Sexual size dimorphism in garter snakes (*Thamnophis sirtalis*), water snakes (*Nerodia sipedon*) and black ratsnakes (*Elaphe obsoleta*)

By

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Abstract

I investigated sexual size dimorphism (SSD) in garter snakes (*Thamnophis sirtalis*), northern water snakes (*Nerodia sipedon*) and black ratsnakes (*Elaphe obsoleta*). My first objective was to examine whether or not structures involved in feeding (head and jaws) are more divergent than body size. Head size in *T. sirtalis* was slightly more divergent than body size, but no such relationship existed for *E. obsoleta*. My 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 head size in *T. sirtalis* for both sexes, but not for *E. obsoleta* or for *N. sipedon*.

Introduction

Sexual size dimorphism (SSD) is a common phenomenon in all animal taxa (Darwin, 1871; Blanckenhorn, 2005; Shine, 1989). Differences in body size between the sexes may be attributed to differences in optimal body size between males and females (Blanckenhorn, 2005). Selective pressure for large body size is most often attributed to sexual selection for males and fertility selection for females; however, there is little consensus regarding selective pressures for small body size (Blanckenhorn, 2005). According to the niche divergence hypothesis, SSD is caused by ecological divergence between the sexes to reduce intersexual competition (Slatkin, 1984; Shine, 1989). Alternatively, according to the Reproductive role hypothesis, SSD is a result of differences in energetic needs resulting from the different reproductive roles of males and females (Slatkin, 1984; Shine, 1989).

Unlike mammals and birds, ectotherms grow continuously throughout life and tend to produce large, indeterminate numbers of offspring, which leads to a strong correlation between fecundity and female body size, and this is likely the reason why SSD in ectotherms is predominantly female-biased (Trivers, 1972). Unless there is strong sexual selection for male body size through combat competition for access to females, snakes follow this pattern (Blanckenhorn, 2005). SSD in snakes is also often associated with dimorphism in trophic structures (head and jaws) (Shine, 1991).

This dimorphism in head size is often used as support for the niche divergence hypothesis. If male and female snakes differ in size to exploit different sized prey items, selection would be expected to act most strongly on structures directly related to prey size (Selander, 1972; Shine, 1989). Snakes are gape-limited predators, and as such, head size directly determines prey size (Shine, 1994). Alternatively, differences in head size may be explained by the Reproductive role hypothesis. Females invest proportionately more in reproduction (Darwin, 1871) and a larger head should maximize energy intake.

I examined SSD in three species of snake, two with female biased SSD, garter snakes (*Thamnophis sirtalis*) and water snakes (*Nerodia sipedon*) and one with male-biased SSD, black ratsnakes (*Elaphe obsoleta*) (Shine, 1991). My first objective was to examine whether or not head size is more sexually dimorphic than body size in the populations under study. My second objective was to examine the relationship between foraging success and head size. If SSD is a result of competition between the sexes, the relationship should be positive in the larger sex, but not in the smaller sex. If SSD is a result of different energetic needs, the relationship should be the same for both sexes or

positive for females only. Body condition (mass relative to length) was used as an indicator of foraging success (Bonnet *et al.*, 2001).

Methods

I captured garter snakes between April 2006 and October 2006 at Leggett's Pancake House and at Queen's University Biological Station, both approximately 40km north of Kingston (Ontario, Canada). I captured water snakes in May 2006 at Barb's Marsh, near Queen's University Biological Station. Black ratsnakes were captured at Queen's University Biological Station between May and October 1996.

I took 6 head measurements on garter snakes and water snakes using digital calipers (Table 1). Due to the high mobility of snake skulls, measurements using calipers may not be reliable, so I also took digital photographs against a ruler of the dorsal, ventral and right lateral sides of the head for each snake, and carried out the same measurements using ImageJ software. I measured snout-vent length (SVL) (mm), tail length (mm) against a ruler and mass (g) using spring scales. The following measurements were taken on black ratsnakes: SVL, tail length, mass, jaw length, prefrontal scale length and parietal scale length. All snakes were sexed using a clean cloacal probe to check for presence of hemipenes. To avoid recapture, I marked all snakes with paint prior to release.

Statistical Analyses

There was minimal difference between the two types of head measurements (less than 5%), except for head height, which is difficult to measure manually without compressing the skull. Therefore, I used results from digital measurements in the

analyses. Variables pertaining to head size were highly correlated, so I performed

principal component analysis of all variables for each species. I then performed an

ANCOVA using head size (the main principal component) as the dependent variable and

Sex and SVL as the independent variables.

I log transformed mass and SVL, and then calculated body condition by

performing a regression of mass on SVL and obtaining a predicted mass for each

individual based on the regression equation. The residuals were divided by the predicted

mass to obtain the condition index (% above or below the predicted mass) (Blouin-

Demers *et al*., 2004). I then performed a regression of body condition on relative head

size (residuals of the regression of head size on SVL).

I also calculated an index of SSD by dividing the mean SVL of the larger sex by

the mean SVL of the smaller sex, subtracting from 1 and assigning a positive sign if

females are larger and a negative sign if males are larger (Shine, 1994).

Results

Principal Component Analysis

For all three species, principle component analysis yielded one component (PC1)

that explained most of the variation (Table 1). For *t. sirtalis*, the variables with the

highest loadings on PC1 were those associated with length (HL, JL and VJL). For *E.*

obsoleta the variable with the highest loading on PC1 was Jaw. For *N. sipedon*, the

variables with the highest loadings on PC1 were JL and HW.

Comparisons between sexes

Indices of SSD for *T. sirtalis* and *E. obsoleta* were 0.14 and -0.05, respectively. ANCOVA revealed that female t. sirtalis had larger heads than males when controlling for SVL but the effect was only marginally significant (partial $R^2 = 0.071$, F = 3.07, df = 1, p = 0.087). *E. obsoleta* showed no significant differences in head size between the sexes when controlling for SVL (partial $R^2 = 0.0035$, F = 0.63, df = 1, p = 0.43). The sample size for male *N. sipedon* was too small to allow comparisons between the sexes.

Condition Analyses

Relative head size was positively correlated with body condition in both male and female *t. sirtalis* but the effect in females was only marginally significant (males, $r^2 = 0.31$, p = 0.0028; females, $r^2 = 0.16$, p = 0.093).

In black rat snakes, head size was not correlated with body condition in either sex (males, $r^2 < 0.001$, p = 0.86; females, $r^2 < 0.001$, p = 0.9749). The same was true for female water snakes ($r^2 = 0.15$, p = 0.27).

Discussion

In *T. sirtalis,* body condition increased with increasing relative head size, suggesting that there is selective pressure to maximize prey size while minimizing body size. Larger animals use more energy (Andrews and Pough, 1985) and thus require more food. By increasing the size of the head relative to the body, snakes could consume larger prey without increasing the maintenance costs associated with a larger body

(Duvall and Beaupre, 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), and it is possible that females have larger heads to maximize prey size and thus maximize growth. 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).

Male and female *E. obsoleta* were not more dimorphic in head size than in body size, which may be due to the direction of SSD in this species. Even though males are under strong selective pressure to attain larger sizes and thus gain an advantage in competitive interactions (Shine, 1994; Blouin-Demers et al., 2002), they do not face the same pressure as females to supply an increasingly larger clutch (Shine, 2003). Thus, the pressure in males to maximize prey size may not be as strong, leading to weaker selection for larger head size and hence less difference in head size between males and females. It is also possible that the lack of head size dimorphism in *E. obsoleta* is due to the smaller degree of SSD. In general, snake species with more pronounced SSD have stronger head size dimorphism (Shine, 1991).

N. sipedon showed no correlation between body condition and relative head size, although Fig. 2C indicates that a correlation might be detected with a larger sample size.

A larger sample would also demonstrate whether or not there is a similar relationship for male *N. sipedon* and whether or not this population is dimorphic in head size.

I found more support for the reproductive role hypothesis as an explanation for head size dimorphism than for the niche divergence hypothesis. If SSD were a result of competition between the sexes, there would not be a positive relationship between body condition and relative head size in male *T. sirtalis*. Future studies ought to examine the relationship between relative head size and reproductive success in female *T. sirtalis*. It would also be informative to perform similar analyses on other species to see if the direction or the degree of SSD explains the difference in results between *T. sirtalis* and *E. obsoleta*.

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Table 1. Head measurements taken on *T. sirtalis* and *N. sipedon*.

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

Table 2. Proportion of variance and loadings for principal components of head length (HL), head width (HW), inter-ocular distance (IOD), jaw length (JL), head height (HH) and ventral jaw length (VJL) for *T. sirtalis* and *N. sipedon* and jaw length (Jaw), length of the prefrontal scale (Pref) and length of the parietal scale (Par) for *E. obsoleta*.

			PC1	PC2	PC3	PC4	PC5	PC6
T. sirtalis	Proportion of variance		0.92	0.030	0.021	0.015	0.0080	0.0055
	Loadings	HL	0.422	0.487	-0.530		0.549	
		HW	0.378	0.368	0.561	0.515		0.369
		IOD	0.214	0.338	-0.321	-0.348	-0.739	0.263
		JL	0.616	-0.711	-0.226	0.160		0.187
		VJL	0.400		0.495	-0.737	0.215	
		HH	0.306			0.210	-0.311	-0.868
E. obsoleta	Proportion of variance		0.99	0.011	0.0025			
	Loadings	Jaw	0.967	-0.254				
		Pref	0.166	0.636	-0.754			
		Par	0.192	0.729	0.657			
N. Sipedon	Proportion of variance		0.68	0.14	0.093	0.045	0.033	0.0093
	Loadings	HL	0.309		-0.275	-0.841	-0.256	0.230
		HW	0.539	-0.315	-0.632	0.334	0.285	0.132
		IOD				-0.298	0.389	-0.863
		JL	0.565	0.672	0.348		0.295	0.123
		VJL	0.367	-0.666		-0.110		
		HH	0.387		0.632	0.270	-0.782	-0.404

Figure captions

Figure 1. Regression of head size on snout-vent length (SVL) for *T. sirtalis* (A) and *E. obsoleta* (B).

Figure 2. Regression of body condition on relative head size (residuals of regression of head size on snout-vent length) for *T. sirtalis* (A), *E. obsoleta* (B) and *N. sipedon* (C).
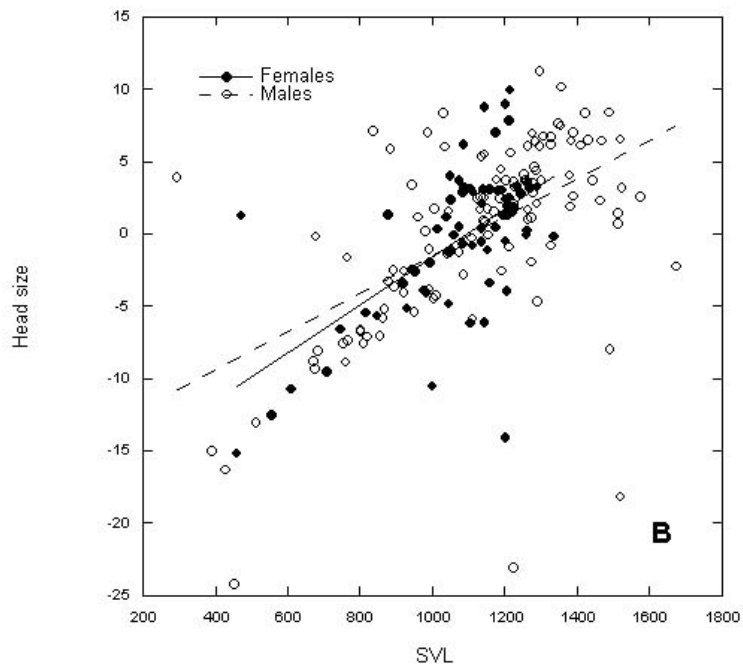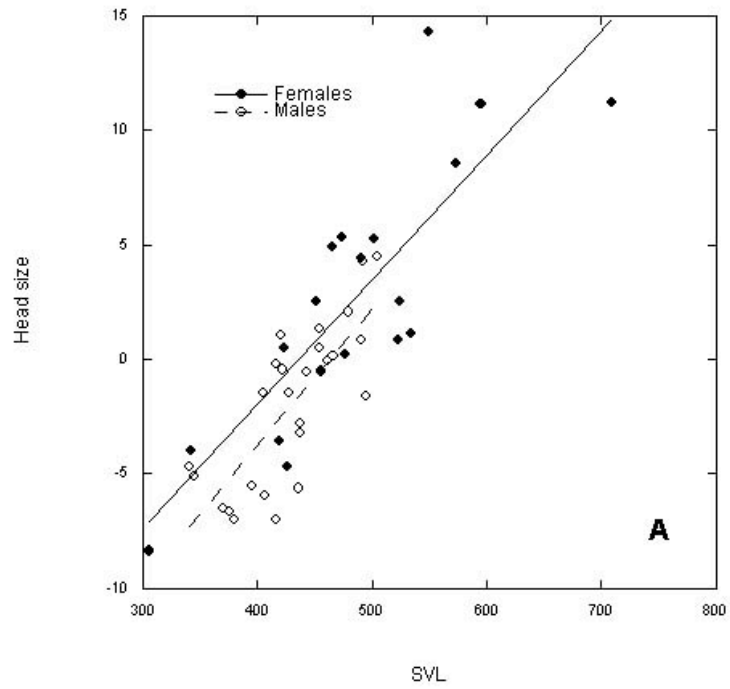
Fig. 1

Fig. 2