

Do a male garter snake's energy stores limit his reproductive effort?

Richard Shine and Robert T. Mason

Abstract: The storage and utilization of energy plays a critical role in reproductive output for females of many species, including snakes. However, links between energy and reproductive effort in males are less clear. Studies at a communal den of red-sided garter snakes (*Thamnophis sirtalis parietalis* (Say, 1823)) in Manitoba suggest that energy is critical to reproduction for males as well as females. Males vary substantially in body condition (mass relative to body length) at the time they emerge from winter inactivity. The energy to be expended in courtship is stored in the muscles rather than the "conventional" sites for energy storage in snakes (abdominal fat bodies or liver). A male's reproductive effort (the duration of his residency at courting aggregations near the den) was linked to his energy stores and to the rate of depletion of those stores. Male snakes that emerged from hibernation in better condition, and that lost mass slowly thereafter, remained in courting aggregations near the den for longer periods than did males that emerged in poor condition (i.e., with less energy resources) and (or) lost mass more rapidly. In outdoor arenas, males that engaged in courtship lost mass more rapidly than did males with no courtship opportunities. These data suggest that courtship is energetically expensive for male garter snakes and that the amount of effort that a male invests in reproduction is determined by his energy stores.

Résumé : La mise en réserve et l'utilisation de l'énergie jouent un rôle fondamental dans le rendement reproductif des femelles de plusieurs espèces, y compris de couleuvres. Les liens entre l'énergie et l'effort reproductif des mâles sont, cependant, moins évidents. Des études faites à un terrier communautaire de couleuvres rayées (*Thamnophis sirtalis parietalis* (Say, 1823)) au Manitoba laissent croire que l'énergie est critique pour la reproduction chez les mâles autant que chez les femelles. Les mâles varient considérablement dans leur condition corporelle (masse en fonction de la longueur du corps) au moment où ils sortent de leur inactivité hivernale. L'énergie qui servira à la cour est stockée dans les muscles plutôt que dans les sites plus « réguliers » de mise en réserve de l'énergie chez les couleuvres, comme les corps gras abdominaux ou le foie. L'effort reproductif du mâle (la durée de son séjour près du terrier dans les rassemblements de cour) est en relation avec ses réserves énergétiques et avec le taux d'utilisation de ces réserves. Les couleuvres mâles qui sortent d'hibernation en meilleure condition et qui subissent une diminution subséquente de masse plus lente demeurent au sein des rassemblements de cour près du terrier plus longtemps que les mâles qui émergent en mauvaise condition (c'est-à-dire avec moins de ressources énergétiques) et (ou) qui subissent une perte de masse plus accélérée. Dans les arènes externes, les mâles qui entreprennent des comportements de cour ont des pertes de masse plus rapides que les mâles qui n'ont aucune occasion de faire la cour. Ces données indiquent que la cour est un processus coûteux en énergie chez les couleuvres rayées mâles et que l'importance de l'effort qu'un mâle investit dans la reproduction est déterminée par ses réserves énergétiques.

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Introduction

Reproducing necessarily involves the expenditure of energy, but whether or not energy availability actually constrains reproductive expenditure remains an open question for most kinds of organisms, and especially for males. The fundamental difference between males and females is that the latter sex produces large, energy-rich gametes whereas the former does not (Williams 1966). Thus, we might expect

a priori that variation in reproductive output among females within a natural population will be driven by variation in their energy stores. Abundant empirical evidence supports this prediction. For example, females of many species delay reproduction until they have accumulated substantial energy reserves, and females able to replenish their reserves more rapidly are able to reproduce at a faster rate (e.g., Frisch and McArthur 1974; Albon et al. 1986; DeRouen et al. 1994; Bonnet et al. 2000, 2001; Harris and Ludwig 2004).

The link between energy availability and reproductive effort is less direct in males. Sperm production requires much less energy than egg production, and males of most species invest nothing except sperm in their offspring; thus, we might expect that variation among males in reproductive effort would be driven by factors other than energy supply. However, this argument neglects the energetically expensive nature of many accessory activities performed by reproductive males, such as mate-searching, male-male combat, and displaying to females or other males (Ryan 1988; Andersson

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1994). To what degree, then, is variation in male reproductive effort within a natural population driven by variation in energy stores and rates of utilization?

This question will be easiest to answer in an ectothermic species. Resting metabolic rates (and thus rates of energy consumption) are very high in endotherms, so that the proportion of an animal's overall energy budget allocated to reproduction inevitably will be much smaller (and thus more difficult to measure) in an endotherm than in an ectotherm. Also, endothermy imposes strong constraints on long-term accumulation of energy reserves because fat storage impedes heat transfer between the animal and its environment (Jönsson 1997). Freed from this constraint, many ectotherms lay down extensive energy reserves over periods of months or years prior to expenditure of those reserves in reproduction (Bull and Shine 1979; Bonnet et al. 1998a, 2001).

One ectothermic group that has attracted considerable research on this topic is the snakes. The effects of energy availability on the reproductive output of females have been the subject of extensive experimental and descriptive studies (Ford and Seigel 1989; Seigel and Ford 1991; Naulleau and Bonnet 1996; Bonnet et al. 1998a, 2001, 2002a, 2002b). This research provides strong evidence that female reproductive output in snakes is causally linked to energy availability. However, the situation with respect to males is less clear. Males do not invest in their offspring except via sperm, but engage in many energetically expensive activities in the course of reproduction (Devine 1984; Schuett and Gillingham 1988; Bonnet and Naulleau 1996; Aubret et al. 2002). Fortunately, empirical assessment of rates of energy expenditure in male snakes is facilitated by the fact that reproductive males of many species show seasonal anorexia, with a complete cessation of feeding during the reproductive season (Madsen and Shine 1993, 2000; Shine et al. 2003). Thus, rates of decrease in body mass over this period indicate rates of decrease in energy stores (Bonnet and Naulleau 1994, 1996; Bonnet et al. 2002b). However, because catabolism of fats provides approximately twice the energy that would be obtained from catabolizing the same mass of protein, we need to know not only the rates of mass loss, but also the nature of the substrate used to generate that energy expenditure (Lourdais et al. 2004). The link between mass loss and energy expenditure during reproduction is more complex in females because the changing water content of developing eggs and embryos modifies maternal mass independent of energy reserves; thus, a female can be heavy-bodied even when she has exhausted all of her energy reserves by directing them into reproductive materials (Bonnet et al. 2002b; Lourdais et al. 2002).

The amount of mass (energy) lost by reproducing male snakes varies considerably but is substantially lower than the amount of mass lost during reproduction by conspecific females (e.g., Madsen and Shine 1993, 2000). In keeping with the putatively low costs of sperm production, male vipers (*Vipera aspis* (L., 1758)) initiate spermatogenesis and courtship even if they are in poor condition (Aubret et al. 2002). However, males in better condition (i.e., with higher energy reserves) exhibit higher plasma testosterone levels (Aubret et al. 2002). Although intuition suggests that mass loss by males is due to energetically expensive activities such as mate-searching, courtship, and male-male combat, detailed

studies of adders (*Vipera berus* (L., 1758)) suggest that a significant part of the energy expenditure occurs before these activities commence and thus may be related instead to hormonal changes and sperm production (Olsson et al. 1997). Thus, to understand the role of energy storage and utilization in male snakes, we need to answer the following questions:

- (1) Is mass lost by males during the reproductive season a direct consequence of reproductive activities? Alternatively, mass loss may simply reflect anorexia coupled with high metabolic rates independent of the intensity of reproductive behaviour.
- (2) Do energy stores and (or) rates of depletion of those stores determine variation in reproductive effort among individual males within the population? Alternatively, behavioural variation among males might be driven by other factors, such as differing tactics or degrees of risk aversion (Andersson 1994; Roff 2002).

To answer these questions, we conducted descriptive and experimental studies of red-sided garter snakes (*Thamnophis sirtalis parietalis* (Say, 1823)) at a communal den on the Canadian Prairies. The work was facilitated by the large number of snakes at the den, their tolerance to human observers, and the ease of monitoring and manipulating male reproductive behaviour.

Material and methods

Study species and area

Red-sided garter snakes (Rossman et al. 1996) are small (snout-vent length (SVL) averages 45 cm in males, 55 cm in females), nonvenomous colubrid snakes. On the Canadian Prairies these snakes gather in large aggregations at suitable den sites each autumn and court and mate during a brief period in spring before they disperse (Gregory 1974; Gregory and Stewart 1975). Males emerge from the den over a period of about 4 weeks and commence courting a day or so after emergence; most leave after 1 or 2 weeks of the 4-week mating season (Shine et al. 2001a). Males do not feed during this period (O'Donnell et al. 2004).

Previous work suggests that energy storage and expenditure may play an important role in the breeding biology of these animals. First, more heavy-bodied males (presumably those with better energy stores) court more vigorously than their thinner rivals and consequently are more likely to obtain matings both in arena trials (Shine et al. 2004) and in the field (Shine et al. 2000). Also, recaptures of males at the den have revealed rapid losses in body mass; these decreases are not due to dehydration, because providing access to drinking water prior to weighing has little effect on estimated rates of mass loss (Shine et al. 2001a).

We worked at a large den 1.5 km north of the town of Inwood, Manitoba (50°31.58'N, 97°29.71'W) in May 2002 and 2003, encompassing most of the snake's emergence period each year. Data on body composition of dissected snakes come from earlier work at the Chatfield dens 30 km further north (see Shine et al. 2001b for details).

Variation in energy stores among males

To quantify the degree of variation in energy stores among males at the time they emerge from hibernation, we can

measure variation in body condition (mass relative to SVL). We did this with a large sample of newly emerged snakes at the Inwood den in 2003 (see below); residual scores from the general linear regression of \ln mass against \ln SVL provided indices of body condition. To clarify the form of energy stores, we can examine the determinants of body condition; for example, how much does variation in the mass of abdominal fat bodies contribute to overall variation in body condition? To obtain these data, we took advantage of a major mortality event at the Chatfield dens in 1997, when 76 males were found suffocated within a den under the weight of an unusually large courting aggregation (see Shine et al. 2001b for details). These animals were dissected to provide data on mass of the fat bodies and liver (the main energy stores previously described in snakes: Bonnet et al. 1998b) relative to that of the rest of the carcass.

Rates of mass loss in the field

Each day in May 2003 we collected newly emerged snakes (i.e., those on their first day out after their 8-month winter inactivity) at the Inwood den. Newly emerged males attract courtship by other males for the first day after emergence (Shine et al. 2001c) and are thus easily recognized. We measured SVL and weighed all of these snakes, painted a unique number on the dorsal surface of each one, then released them in the den on the same day (or, rarely, the following day). Recaptures of these animals provided data on rates of mass loss. To recapture these animals as they dispersed from the den, we set up a 60-m drift fence of wire mesh with funnel traps at 10-m intervals, 100 m from the main Inwood den. Traps were checked and cleared at least twice daily; recaptured snakes were reweighed before release the following morning on the opposite side of the fence. Male snakes switch from courting to feeding as they leave the vicinity of the den (O'Donnell et al. 2004), so snakes that leave sooner presumably spend less time engaged in reproductive activities.

Rates of mass loss in outdoor arenas

To see whether mass loss by males was causally connected to courtship, we set out 10 open-topped nylon arenas (1 m \times 1 m \times 0.8 m) and placed 10 numbered (paint-marked) and weighed males in each arena. We added two reproductive females to each of half of the arenas but not the other half, and replaced these females on a daily basis. We taped the cloaca of each female to prevent mating. Under these conditions, male garter snakes court vigorously (e.g., Shine et al. 2000). Thus, half of the males actively engaged in courtship every day, whereas the other half did not. We reweighed all the males 6 days later.

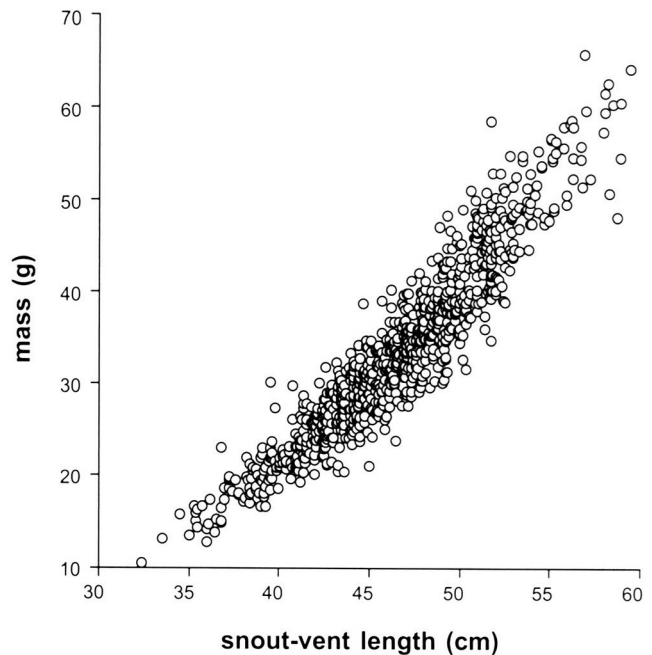
All experiments were conducted in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Results

Variation in energy stores among males

Newly emerging male garter snakes varied substantially in body condition (mass relative to SVL; Fig. 1). For example, at 50 cm body length, mass varied from 30 to 50 g (Fig. 1). However, dissection revealed that males had tiny abdominal

Fig. 1. Mass relative to snout-vent length for 936 male garter snakes (*Thamnophis sirtalis parietalis*), as measured on the day they first emerged from their 8-month period of winter inactivity in a Manitoba den.



fat bodies (mean = 0.86 g in an average-sized, 31.5-g male (2.7% of body mass)). Although larger, the liver was also only a small proportion of total body mass (mean = 1.52 g (4.8%)). Thus, most of the variation in male body mass was due to lean mass (muscle, skeleton, etc., versus total mass; $n = 76$, $r^2 = 0.997$, $P < 0.0001$). Hence, the proportions of fat-body mass and liver mass relative to total mass had no significant influence on body condition (residual score of \ln mass vs. \ln SVL: fat-body mass, $r^2 = 0.0004$, $P = 0.87$; liver mass, $r^2 = 0.006$, $P = 0.51$).

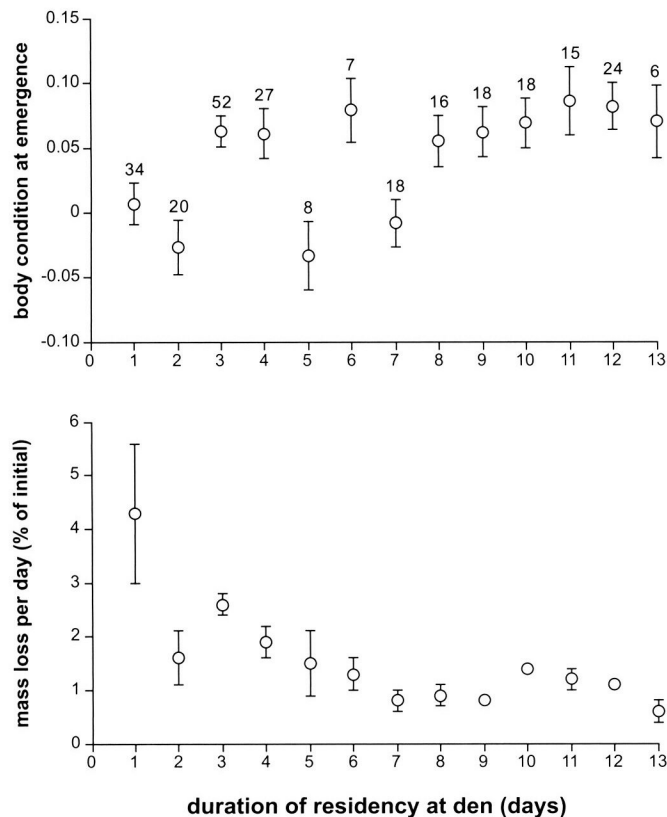
Rates of mass loss in the field

Some male snakes stayed at the den for at least 13 days after emerging, whereas others left the same day they emerged (mean = 4.78 days, mode = 3 days). Males lost mass over this period at an average rate of 2.3% per day (range 0%–8.9%). As predicted by the hypothesis that energy resources determine the duration of a male snake's stay at the den, multiple regression showed that males were likely to stay longer at the den if:

- (1) they were heavy-bodied at emergence (using residual scores from the general linear regression of \ln mass vs. \ln SVL as a measure of body condition versus duration of residency at the den; $n = 262$ males, Spearman's $\rho = 0.23$, $P < 0.0005$; see Fig. 2) and;
- (2) they lost mass only slowly (ANCOVA with duration of residency at the den as the factor, mass lost per day between emergence and recapture at the fence as the dependent variable, and initial SVL as the covariate; effect of residency duration on daily rates of mass loss, $F_{1|2,241} = 7.65$, $P < 0.0001$; see Fig. 2).

The first of these patterns is unambiguous, but the second is not. A correlation between recapture interval and daily

Fig. 2. Duration of residency of male garter snakes at a breeding aggregation relative to the snakes' initial body condition at emergence from overwinter inactivity (residual score from \ln mass vs. \ln snout-vent length for all snakes combined) and the rates at which the snakes lost mass during the breeding period (percent of initial mass lost per day). The graphs show mean values and standard errors for each 1-day category for duration of residency; numbers are sample sizes and are the same for both data sets. Although data are shown this way for ease of interpretation, statistical analyses were based on raw data, rather than ratio measures, to avoid statistical artefacts.



rate of mass loss might arise not because males that maintained mass stayed longer at the den, but because:

- (1) rates of mass loss declined with time since emergence overall. That is, all snakes might rapidly lose mass soon after emergence and then remain relatively constant in mass. We can test this alternative interpretation by comparing sequential rates of mass loss in snakes recaptured more than once. Daily mass loss rates did not differ significantly between the first and second recapture intervals for individual snakes (means: 2.1% vs. 2.7%, $F_{[1,43]} = 0.25$, $P = 0.62$). Thus, the strong relationship between duration of residency and rates of mass loss (Fig. 2) cannot be attributed to declining rates of mass loss as a function of time since emergence.
- (2) rates of mass loss were lower early in the emergence season, when ambient temperatures were lower. Because snakes that remained at the den longer were, on average, those that emerged from the den earlier in the season, this bias might generate an artefactual correlation between duration of residency and rates of mass loss. We tested this idea by including the date (number of days

after the beginning of our study) as an additional independent variable in the ANCOVA. As predicted, earlier emergence was associated with lower rates of mass loss ($F_{[12,240]} = 48.66$, $P < 0.0001$), but including date as a variable strengthened rather than weakened the association between duration of den residency and daily rates of mass loss ($F_{[12,240]} = 13.10$, $P < 0.0001$).

Rates of mass loss in outdoor arenas

We used nested ANOVA to examine experimental data from individual animals nested within the arena in which the animals were maintained. Mass after 6 days was the dependent variable, and initial mass was included as a covariate. Treatment (presence or absence of females) significantly affected the amount of mass lost by male snakes ($F_{[1,4]} = 10.86$, $P < 0.035$; significance tested against the nested term rather than the residual error term). Simple ratio calculations showed that mean rates of mass loss were twice as high for males allowed to court females ($2.9\% \pm 0.5\%$ of initial mass per day) as for males kept without access to females ($1.4\% \pm 0.5\%$ per day).

Discussion

Our data support the hypotheses that:

- (1) the rate at which an anorexic reproductive male snake loses mass (presumably because of depletion of energy resources) is influenced by his energy expenditure in courtship activities per se rather than by his general physiological condition; and
- (2) a male snake modifies his reproductive expenditure (i.e., duration of his participation in courting aggregations near the den) during the current breeding episode as a function of his energy resources and the rate at which those resources decrease through time.

Our results constitute the strongest empirical support yet available for these conclusions, but accord with intuition. First, male garter snakes are extraordinarily active during the courtship season; focal observations suggest that males typically move almost constantly and may average >6 m of displacement per minute (Shine et al. 2001a; R. Shine et al., unpublished data). This frenetic activity inevitably makes severe demands on the animal's energy stores. In some other snake species, males move about more slowly and court much less vigorously (e.g., Shetty and Shine 2002); hence, metabolic costs are, presumably, correspondingly lower.

Second, matching total investment in energetically expensive reproductive behaviours to energy stores makes intuitive sense and accords well with the observation that plasma testosterone levels correlate with energy reserves in male vipers (Aubret et al. 2002). At the Manitoba dens, male snakes with lowered energy resources are less likely to obtain matings; extensive data both from the field and from outdoor arena studies document a strong trend for more heavy-bodied males to obtain more matings (Shine et al. 2000, 2004). Also, males with lowered energy resources may be less able to make the long-distance (up to 18 km; Gregory 1974) migrations from the dens to their summer feeding ranges. Accordingly, male garter snakes shift their priorities from courtship to feeding as the reproductive season pro-

gresses and their own body condition declines (O'Donnell et al. 2004).

Darwinian fitness depends upon successful reproduction, and thus an organism must allocate time, energy, and nutrients to reproductive expenditure, often experiencing substantial risk in the process. Mathematical models suggest that natural selection will balance these "costs" (to probable future reproductive output) against the benefits (successful production of progeny in the current episode), such that organisms will allocate optimal amounts of resources to reproduction each season (Williams 1966; Roff 2002). However, this simple prediction from simple mathematics has proved frustratingly difficult to test. It is relatively straightforward to detect the presence of costs (such as loss in body mass), but much harder to determine their relationship to reproductive investment. The Manitoba dens facilitate the detection of such relationships, especially because mass loss can be used as an index of energy depletion in these anorexic ectotherms.

Nonetheless, many puzzles remain. Chief among them is the site of storage for the energy that male garter snakes use to fuel their reproductive activities. Data from our dissections show that this energy is not stored in the "conventional" sites (abdominal fat bodies or the liver; see Bonnet et al. 1998b for data on fat-body and liver masses in males of other snake species); these are too small, and variation in their size is unrelated to the body condition of males. Our mark-recapture studies show that male snakes often lose >10% of their initial body mass during their tenure at the den, a far greater loss than can be explained by utilization of lipids from either the fat bodies or the liver. Instead, the energy stores are somehow included within the muscle mass of the snakes. Previous literature has generally assumed that abdominal fat bodies and the liver are the primary storage sites for energy reserves to be used during reproduction. However, the reality may be more complex. Recent work has shown that female boid snakes break down muscle tissue to support energy expenditure during long periods of fasting associated with pregnancy, but suffer substantial reductions in locomotor performance and strength as a result (Lourdais et al. 2004). The location and functional consequences of energy storage to maintain reproductive output thus remain significant open questions.

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