Why do male snakes have longer tails than females?

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In most snake species, males have longer tails than females of the same body length. The adaptive significance of this widespread dimorphism has attracted much speculation, but few tests. We took advantage of huge mating aggregations of red-sided gartersnakes (*Thamnophis sirtalis parietalis*) in southern Manitoba to test two (non-exclusive) hypotheses about the selective forces responsible for this dimorphism. Our data support both hypotheses. First, relative tail length affects the size of the male copulatory organs (hemipenes). Males with longer tails relative to body length have longer hemipenes, presumably because of the additional space available (the hemipenes are housed inside the tail base). Second, relative tail length affects male mating success. Males with partial tail loss (due to predation or misadventure) experienced a threefold reduction in mating success. Among males with intact tails, we detected strong stabilizing selection on relative tail length in one of the two years of our study. Thus, our data support the notion that sex divergence in tail length relative to body length in snakes reflects the action of sexual selection for male mating success.

Keywords: male combat; mating success; sexual selection; tail wrestling; *Thamnophis sirtalis parietalis*

1. INTRODUCTION

The selective forces responsible for the evolution of sexually dimorphic traits have attracted considerable scientific attention, because the ability to carry out strictly controlled comparisons (i.e. between conspecific males and females) provides an opportunity for exceptionally powerful tests of evolutionary hypotheses (e.g. Andersson 1994). The myriad forces that confound interspecific comparisons and, thus, complicate any attempt to understand the selective basis of interspecific divergences (e.g. Harvey & Pagel 1991) do not apply to analyses of sexual dimorphism. This advantage is carried to its extreme in organisms with a highly simplified morphology, in which sex differences are necessarily few in number and simple in form. Snakes offer a good example of such organisms: because of their highly simplified external morphology, there are few ways in which snakes can display significant sexual dimorphism (e.g. Shine 1993; Bonnet *et al.* 1998). A sex divergence in tail length relative to body length (at the same body length, males have longer tails than females) is the most widespread example of overt sexual dimorphism in these animals (King 1989; Shine 1993).

Even for such a straightforward trait, a detailed consideration reveals that there are several possible explanations for the evolution of the tail-length dimorphism (King 1989). For example, males might benefit from a longer tail because it thereby provides more space for larger hemipenes (the male copulatory organ is housed inside the tail base) or because it confers an advantage in 'tail

wrestling' with other males during courtship. King (1989) attempted to evaluate the plausibility of such hypotheses by deriving and testing predictions about the patterns in the magnitude of tail-length dimorphism. Although several patterns were apparent, the scarcity of detailed data—particularly data on the direct consequences of relative tail length for male reproductive success—made it difficult to draw firm conclusions on this topic (King 1989). This scarcity in turn reflects empirical constraints. Snakes are generally scarce and secretive, so that it is difficult to gather the extensive data sets necessary for an analysis of this kind. However, at least one snake species forms huge mating aggregations where such data are relatively easy to obtain. We have taken advantage of this opportunity to gather the first data on the reproductive consequences of tail-length dimorphism in snakes.

2. MATERIAL AND METHODS

Red-sided gartersnakes (*Thamnophis sirtalis parietalis*) over-winter in large communal dens in south-central Manitoba (Chatfield Community Pasture, 50°44′N, 97°34′W; Mason & Crews 1985) and mate immediately after emerging in spring (Gregory 1974, 1977; Gregory & Stewart 1975). At this time, it is possible to find copulating pairs of snakes in the midst of large 'mating balls' in and near the dens (Gregory 1974; Mason & Crews 1985). We collected such mating pairs over two-week periods in May 1997 and 1998, as well as a large sample of courting males from the same aggregations. These samples enabled us to compare the relative tail lengths of males that succeeded in gaining copulations compared to those that were unsuccessful (at least at the time we collected them).
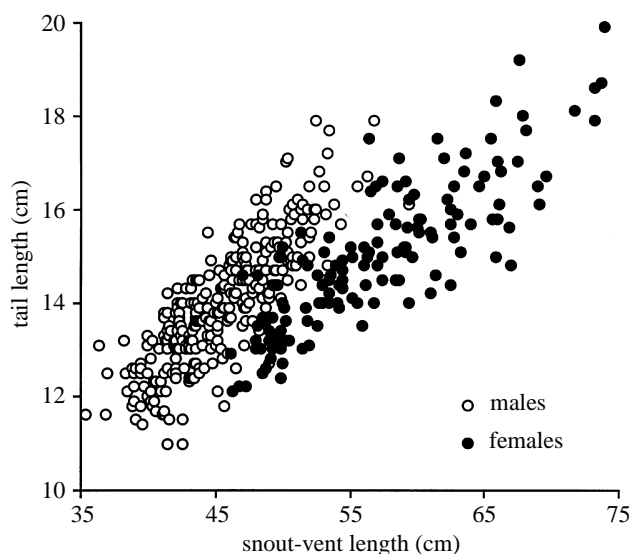
Figure 1. Sex divergence in tail length relative to snout–vent length within red-sided gartersnakes (*T. s. parietalis*) from southern Manitoba. Stub-tailed snakes are not included in this figure. See the text for statistical tests.

We also took advantage of an unusual mass mortality event to gather an extensive data set on the morphological correlates of relative tail length among the male snakes. We found > 100 recently killed male snakes under a large pile of other snakes on 8 May 1997. These animals were almost certainly suffocated by the weight of the overlying males; they had been dead for only a few hours (at most) when we found them. We stored the carcasses in a snowdrift overnight and dissected most of them the next day to quantify their body and organ sizes. We measured snout–vent length (SVL), tail length and the dimensions (length and width) of the kidneys, testes and each fully everted hemipenis. The liver and the abdominal fat bodies were dissected out and weighed.

We used these data to test predictions from two of King's (1989) hypotheses. His 'morphological constraint' hypothesis predicts that relative tail length will correlate with the size of the hemipenes or other male reproductive structures. His 'male mating ability' hypothesis predicts that tail length will correlate with male mating success. The natural level of variation in relative tail length among males within the Manitoba gartersnake population is amplified by the common occurrence of partial tail loss, presumably reflecting predation attempts (e.g. Fitch 1999) or other accidents (e.g. parasites; Degenhardt & Degenhardt 1965) in a substantial proportion of these animals. This tail loss constitutes a 'natural experiment', because it generates a set of 'stub-tailed' males whose reproductive success can be compared to that of males with entire tails.

3. RESULTS

(a) *Sexual dimorphism in relative tail length*

Red-sided gartersnakes display substantial sexual dimorphism in tail length relative to body length. At the same SVL, males have longer tails than do conspecific females (figure 1) (one-factor heterogeneity of slopes test with sex as the factor, SVL as the covariate and tail length as the dependent variable, $F_{1,620} = 5.07$ and $p < 0.03$). In both sexes, tails are longest relative to SVL

(i.e. the ratio of tail length to SVL is highest) in small animals, with relative tail length decreasing gradually in larger animals (plotting this ratio against SVL, excluding stub-tailed animals, for 1425 males and for 142 females, $r = -0.16$ and $p < 0.0001$, and $r = -0.38$ and $p < 0.0001$, respectively).

(b) *Morphological correlates of relative tail length*

The morphological constraint hypothesis (King 1989) predicts that males with relatively longer tails should have larger hemipenes. Our analysis of the data from the dissected snakes supports this prediction; hemipenes were longer (but not wider) in males with relatively longer tails (figure 2). To analyse these patterns, we used residual scores from the least-squares linear regression of tail length versus male SVL as our index of relative tail length; a negative score means that the male had a shorter than average tail for its SVL. This index was significantly associated with the length of the hemipenes on both sides of the body (relative tail length versus length of the left hemipenis, $n = 68$, $r = 0.29$ and $p < 0.02$, and relative tail length versus length of the right hemipenis, $n = 68$, $r = 0.38$ and $p < 0.002$). However, the hemipenis width was not significantly linked to relative tail length (relative tail length versus width of the left hemipenis, $n = 68$, $r = 0.10$ and $p = 0.40$, and relative tail length versus width of the right hemipenis, $n = 68$, $r = 0.03$ and $p = 0.83$). Relative tail length was not significantly correlated with the size of any other body component that we measured, except for the size of the abdominal fat bodies. Longer-tailed males tended to have smaller fat stores (using residual scores as above, $n = 68$, $r = -0.26$ and $p < 0.04$).

(c) *Consequences of tail length for male mating success*

The male mating ability hypothesis (King 1989) predicts that the males found *in copulo* should differ in relative tail length from those that were not mating when collected. The difference could involve either the mean tail length (i.e. directional selection, whereby longer-tailed males obtain more matings) or different levels of variation in tail length around the same mean value (i.e. stabilizing selection, whereby males with closer to average length tails obtain more matings). Our analyses were performed separately for 1997 and 1998, because the distributions of male body size differed between the two years (Shine *et al.* 1999), thereby possibly influencing the magnitude of selection on relative tail length. We excluded stub-tailed males from these analyses, but consider them separately (below).

In both years of our study, males with longer tails obtained more matings (one-factor ANOVA comparing absolute tail length in mated versus unmated males, $F_{1,625} = 5.67$ and $p < 0.02$ for 1997, and $F_{1,899} = 8.15$ and $p < 0.005$ for 1998). However, this result tells us nothing about the significance of tail length relative to SVL; it could simply reflect the considerable mating advantage accruing to larger overall body size in males in this system (Shine *et al.* 1999; contra Joy & Crews 1988). Our comparisons of relative tail length in mated versus unmated males revealed no significant directional selection for longer tails in either year (one-factor ANOVA on
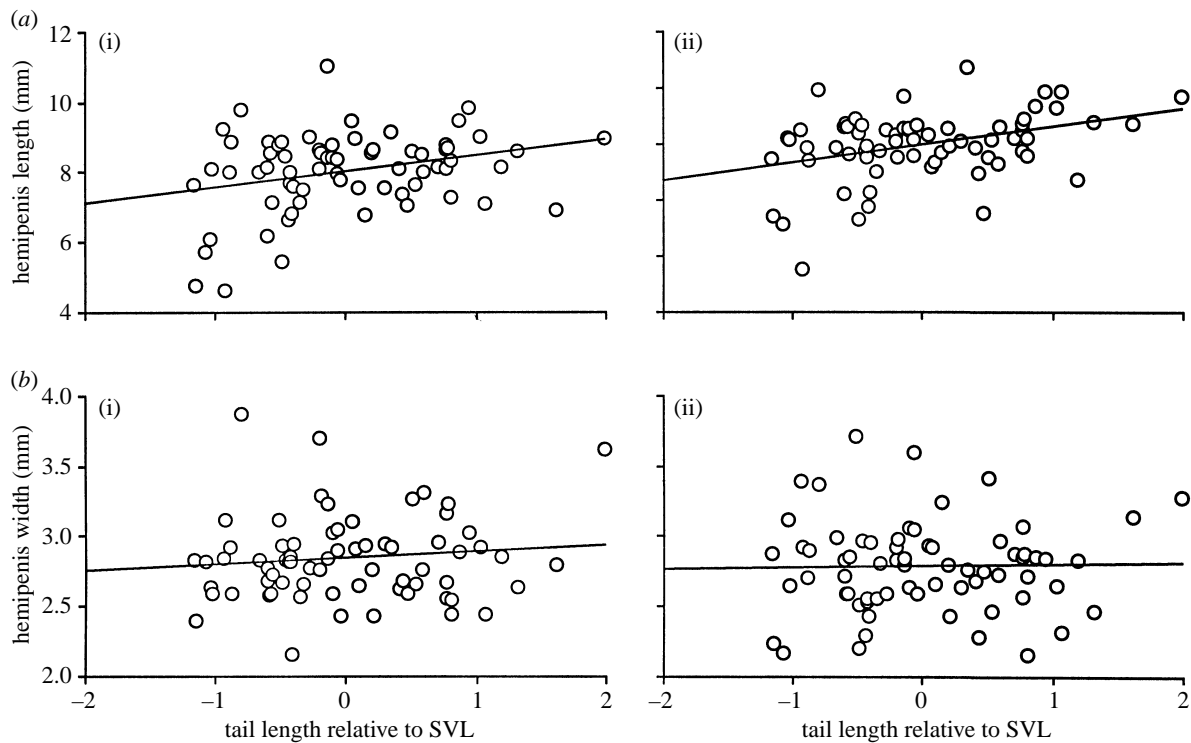
Figure 2. (*a*) Lengths and (*b*) widths of fully everted hemipenes ((i) left hemipenis, (ii) right hemipenis) from gartersnakes as a function of relative tail length of the male snake. Relative tail length was calculated as the residual score from the linear regression of tail length on snout–vent length (SVL). See the text for statistical tests.
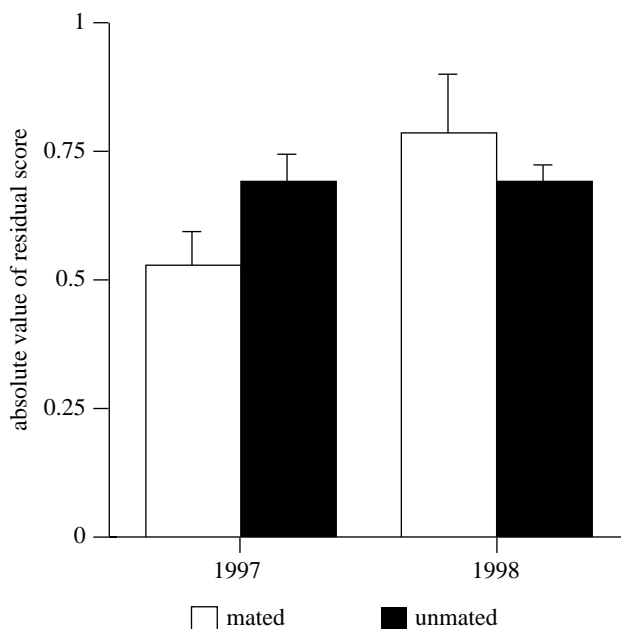

Figure 3. Comparisons of the degree to which relative tail length deviated from the expected (average) value for this trait in mated versus unmated male gartersnakes in two mating seasons (May 1997 and 1998). Relative tail length was calculated as the residual score from the linear regression of tail length on snout–vent length (SVL). The absolute value of this residual score was used to calculate the degree to which any given tail differed from the length expected in a male of that SVL. See the text for statistical tests.

residual score from tail length versus SVL, $F_{1,605} = 3.13$ and $p = 0.08$ for 1997, and $F_{1,824} = 2.16$ and $p = 0.14$ for 1998). No significant stabilizing selection was evident in 1998 (using the absolute value of each residual score $F_{1,824} = 2.68$ and $p = 0.10$), but stabilizing selection was highly significant in 1997 ($F_{1,605} = 10.92$ and $p < 0.001$; see figure 3). That is, males that obtained matings in 1997 were closer to the average in terms of tail length relative to SVL than were the random sample of non-mating males.

The analyses above are based on males with complete tails only. The effects of tail length on male mating success can be seen more clearly by comparing stub-tailed males with individuals possessing entire tails. The degree of truncation of the tail in these individuals was variable, with the ratio of tail length to SVL in the stub-tailed males averaging 21.4% (range 9.2–27.2%) versus 30.8% (range 25.5–40.9%) for males with entire tails and 25.8% (range 11–31%) for females. In both years, the proportion of stub-tailed males obtaining matings was lower than for males with entire tails. In 1997, three out of 42 (7%) stub-tailed males mated versus 133 out of 589 (23%) entire-tailed males ($\chi^2 = 4.65$, d.f. $= 1$ and $p < 0.04$) and in 1998 ten out of 128 (8%) stub-tailed males mated versus 81 out of 369 (22%) entire-tailed males ($\chi^2 = 11.77$, d.f. $= 1$ and $p < 0.001$). In both years, males with entire tails were approximately three times as likely to obtain a mating as were males that had lost a portion of their tails. The difference in mating success is not an artefact of differences in body size between entire-tailed versus stub-tailed males (for SVL means of 44.8 cm versus 44.9 cm and for mass means of 31.1 g versus 31.3 g; in both cases $p > 0.50$ in one-factor ANOVAs), nor is it due to physical

impairment of the copulatory apparatus: all stub-tailed males had long-enough tail remnants to include the hemipenes and associated musculature.

4. DISCUSSION

Sex differences in relative tail length are very widespread in snakes (King 1989; Shine 1993) and have been recognized for a long time (with one of the first reports being Burt's (1928) paper on *T. sirtalis*). Nonetheless, there have been few published attempts to test alternative possible explanations for this phenomenon (Klauber 1943; King 1989). Our study provides the most direct evidence yet available on the consequences of tail length in male snakes. Within the Manitoba population of *T. sirtalis*, males with relatively longer tails had longer hemipenes and accidental loss of part of the tail was associated with a threefold decrease in male mating success. In addition, even when the analysis was confined to males with entire tails, we detected significant stabilizing selection on male tail length (relative to SVL) in one of the two years of our study.

In combination, these data support the notion that relative tail length in male snakes is a biologically relevant trait which affects male mating success. In particular, our work provides empirical support for two of King's (1989) hypotheses: the ideas that longer tails enhance male fitness by providing space for larger hemipenes (the morphological constraint hypothesis) and enhance a male's ability to obtain matings (the male mating ability hypothesis). It is important to note that these are not mutually exclusive alternatives; it may well be true that both of these advantages have played a role in the evolution of tail-length dimorphism.

Two caveats are attached to this conclusion. First, we have only demonstrated phenotypic effects; selection on such traits will not change gene frequencies (i.e. affect the evolution of tail length) unless there is an underlying genetic basis for the observed variation. Previous work supports this assumption (Arnold 1988; Dohm & Garland 1993). Second, our analyses rely on correlations rather than experimental manipulation of tail length. These correlations might not reflect functional associations. The simplest interpretation of the association between longer tails and longer hemipenes (figure 2) involves a direct functional relationship: longer tails provide more space for hemipenes. Alternatively, however, the same correlation could ensue if sexually dimorphic traits were under common endocrine control. Thus, for example, males with higher androgen levels might exhibit more pronounced dimorphism in tail length as well as larger hemipenes, even if there was no functional relationship between the two latter traits. This hypothesis is difficult to reconcile with the observation that relative tail length does not correlate with the size of any other reproductive structure (including the width of the hemipenes). Hence, the link between tail length and hemipenis length probably reflects a functional association. We have no evidence that a larger hemipenis enhances male reproductive success, although it might plausibly provide a firmer attachment to a female during copulation.

The nature of the mating disadvantage to stub-tailed males also warrants closer examination, although it clearly cannot be attributed to endocrine factors. The simplest explanation for the lower success of stub-tailed males is that a shorter tail impedes a male's ability to displace the tails of his rivals from the vicinity of the female's cloaca during courtship (see below). However, other possibilities need to be considered. If tail loss is disproportionately common among larger snakes or is correlated with lower body condition, the apparent disadvantage to stub-tailed males could be due to a common correlation with these other factors. The equivalence in body size between stub-tailed and intact-tailed males (see above) means that this possibility can be discounted. The only other artefact we can envisage would be if the injuries to the tails were recent and associated with a reduction in vigour, activity or mobility. This was not the case: all of the tail losses were injuries from preceding seasons and appeared to be completely healed. Thus, we interpret the lowered mating success of stub-tailed males as a direct consequence of their partial tail loss.

The effect of tail length on mating success is probably mediated via tail wrestling with rival males during courtship. The female gartersnakes in our study population were simultaneously courted by many males, with several males orientating along the female's body and vying for the opportunity to insert a hemipenis when the female lifted her tail (e.g. Whittier *et al.* 1985). Males actively displace the tails of their rivals and the system consequently confers strong mating advantages to larger, heavier males (Shine *et al.* 1999; contra Joy & Crews 1988). Males with shorter or less muscular tails may therefore be at a considerable disadvantage in such struggles. An alternative possibility involves female choice, with females actively selecting male partners based on the relative length of their tails. We doubt this possibility, because we doubt that females within large mating balls have the opportunity to select their mates.

Why was there strong stabilizing selection on relative tail length in one year of our study but not the other, particularly since stub-tailed males were at a similar disadvantage in both years? We do not know, but part of the reason may lie in the differences in the body-size distributions of the males between the two years of our study. Larger males obtained more matings in both years (Shine *et al.* 1999), but the wider range of male body sizes in 1998 may have made more subtle influences on male mating success (such as that due to tail-length differences among males of similar body sizes) more difficult to detect in this year than in 1997.

Partial tail loss does not reduce locomotor speed substantially in gartersnakes (Jayne & Bennett 1989), but it can reduce a snake's probability of survival (Willis *et al.* 1982) and its mating success (present study). Thus, an apparently trivial injury may impose a considerable fitness disadvantage. The disadvantages may be particularly great for males, perhaps favouring a greater reluctance to autotomize the tail in this sex. Such a sex difference might explain the observation that tail loss is less common in males than in same-aged female conspecifics within a Kansas population of *T. s. parietalis* (Fitch 1999). If much of the variation among males in relative tail length is due to predation rather than heritable factors, the result will be a complex interplay between sexual selection and natural selection.

Given the wide occurrence of sexual dimorphism in relative tail length among snakes (King 1989; Shine 1993), it is clear that this trait evolved early in snake phylogeny. Hence, our data tell us little about the factors initially responsible for that divergence. Nonetheless, the magnitude of the sexual dimorphism in tail length and the nature of the allometric shifts in relative tail length during male and female ontogeny vary considerably even between species within the genus *Thamnophis* (e.g. Rossman & Gongora 1997). Thus, our data may illuminate the factors that act to maintain the sex difference in proportion. The stabilizing selection on male tail length relative to SVL fits well with this scenario. The stub-tailed males are particularly interesting, because these animals comprise a natural experiment: the magnitude of the decrease in mating success in these stub-tailed males suggests that males with female-sized tails are likely to be at a strong disadvantage in sexual rivalry. Overall, our data provide strong support for the hypothesis that tail length in male snakes is a significant target of sexual selection.

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