Eastern Garter Snakes (*Thamnophis sirtalis*) with proportionally larger heads are in better condition

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Abstract. We investigated sexual size dimorphism and trophic morphology dimorphism in Eastern Garter Snakes (*Thamnophis sirtalis*) to test predictions derived from the reproductive role hypothesis. Our first objective was to examine whether structures involved in feeding (head and jaws) are more divergent than body size. Female *T. sirtalis* were larger than males and had proportionally larger heads. Our second objective was to look for an advantage of large head size by examining the relationship between body condition and head size. Body condition was positively correlated with relative head size in *T. sirtalis* for both sexes, in agreement with the reproductive role hypothesis.

Keywords: fecundity selection, reproductive role hypothesis, sexual size dimorphism, trophic morphology dimorphism.

Sexual dimorphism is common and often spectacular in animals (Blanckenhorn, 2005). Sexual size dimorphism (SSD), for instance, arises because of differences in optimal body size between males and females (Blanckenhorn, 2005). Selective pressure for large body size is most often attributed to mating advantages between competing males (sexual selection) or to fertility selection in females (Blanckenhorn, 2005). According to the reproductive role hypothesis, SSD can be a result of differences in energetic needs resulting from the different reproductive roles of males and females (Slatkin, 1984).

Unlike mammals and birds, most ectotherms grow throughout life, which leads to large variation in adult body size. Because there often is a strong correlation between reproductive output and female body size (Blouin-Demers and Weatherhead, 2007; Bulté et al., 2008), there is strong selection on female body size in ectotherms, and this fertility selection is likely why SSD is predominantly female-biased in this group (Trivers, 1972). The potential selective advantage of a large body size in females, however, cannot be realized unless there is a concomitant increase in energy acquisition (Bulté

et al., 2008). To realize the reproductive advantage of a large body size, females need to allocate more energy to growth and egg production. In gape-limited predators such as snakes and durophagous turtles, this requirement for additional energy often results in trophic morphology dimorphism (TMD): in addition to a larger body size, females may have proportionally larger feeding structures than males (Shine, 1989, 1991; Bulté et al., 2008).

We examined SSD and TMD in Eastern Garter Snakes (*Thamnophis sirtalis*). Our first objective was to verify the presence of TMD: whether or not head size is more sexually dimorphic than body size in the population under study. Our second objective was to test the prediction arising from the reproductive role hypothesis that if TMD evolves because it allows the harvest of more energy, individuals with proportionally larger heads should be in better body condition. Adaptive explanations for the evolution of TMD, such as the reproductive role hypothesis, require the dimorphism to have a genetic basis. While there is evidence for some phenotypic plasticity in head size in snakes (Queral-Regil and King, 1998; Bonnet et al., 2001), others have failed to unveil such plasticity (Forsman, 1996) and nonadaptive hypotheses for intraspecific variation in head size of snakes have been rejected (Fors-

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Table 1. Acronyms and descriptions of head measurements of *Thamnophis sirtalis* from Ontario, Canada.

Head dimension	Description
HL	Head length: from tip of snout to back of parietal scales
HW	Head width: taken at the widest point
IOD	Inter-ocular distance: distance between the eyes
JL	Jaw length: from tip of snout to the back of the last supralabial scale
VJL	Ventral jaw length: from tip of lower jaw to first ventral scale

Table 2. Proportion of variance explained and variable loadings for principal component analysis of head length (HL), head width (HW), inter-ocular distance (IOD), jaw length (JL), and ventral jaw length (VJL) of *Thamnophis sirtalis* from Ontario, Canada.

Component		PC1	PC2	PC3
Proportion of variance explained		0.920	0.030	0.021
Loadings	HL	0.422	0.487	−0.530
	HW	0.378	0.368	0.561
	IOD	0.214	0.338	−0.321
	JL	0.616	−0.711	−0.226
	VJL	0.400	−0.666	0.495

man and Shine, 1997). Finally, phenotypic plasticity in itself may be an adaptation (Aubret et al., 2004).

We captured 63 garter snakes during egress and ingress from a communal hibernaculum in the vicinity of the Queen's University Biological Station, approximately 100 km south of Ottawa, Ontario, Canada. We took 5 head measurements with digital calipers (table 1). Due to the highly kinetic skulls of snakes, however, measurements with calipers may not be reliable. Therefore, we also took digital photographs against a ruler of the dorsal, ventral, and right lateral sides of the head of each snake, and took the same measurements with ImageJ software (National Institute of Health, USA). We measured snout-vent length (SVL) by juxtaposing the snake against a ruler and mass with a spring scale. Snakes were sexed with a clean probe inserted in the cloaca to check for presence of hemipenes. To avoid recapture, we marked all snakes with paint prior to release.

There were small differences between head dimensions measured with calipers and those measured from digital photographs (ca. 5%). Therefore, we used measurements from the digital images in the analyses. Head dimensions were highly correlated, so we performed a principal component analysis to summarize the variation. We calculated body condition by performing a regression of mass on SVL (both log transformed) for each sex. The residuals of these regressions were divided by the predicted mass for each sex (obtained from the regression equations) to yield an index of condition (% above or below the predicted mass) (Blouin-Demers et al., 2005). Because we only captured snakes just after exit or just before entry into hibernation, they had empty stomachs and our body condition index is thus unaffected by variation in stomach content. We conducted all analyses on JMP version 7 (Statistical Analysis Systems,

Cary, North Carolina). All assumptions of normality and homogeneity of variance were met and verified by examining box-plots. We accepted significance of tests at $\alpha = 0.05$.

Principal component analysis on head dimensions yielded one component (PC1) that explained most of the variation (table 2). The variables with the highest loadings on PC1 were those associated with head length (head length, jaw length, and ventral jaw length). ANCOVA with sex and SVL as independent variables and PC1 scores as the dependent variable revealed that females have significantly larger heads than males when controlling for SVL (partial R^2 of sex $= 0.071$, $F_{1,59} = 4.39$, $P = 0.040$, fig. 1). ANCOVA with PC1 scores, sex, SVL, and the interaction sex∗SVL as independent variables and body condition as the dependent variable revealed that males and females with bigger heads for their body size are in better condition (partial R^2 of PC1 scores $= 0.158$, $F_{1,56} = 10.63$, $P = 0.002$, fig. 2).

Female *T. sirtalis* were larger, and had proportionally larger heads, than males. Individuals of both sexes with proportionally larger heads were in better condition. Larger animals use more energy (Andrews and Pough, 1985) and thus require more food. By increasing head size relative to body size, snakes could consume
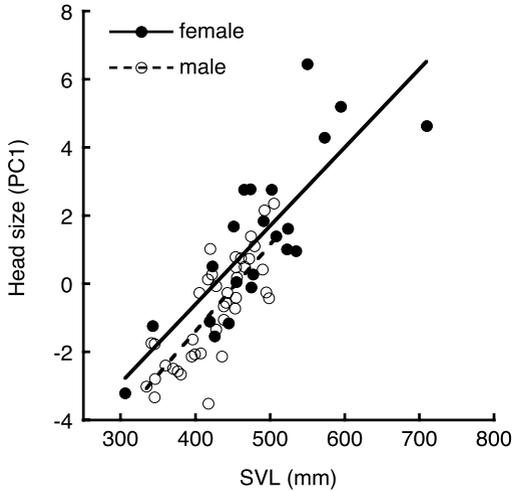
Figure 1. Principal component scores of five head dimensions as a function of snout-vent length indicate that female *Thamnophis sirtalis* from Ontario, Canada have proportionally bigger heads than males.
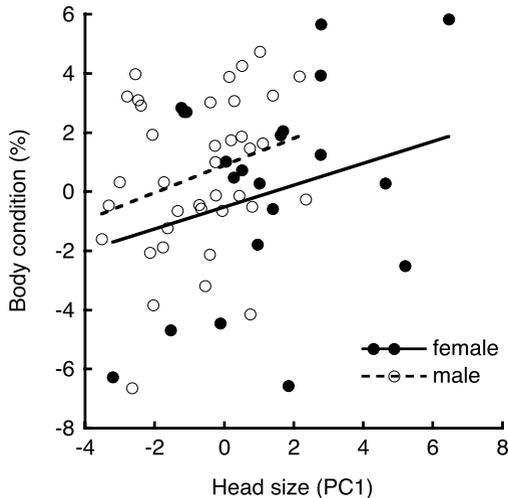
Figure 2. Body condition as a function of principal component scores of five head dimensions indicate that male and female *Thamnophis sirtalis* from Ontario, Canada with proportionally larger heads are in better condition.

larger prey without increasing the maintenance costs associated with a larger body (Duvall and Beaupré, 1998). Thus, they would be able to allocate more resources to other energetically costly activities, such as reproduction (Blanckenhorn, 2005).

Despite the similar relationship between head size and body condition for male and female *T. sirtalis*, females still had larger heads for their body size. The larger body size in females of this species is associated with more rapid growth rates (Shine and Crews, 1988), which can be facilitated by greater food quantity or quality (Bronikowski and Arnold, 1999). It seems plausible that females have larger heads to maximize prey size and thus maximize energy acquisition that can then be allocated to growth and reproduction (Vincent and Herrel, 2007). Clutch size increases with body size, which likely creates additional selective pressure for females to be able to acquire enough resources to supply a large clutch (Shine, 1994; Shine et al., 1998) because females cannot reap the reproductive benefits of a large body without a concomitant increase in energy acquisition (Bulté et al., 2008).

An important caveat must be made with regard to our observation that snakes with relatively large heads are in better condition. We assumed that our measurement of SVL was unaffected by body condition. Thomas Madsen's (pers. comm.) data on water pythons (*Liasis fuscus*) suggest that snakes in good condition are more difficult to stretch for SVL measurements than snakes in poor condition, thus leading to a systematic underestimation of SVL for snakes in good condition. Because relative head size is measured in relationship to SVL, snakes in good condition would appear to have large heads relative to their SVL if their SVL is systematically underestimated. We do not believe this applies to our results on garter snakes because we did not attempt to stretch snakes for SVL measurement. Formally addressing this intriguing alternative hypothesis, however, would require measuring SVL of snakes in good and in poor condition while fully awake and while under anesthesia to determine whether the true SVL of snakes in good condition is consistently underestimated compared to the true SVL of those in poor condition.

Our findings are consistent with the reproductive role hypothesis as an explanation for both sexual size dimorphism and head size dimorphism in our population of *T. sirtalis*. Future studies ought to examine the relationship between relative head size and reproductive success in female *T. sirtalis*. In addition, a formal quantification of the contribution of genetic effects versus phenotypic plasticity on head size dimorphism would be helpful.

References

Andrews, R.M., Pough, H. (1985): Metabolism of squamate reptiles: allometric and ecological relationships. Physiol. Zool. **58**: 214-231.

Aubret, F., Shine, R., Bonnet, X. (2004): Adaptive developmental plasticity in snakes. Nature **431**: 261-262.

Blanckenhorn, W.U. (2005): Behavioral causes and consequences of sexual size dimorphism. Ethology **111**: 977-1016.

Blouin-Demers, G., Gibbs, H.L., Weatherhead, P.J. (2005): Genetic evidence for sexual selection in black ratsnakes (*Elaphe obsoleta*). An. Behav. **69**: 225-234.

Blouin-Demers, G., Weatherhead, P.J. (2007): Allocation of offspring size and sex by female black ratsnakes. Oikos **116**: 1759-1767.

Bonnet, X., Shine, R., Naulleau, G., Thiburce, C. (2001): Plastic vipers: influence of food intake on the size and shape of Gaboon vipers (*Bitis gabonica*). J. Zool. **255**: 341-351.

Bronikowski, A.M., Arnold, S.J. (1999): The evolutionary ecology of life history variation in the garter snake *Thamnophis elegans*. Ecology **80**: 2314-2325.

Bulté, G., Irschick, D.J., Blouin-Demers, G. (2008): The reproductive role hypothesis explains trophic morphology dimorphism in northern map turtles. Func. Ecol. **22**: 824-830.

Duvall, D., Beaupré, S.J. (1998): Sexual strategy and size dimorphism in rattlesnakes: integrating proximate and ultimate causation. Am. Zool. **38**: 152-165.

Forsman, A. (1996): An experimental test for food effects on head size allometry in juvenile snakes. Evolution **50**: 2536-2542.

Forsman, A., Shine, R. (1997): Rejection of non-adaptive hypotheses for intraspecific variation in trophic morphology in gape-limited predators. Biol. J. Lin. Soc. **62**: 209-223.

Queral-Regil, A., King, R.B. (1998): Evidence for phenotypic plasticity in snake body size and relative head dimensions in response to amount and size of prey. Copeia **1998**: 423-429.

Shine, R. (1989): Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quart. Rev. Biol. **64**: 419-431.

Shine, R. (1991): Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. Am. Nat. **138**: 103-122.

Shine, R. (1994): Sexual size dimorphism in snakes revisited. Copeia **1994**: 326-346.

Shine, R., Crews, D. (1988): Why male garter snakes have small heads: the evolution and endocrine control of sexual dimorphism. Evolution **42**: 1105-1110.

Shine, R., Harlow, S., Keogh, J.S., Boeadi (1998): The influence of sex and body size of the food habits of a giant tropical snake, *Python reticulatus*. Funct. Ecol. **12**: 248-258.

Slatkin, M. (1984): Ecological causes of sexual dimorphism. Evolution **38**: 622-630.

Trivers, R.L. (1972): Parental investment and sexual selection. In: Sexual Selection and the Descent of Man, p. 136-179. Campbell, B., Ed., London, Heinemann Educational Books.

Vincent, S.E., Herrel, A. (2007): Functional and ecological correlates of ecologically-based dimorphisms in squamate reptiles. Integ. Comp. Biol. **47**: 172-188.