nine males went right, and seven went left (binomial test, $P=0.80$).

Over time, males switched from following the female pheromone trail to following the worm trail (Fig. 2). Slopes of individual logistic regressions were significantly positive (two-tailed Wilcoxon signed-rank test, $Z=3.00$, $P=0.0027$).

Time significantly affected the choice when all males were included in a logistic regression (Wald test, $Z=2.56$, $P=0.01$). Allowing for individual differences in slope and intercept did not significantly increase the fit when compared to a model that did not consider individual differences ($F=60.12$, $df=46$, $P=0.08$). Allowing for an effect of mass loss also did not significantly increase the fit ($F=1.51$, $df=2$, $P=0.47$). Mass loss was not affected by whether the male ate a worm in the first feeding trial (two-tailed Wilcoxon rank-sum test, $Z=0.41$, $P=0.68$). On average, males lost 2.5 ± 0.17 g between days 1 and 24. This was $8.4\pm0.52\%$ of their body mass.

Experiment 3: does feeding behavior change over time?

There were significant increases in feeding over time within each year of the study. In 2002, significantly more males fed on day 40 than on day 4 (19/20 vs 2/20, two-tailed Wilcoxon signed-rank test, $Z=4.24$, $P<0.0001$). Males also attacked the worm faster on day 48 than on day 4 (57.8 ± 12.1 s vs 195 ± 45 s, two-tailed Wilcoxon

signed-rank test, $Z=-4.00$, $P=0.0001$). In 2003, significantly more males fed on day 24 than on day 9 (10/24 vs 17/24, two-tailed Wilcoxon signed-rank test, $Z=2.33$, $P=0.020$). However, males did not attack worms significantly faster or slower on day 24 than on day 9 (52.9 ± 25.1 s vs 102.6 ± 27.3 s, two-tailed Wilcoxon signed-rank test, $Z=-1.71$, $P=0.09$).

Experiment 4: does courtship behavior change over time?

The change in feeding behavior over time in experiment 3 could alone explain the results of experiments 1 and 2, or courtship behavior could also have changed simultaneously. The latter was found to be the case; there were significant decreases in courtship over time within each year of the study. In 2002, significantly more males courted on day 1 than on day 60. Among 20 males, 20 courted on day 1, and 0 courted on day 60 (two-tailed Wilcoxon signed-rank test, $Z=-4.47$, $P<0.0001$). In 2003, significantly more males courted on day 3 than on day 24. Among 24 males, 24 courted on day 3, and 7 courted on day 24 (two-tailed Wilcoxon signed-rank test, $Z=-4.12$, $P<0.0001$).

Discussion

Aphagia in male garter snakes over the 4-week courtship period might be caused by a single mechanism. Snakes concentrate on courtship rather than feeding either because of some intrinsic behavioral mechanism (anorexia), or because they do not encounter potential prey in the locations where courtship occurs. Indeed, previous literature has assumed such a dichotomy, leading to directly contradictory conclusions—either that reproducing male red-sided garter snakes refuse to feed even if food is available (Crews et al. 1987; Morris and Crews 1990) or that the aphagia of these animals is a result of failure to encounter prey rather than their refusal to consume prey if encountered (Shine et al. 2002). Our data resolve this contradiction, showing that both mechanisms may be at work, depending on the timing of migration from the hibernaculum where courtship occurs to the fields and marshes where feeding occurs. That is, in the early part of the mating period, male garter snakes simply refuse to feed even when food is available—but at the end of the mating period, they may readily accept prey if it is available. Future work should investigate the coincidence between the timing of this intrinsic shift in behavior and the migration to the feeding grounds. We predict that the shift in behavior will coincide with the migration to the feeding grounds where prey are abundant and receptive females are absent.

In years when the intrinsic shift occurs before migration, a single phenomenon (aphagia during breeding) may actually reflect two different proximate mechanisms, both an intrinsic anorexia and an extrinsic absence of prey items at the den. Previous studies have failed to document

this complexity, but our study improves upon previous designs by (1) incorporating time within the breeding season as a factor in the analyses; and (2) using a behavioral test (trail-following) that forced males to select between the two competing priorities of feeding versus breeding. This within-season shift in male behavior fits well with other recent research on the Manitoba garter snakes, which has revealed substantial shifts in important behaviors over the course of the spring mating period (Shine et al. 2002).

Our experiment using standardized female pheromone trails (experiment 2) confirms that the shift in male behavior was dependent on male response to, or perception of, the pheromone. However, this result does not exclude the possibility that the pheromones of the live females changed through the course of the breeding season. Female pheromone profiles do change seasonally, but it is not known whether these changes require a shedding of the skin or on what timescale these changes occur (Mason et al. 1987; Mason 1992). If changes in female pheromones do occur during the breeding season, they could partly explain the lowered intensity of courtship to females later in the breeding season (Shine et al. 2002). Alternatively, reduced exposure to female pheromones in the environment (either on females or deposited on the substrate) could cue males to shift from breeding to feeding behavior.

While the regulation of the shift from courtship to feeding is not well understood, a number of cues stand out as candidates. One possible cue is mass loss. Males may switch from mating to feeding once they reach a critical reduction in body mass. However, data from this experiment suggest that this is not the case. Mass loss had no effect on the decision to pursue a breeding or feeding opportunity in either year of this study.

The switch from mating to feeding may also be a product of the time required to reactivate the digestive system after 8 months of aphagia. However, the shift in *T. s. parietalis* took much longer than required for stomach activation in other snake species. The rattlesnake *Crotalus cerastes* takes 12–24 h to activate its digestive system after ingesting a meal, and the Burmese python, *Python molurus*, takes 24–48 h (Secor et al. 1994; Secor et al. 2002). Furthermore, these snakes ingest food while their stomachs are inactive. The presence of nutrients in the digestive tract activates the stomach. It is unlikely that the garter snake delays feeding because the digestive tract is inactive upon emergence because in these other snake species it is the ingestion of food that activates the digestive tract, not vice versa.

Temperature could potentially affect the switch from courting to feeding. The lower thermal threshold for courtship in Manitoba *T. s. parietalis* varies between individuals from 4.5 to 25°C (Aleksiuk and Gregory 1974; Hawley and Aleksiuk 1975). Similarly, the minimum temperature required for courtship in Michigan *T. s. sirtalis* is 4.5°C, and the minimum temperature for copulation is 15.5°C (Blanchard and Blanchard 1941). Feeding is also affected by temperature. Western terrestrial garter snakes (*T. elegans*) regurgitate mice if they are ingested when the snake's body temperature is below 10°C (Stevenson et al. 1985). The lower limit for courtship is approximately equivalent to the lower limit for feeding, but there is an apparent upper limit on copulation, if not courtship. Female *T. s. parietalis* with body temperatures over 20°C refuse to mate (Garstka et al. 1982). More data are required on the lower thermal limit of feeding and the upper thermal limits of courtship and feeding to determine whether temperature alone could regulate the shift between these behaviors in *T. s. parietalis*. However, both behaviors are observed over a broad range of temperatures. While the chronic thermal regime may regulate the switch, current body temperature alone probably does not.

Changes in day length could potentially regulate the timing of the shift from feeding to mating, as it does in some mammals (Morgan and Mercer 2001). Because red-sided garter snakes spend 8 months of the year underground in total darkness, light cues are expected to be less important than in other species (Garstka et al. 1982; Whittier et al. 1987). For example, emergence from the hibernaculum, and thus the initiation of the breeding season, is regulated by temperature and not by light (Aleksiuk and Gregory 1974; Whittier et al. 1987). Captive males switched from breeding to feeding over a period of about 10 days when on an artificial 12L:12D photoperiod after emergence (Aleksiuk and Gregory 1974), so the switch can occur without any change in photoperiod. The possibility remains that the shift in behavior may be related to changes in photoperiod; however this hypothesis remains to be tested.

Whatever the environmental cue is that regulates the shift from mating to feeding, the proximate transducer of that signal also remains an enigma. While there could be two separate signals regulating courtship and feeding, the inverse relationship between these behaviors suggests that they may be regulated by the same signal (Aleksiuk and Gregory 1974). Based primarily on studies in rodents, some specific hormones have been identified as potential regulators of the behavioral switch from mating to feeding. These hormones include leptin (Aubert et al. 1998), neuropeptide Y (Morris and Crews 1990), galanin (Crawley 1995), and cholecystokinin (Jensen 2001).

The evolutionary advantage of refusing food during the breeding season, even if food is available, is unclear. The handling time of a worm is not considerable, taking less than 2 min in most cases (Shine et al. 2002). But many snakes reduce or cease feeding during the reproductive season (Shine 1980; Madsen and Shine 2000; but see Aldridge et al. 2003). Given the short duration of the breeding season, the scarcity of prey close to the den, and the very high emergence rate of females (and thus, the high opportunities for mating), the optimal male tactic may be to focus on courtship to the exclusion of all else (Gregory and Stewart 1975; Mrosovsky and Sherry 1980). In keeping with this interpretation, courting male garter snakes show little overt response to stress (Moore et al. 2000) or to predator cues (Shine et al. 2002). Alternatively, refusing food may not be in itself adaptive for

snakes. This seasonal anorexia may be simply due to some physiological constraint inherent to reproduction. In any case, being willing to ingest food during the breeding season would be unlikely to present a significant evolutionary advantage in this population because of the virtual absence of prey items at the dens (Aleksiuk and Stewart 1971; Gregory and Stewart 1975; Crews et al. 1987). Two additional questions may shed light on these hypothesized explanations for the observed shift in male behavior. First, do males show a similar inhibition of feeding in the fall breeding season? Males are already known to refuse food in the fall, but this has been assumed to be a result of the costs associated with hibernating with stomach contents (i.e. rotting food in the digestive tract) (Aleksiuk and Stewart 1971). Second, do females show similar shifts in behavior in the spring? If so, then the inhibition of feeding reported here is not likely explained by the costs of mate searching.

The red-sided garter snake provides an excellent model for the study of certain aspects of the regulation of feeding behavior. While the value of mammalian models of anorexia and obesity with known genetic backgrounds is not to be understated, the dramatic shifts in feeding and reproductive behavior in the garter snake allow the study of the hormonal regulation of these behaviors within a single animal, rather than comparing multiple genetic mutants. In the future, the red-sided garter snake may prove to be a valuable model for the study of the regulation of courtship and feeding behavior.

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