

Sexual dimorphism of body and relative head sizes in neonatal common garter snakes

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Keywords

sexual dimorphism; neonate; garter snake; *Thamnophis sirtalis*.

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Received 14 April 2006; accepted
17 July 2006

doi:10.1111/j.1469-7998.2006.00251.x

Abstract

Morphological and behavioral differences between sexes are commonplace throughout the animal kingdom. Body size is one of the most obvious sex differences frequently found in snakes. However, the developmental origins of size differences in many species, including snakes, are not well known. We examined postnatal variation in sexual size dimorphism in garter snakes *Thamnophis sirtalis*. The weights, body and tail lengths, and head sizes of male and female neonates born to mothers collected from ecologically dissimilar habitats on Beaver Island, Lake Michigan were compared. Sexual size dimorphism was prominent. Overall, males had significantly longer bodies and tails than females. Females were significantly heavier and had larger heads than male snakes. Maternal site affected head but not body measurements, perhaps due to differences in prey availability. The body condition of maternal females predicted neonatal body length. Significant litter variation suggests heritable variation in morphological traits possibly correlated with feeding success and survival.

Introduction

Males and females of many species have evolved unique adaptive variations in morphology and behavior. Body size frequently differs between males and females, which can be explained by at least three different mechanisms. First, in species for which male–male combat and direct competition is common, male-biased size dimorphism is often found. However, this rule is also constrained by other factors within lineages. Thus, phylogenetic factors should be taken into account when testing hypotheses for sexual size dimorphism. For example, larger species of shorebirds show male-biased sexual size dimorphism and smaller species show female-biased size dimorphism. This pattern, called Rensch's rule, can be attributed to intense selection on male body size in larger species, and selection for agility in smaller species (Székely, Freckleton & Reynolds, 2004). Size dimorphism may result from female choice; females may preferentially mate with males of a particular size. Thus, inter- and intrasexual selection set conditions for which sexually dimorphic body sizes might evolve (Andersson, 1994).

Another possible cause of dimorphic features is differential niche utilization between the sexes (Slatkin, 1984). For example, males and females may feed upon different but mutually available resources. Resource partitioning such as this occurs in snakes, in which body and head sizes for these mouth-gape-limited animals frequently differ between males and females (Houston & Shine, 1993). Furthermore, intra-

specific variation of reaction norms may account for geographic variation in relative sexual size dimorphism, as suggested in data gathered on marine iguanas *Amblyrhynchus cristatus* (Wikelski & Trillmich, 1997) and carpet pythons *Morelia spilota* (Pearson, Shine & Williams, 2002).

Sexual size dimorphism is common in snakes, and in most species for which there are data the females are the longer sex (Shine, 1993). Sexual selection accounts for some exceptions to the general rule of larger female body size. Some species, including rat snakes *Elaphe obsoleta* and copperheads *Agkistrodon contortrix*, undergo male–male combat during courtship (Gillingham, 1980), which favors larger males. However, Shine (1994) concludes that many species of snakes are female biased in body size [snout–vent length (SVL)], an observation underlying recent arguments and theory on the evolution of mating systems in snakes (Rivas & Burghardt, 2005). Larger female snakes appear to have reproductive advantages, in the form of greater clutch sizes and fecundity, over smaller females (Seigel & Ford, 1987; Ford & Seigel, 1989). Thus, intrasexual selection may account for the widespread tendency toward large females. One trait that is consistently larger in male snakes is tail length (TL). Males with greater relative TLs tend to have larger hemipenes and greater mating success relative to males with smaller tails (Shine *et al.*, 1999).

In addition to body size measures, other characteristics related to the feeding ecology of snakes may be sexually

dimorphic. The head shapes of cottonmouths *Agkistrodon piscivorus* differ between males and females (Vincent, Herrel & Irschick, 2004). Male cottonmouths, the larger sex, have both absolutely and relatively longer quadrate bones and lateral head surface areas than do female snakes. The males of this species also consume prey of greater diameter than similar-sized females. This finding suggests that niche divergence is a condition driving sexually dimorphic head shape in this species. Similar to overall body length and size, the relative head-to-body sizes are female biased in many species of snakes (King *et al.*, 1999).

Although there are numerous well-known examples of body size dimorphism in snakes, much less is known about how and why the sex difference arises. Previous reports reveal head size dimorphism in neonatal common garter snakes (Shine & Crews, 1988). Phenotypic plasticity is one mechanism that accounts for some of the variation in snake head and body sizes (Forsman, 1996). Snakes that eat more frequently or eat relatively large prey grow larger than do littermates that feed less frequently or upon smaller prey (Queral-Regil & King, 1998). Field studies have confirmed that dietary factors account for some geographic variation in snake morphology (Forsman & Lindell, 1991a,b). However, environmental influences on morphology are constrained by factors such as population-based genetic differences, litter and sex. For example, Schuett *et al.* (2005) report sexual dimorphism of head size in young boa constrictors after controlling prey size and feeding frequency for both sexes.

The species examined in this study was the common garter snake *Thamnophis sirtalis*, a widely distributed generalist species found across North America. Across its geographic range, *T. sirtalis* varies in diet and habitat use. Intensive studies of garter snake diet, morphology and behavior have been carried out on animals inhabiting several Midwestern states (Ohio, Michigan, Illinois, Wisconsin; see Fitch, 1965; Burghardt & Schwartz, 1999). The snakes were collected on Beaver Island, which has been the focus of studies of geographic variation in morphology and behavior (Krause, 2000; Placyk, 2006). Garter snakes from several mainland and island populations of the Beaver Archipelago differ in relative head sizes, and this appears to correspond with differences in available diets (Grudzien *et al.*, 1992). Previous work examining adult garter snakes from the Beaver Island populations found significant sexual size dimorphism in adult animals collected at two ecologically dissimilar habitats (Krause, Burghardt & Gillingham, 2003).

Neonates born to mothers from the two ecologically dissimilar habitats were measured for body weight, SVL, TL and relative head sizes. We examined litter, sex and site effects on these traits, each of which influence morphological variation in snakes (Gregory & Prelypchan, 1994). Adult females, but not males, from one of the sites, Miller's marsh, are significantly larger than females inhabiting another site, McCafferty farm. Miller's marsh hosts a wide array of prey species, including anurans, which are lacking at McCafferty farm.

Given the site and sex differences in body size reported in Krause *et al.* (2003), we sought to test the degree to which

these differences are found in neonates born to resident pregnant females. The objectives of this study were to (1) test for sexual size dimorphism in neonates, (2) test for the effects of site on neonatal size differences and sexually dimorphic characteristics, and (3) evaluate potential maternal and dietary influences on the observed patterns.

Materials and methods

Seventeen pregnant females from Miller's marsh and 16 pregnant females from McCafferty farm were captured and brought to the University of Tennessee in August 1998 ($n = 22$ litters) and 1999 ($n = 11$ litters). The females were housed separately in cages that included a shelter box, water dish and paper board substrate. They were fed either minnows *Pimephales promelas* or earthworms *Lumbricus terrestris* once a week. Heat strips were placed beneath each cage to provide a surface temperature gradient. Room temperature was kept at 25 °C and relative humidity at 30%, and a 12:12 light:dark cycle was maintained. Females were checked for parturition at least once daily. When a litter was born, the neonates were removed and housed separately in clear plastic cages (13.5 × 18.5 × 4.0 cm or 12.0 × 17.0 × 9.0 cm), each including a cardboard substrate, shelter and water dish. Cages were cleaned as needed and water was available *ad libitum*. Mothers were weighed and measured pre- and post-parturition. After giving birth the adult females were returned to their capture sites on Beaver Island.

Morphological measurements

Within 24 h of birth, the following measurements were taken on each neonate: mass, SVL, TL, head length (HL, distance between snout tip and posterior margin of the parietal scales), jaw length (JL, distance between snout tip and posterior margin of the posteriormost upper labial scale on the left side of the head), head width (HW, widest anterior point to posterior margin of parietal scales) and interocular distance (IOD, distance between junction points of supraocular scale, parietal scale and eyes). Mass was measured to the nearest 0.01 g with a digital scale. SVL and TL were measured in millimeters by stretching each snake across a meterstick, and head measurements (to 0.01 mm) were made with a hand-held digital caliper. Figures showing the location of each head scale can be found in Conant & Collins (1991). Sex was determined by cloacal probing. JL, HW and IOD were not measured on neonates during the 1999 season. Multivariate analyses on head morphology are thus restricted to 156 of the neonates born in 1998.

Statistical analyses

Sex, litter and site differences in neonatal SVL, mass and TL were tested with ANOVA, with sex and site specified as fixed factors, and litter as a random factor nested within site. SVL was treated as a covariate for comparisons of mass and TL. Head measurements were analyzed using MANCOVA, with sex and site treated as fixed factors, and litter nested in site as a random factor and SVL included as a covariate. Equality

of slopes was tested and confirmed by non-significant interactions between SVL and sex, and SVL and site. Multivariate significance for SVL, sex, site and litter was tested using Wilk's λ , and effects for each of these factors on all four head measurements were tested with univariate F -tests. Phenotypic correlations among HL, JL, HW and IOD were determined using partial correlation coefficients, with SVL factored out. Relationships between maternal SVL and litter size, and mean neonatal SVL and mass were tested using simple linear regression. All data were normalized using natural log transformations.

Results

A total of 286 neonates of a roughly equal sex ratio was born during the two seasons (Table 1). Eleven litters from each site were collected in 1998, and six litters were collected from Miller's marsh and five from McCafferty farm in 1999. Neonatal head and body measurements taken during the two collecting seasons did not differ significantly. Therefore, data from the 2 years are combined in all analyses that follow. Adult females from Miller's marsh had significantly greater mean SVLs ($M = 552.5$ mm, $SE = 9.2$) than females from McCafferty farm ($M = 512.9$ mm, $SE = 9.3$), $F(1,29) = 9.2$, $P < 0.01$. Females from Miller's marsh gave birth to significantly larger litters than did snakes from McCafferty farm, $t(31) = 3.1$, $P < 0.01$. Comparisons by sex, site and litter for SVL, tail and mass were made with all 286 snakes. Analyses of head measurements were conducted on the 22 litters born in 1998. Descriptive statistics ($M \pm 1SE$) on mass, SVL, TL, HL, JL, HW and IOD at birth for snakes within each litter,

Table 1 Litter sizes and frequencies of each sex for snakes born to mothers from Miller's marsh (MM) and McCafferty farm (MF) during 1998 and 1999

Site	n	No. of litters	M (SD) litter size	Range	Males (n)	Females (n)
MM	175	17	10.3 (3.4)	3–17	84	91
MF	111	16	6.9 (2.8)	2–13	58	53
Total	286	33	8.7 (3.5)	2–17	142	144

These snakes were used in analyses for litter, sex and site differences in post-partum snout–vent length, tail length and mass.

Table 2 Descriptive statistics ($M \pm 1SE$) by site and sex for mass, snout–vent length (SVL), tail length (TL), head length (HL), jaw length (JL), head width (HW) and interocular distance (IOD) for neonates born in 1998 and 1999 to mothers from McCafferty farm (MF) and Miller's marsh (MM)

Site	Sex	Mass (0.1 g)	SVL (1.0 mm)	TL (1.0 mm)	HL (0.01 mm)	JL (0.01 mm)	HW (0.01 mm)	IOD (0.01 mm)
MF	M	2.07 (0.04)	162.3 (1.04)	48.9 (0.51)	9.98 (0.05)	9.80 (0.05)	4.54 (0.03)	4.00 (0.02)
	F	2.16 (0.04)	161.9 (1.30)	45.0 (0.60)	10.13 (0.06)	10.06 (0.11)	4.63 (0.03)	4.07 (0.03)
	Total	2.11 (0.03)	162.1 (0.82)	47.1 (0.43)	10.05 (0.04)	9.90 (0.06)	4.58 (0.02)	4.03 (0.02)
MM	M	2.22 (0.05)	166.1 (1.14)	48.3 (0.47)	10.04 (0.04)	9.94 (0.05)	4.61 (0.02)	4.04 (0.02)
	F	2.23 (0.04)	162.7 (1.08)	45.5 (0.54)	10.20 (0.04)	10.13 (0.04)	4.69 (0.02)	4.09 (0.02)
	Total	2.23 (0.03)	164.3 (0.79)	46.8 (0.37)	10.13 (0.03)	10.05 (0.03)	4.65 (0.01)	4.07 (0.01)
Grand total	M	2.16 (0.03)	164.5 (0.81)	48.6 (0.35)	10.02 (0.03)	9.88 (0.04)	4.58 (0.02)	4.02 (0.02)
	F	2.21 (0.03)	162.4 (0.83)	45.3 (0.40)	10.17 (0.04)	10.11 (0.04)	4.67 (0.02)	4.09 (0.02)
	Total	2.18 (0.02)	163.5 (0.58)	46.9 (0.28)	10.10 (0.02)	9.99 (0.03)	4.62 (0.01)	4.06 (0.01)

JL, HW and IOD were not measured for 1999 neonates. Head measurements for two litters born late in 1998 were not taken.

sex and site are shown in Table 2. Mass and SVL were significantly correlated at birth for both males and females. The linear relationship between SVL and mass was significant for both males and females, $R^2 = 0.44$, $F(1,31) = 24.0$, $P < 0.001$ (combined in Fig. 1).

Our sub-sample, along with a much larger sample of adult females from Miller's marsh, was significantly longer and heavier than that from McCafferty farm (Krause *et al.*, 2003). This is probably due to the relatively more diverse and abundant sources of food available at Miller's marsh. However, the dietary and size differences in adult snakes from the two sites on Beaver Island did not appear to have a significant effect on neonatal body size, mass or TL. At birth, neonates born to mothers collected at Miller's marsh were slightly heavier and had longer SVLs than neonates from McCafferty farm, but the differences were not significant and no site effect was found for TL (Table 3).

There were marked body size differences between male and female neonates (Table 2). Overall, females from both sites were significantly heavier than males ($P = 0.033$, Table 3). The magnitude of the difference in mass between sexes was greater in neonates from McCafferty farm. The

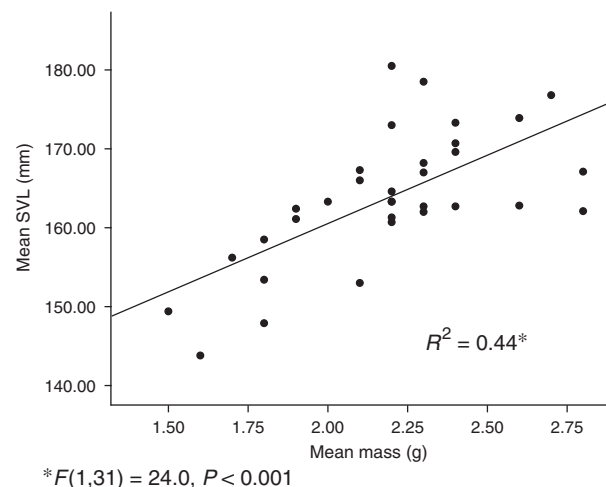


Figure 1 Relationship between snout–vent length (SVL) and mass in neonatal garter snakes *Thamnophis sirtalis* ($n = 33$ litters). Litter means for sexes combined are plotted.

Table 3 Results of univariate ANOVA testing for litter, sex and site effects on neonatal snout-vent length (SVL), mass and tail length (TL)

Measure	Source	d.f.	MS ^a	F	P
SVL	Litter within site	31, 251	2.38E-02	19.75	< 0.001
			1.21E-03		
	Sex	1, 251	2.16E-02	17.86	0.001
			1.21E-03		
Site	1, 32	1.34E-02	0.70	0.408	
		1.90E-02			
Mass	Covariate (SVL)	1, 250	0.46	180.23	< 0.001
			2.54E-03		
	Litter within site	31, 250	4.78E-02	18.83	0.001
			2.54E-03		
Sex	1, 250	1.16E-02	4.59	0.033	
		2.54E-03			
Site	1, 32	4.99E-02	1.33	0.258	
		3.76E-02			
TL	Covariate (SVL)	1, 250	0.18	64.99	< 0.001
			2.81E-03		
	Litter within site	31, 250	3.61E-02	12.85	0.001
			2.81E-03		
Sex	1, 250	0.22	78.62	0.001	
		2.81E-03			
Site	1, 32	2.25E-02	0.79	0.382	
		2.86E-02			

^aMS, hypothesis mean squared error. Significant results are in bold.

sexes also differed significantly in SVL and TL. Males born to mothers from both sites had significantly longer SVLs and TLs than females (Tables 2 and 3). Sex by site interactions were not significant for SVL, mass and TL and were therefore omitted from the results shown in Table 3. Among the neonates, litter was a significant factor for all body measures. SVLs, body weights and TLs differed significantly among the 33 litters (Table 3). Heritabilities were not calculated because multiple paternity is common in *T. sirtalis* (Garner *et al.*, 2002), and we did not assess its presence in this study.

Head size variation

Phenotypic correlations among the four head measurements were computed with SVL as a covariate. At birth, there were significant (all P 's < 0.001) positive phenotypic correlations among the four head measurements (Table 4). Adjusting significance levels for the six correlations using the Bonferroni procedure ($0.05/6 = 0.008$) and Holm's sequentially rejective procedure (Holm, 1979) did not change the outcome of the tests.

SVL covaried significantly with the four head measurements ($\lambda = 0.595$, $F = 19.21$, d.f. = 4, 113, $P < 0.001$). The overall effect for site on neonatal head size was not significant ($\lambda = 0.58$, $F = 2.53$, d.f. = 4, 14, $P = 0.087$), but snakes from Miller's marsh had significantly greater JLs and IODs (see Tables 2 and 5). There was a significant overall effect for sex ($\lambda = 0.422$, $F = 4.80$, d.f. = 4, 14, $P = 0.012$), with neonatal females having greater JLs, HLs, HWs and IODs

Table 4 Phenotypic correlations among four head measurements in 155 neonatal garter snakes *Thamnophis sirtalis*

	Jaw length	Head width	Interocular distance
Head length	0.578**	0.563**	0.405**
Jaw length		0.543**	0.450**
Head width			0.599**

All P values are two-tailed after controlling for multiple comparisons. ** $P < 0.001$.

Table 5 Results of MANCOVA testing for site, sex and litter effects on head length (HL), jaw length (JL), head width (HW) and interocular distance (IOD) in 155 neonatal garter snakes *Thamnophis sirtalis*

Source of variation	d.f.	Hypothesis MS	Error MS	F	P
Covariate (SVL)					
HL	1	2.15E-02	6.0E-04	35.69	< 0.001
JL	1	4.76E-02	7.0E-04	67.63	0.001
HW	1	1.10E-02	5.7E-04	19.22	0.001
IOD	1	1.12E-02	6.9E-04	16.26	0.001
	116				
Site					
HL	1	1.83E-03	1.52E-03	1.21	0.287
JL	1	1.67E-02	2.25E-03	7.41	0.015
HW	1	2.0E-03	1.17E-03	1.71	0.208
IOD	1	1.55E-02	2.97E-03	5.22	0.035
	17				
Sex					
HL	1	3.79E-03	6.0E-04	5.71	0.029
JL	1	2.05E-02	7.0E-04	22.23	0.001
HW	1	8.29E-03	5.7E-04	12.25	0.003
IOD	1	3.20E-03	6.9E-04	8.45	0.010
	17				
Litter within site					
HL	17	1.52E-03	6.0E-04	2.52	0.002
JL	17	2.25E-03	7.0E-04	3.20	0.001
HW	17	1.17E-03	5.7E-04	2.05	0.013
IOD	17	2.97E-03	6.9E-04	4.30	0.001
	116				
Litter by sex					
HL	17	6.6E-04	6.0E-04	1.10	0.363
JL	17	9.2E-04	7.0E-04	1.31	0.198
HW	17	6.8E-04	5.7E-04	1.19	0.286
IOD	17	3.8E-04	6.9E-04	0.55	0.922
	116				
Sex by site					
HL	1	2.2E-04	6.0E-04	0.36	0.548
JL	1	5.0E-05	7.0E-04	0.07	0.785
HW	1	4.6E-04	5.7E-04	0.80	0.373
IOD	1	1.1E-4	6.9E-04	0.16	0.160
	116				

SVL, snout-vent length; MS, hypothesis mean squared error. Significant results are in bold.

(Table 5). The overall effect for litter was significant ($\lambda = 0.283$, $F = 2.49$, d.f. = 68, 464, $P < 0.001$), with all four head measurements showing significant variation among litters (Table 5). The litter by sex and sex by site interactions were not significant for any of the head measurements.

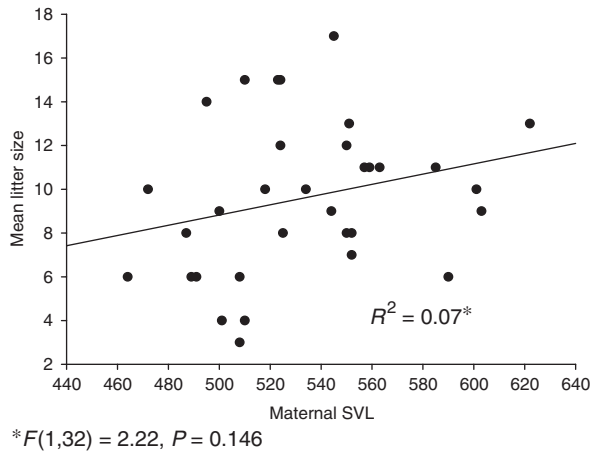


Figure 2 Relationship between litter size ($n=33$) and maternal snout-vent length (SVL) in garter snakes *Thamnophis sirtalis* from both sites.

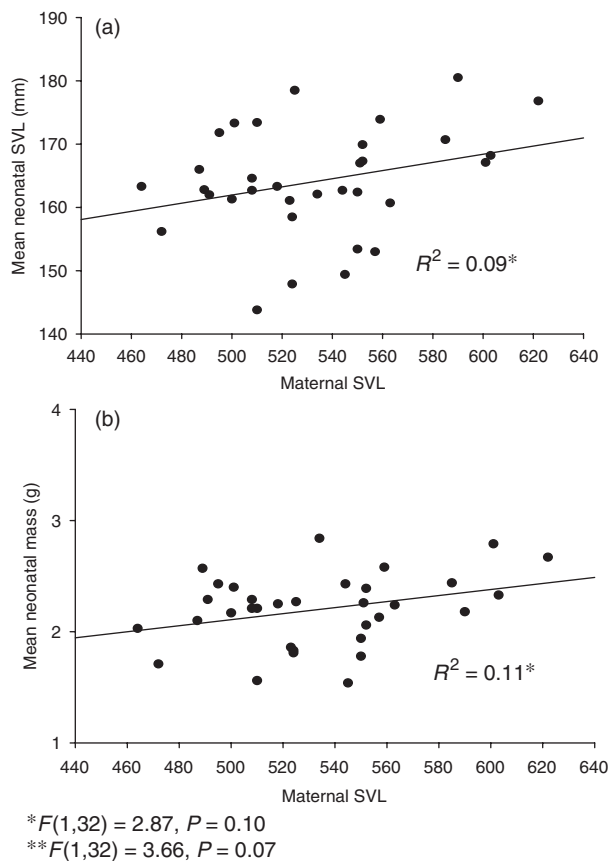


Figure 3 Relationship between mean neonatal and maternal snout-vent length (SVL) (a), and mean neonatal mass and maternal SVL (b) in 33 garter snake *Thamnophis sirtalis* litters.

Maternal size effects

Maternal size influences on litter size and mean neonatal SVL and mass were tested with linear regression coefficients.

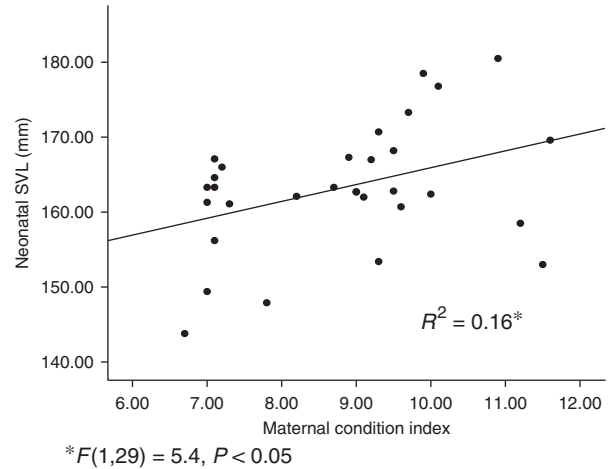


Figure 4 Relationship between mean neonatal snout-vent length (SVL) and maternal condition index in 31 garter snake *Thamnophis sirtalis* litters (data were missing for two adult females), $R^2=0.16$, $F(1,29)=5.4$, $P<0.05$.

Maternal SVL did not predict mean litter size for the 33 litters born during the 1998 and 1999 seasons (Fig. 2). Maternal SVL was also not significantly related to offspring SVL (Fig. 3a), and a marginal relationship was found between maternal SVL and mean neonatal body mass (Fig. 3b). Nevertheless, all of the slopes were positive, suggesting that larger females have a tendency to have more and larger offspring.

Post-partum maternal size was also converted into a composite variable called a condition index (Rivas, 2000). The condition index is calculated by taking the cubic root of mass, dividing by SVL and multiplying this ratio by 100. The resulting number is a measure of the 'health' of a snake, as determined by the ratio between weight and length. Taking the cubic root of mass enables size-independent comparisons of maternal condition to be made. Maternal condition index was a significant predictor of neonatal SVL [$R^2=0.16$, $F(1,29)=5.4$, $P<0.05$; Fig. 4], but not mass ($R^2=0.07$, $P=0.17$). The condition index was not a significant predictor of litter size ($F<1.0$).

The pre-natal hormonal environment in garter snakes is known to influence sexually dimorphic characteristics, namely scale counts (Osypka & Arnold, 2000). It is possible that sex steroid levels of neighboring embryos influence the degree to which sexually dimorphic characters differ at birth. We did not determine the relative positions of males and females within the pregnant females. Rather, we tested whether body and head measurements are also influenced by the sex ratio of each litter. Of our sample, 13 litters were male biased, 14 were female biased and six were of equal sex ratio. To maximize the likelihood of detecting a relationship, we analyzed only those litters in which one sex was at least twice as numerous as the other, resulting in seven female-biased and eight male-biased litters. We then attempted to predict the ratio of male:female SVL, mass, TL and

HL based on the sex ratio of each litter. If sex ratio determines the degree to which these characters are dimorphic, then litters with male-biased sex ratios should have greater SVL and TL (measures showing an overall male size bias) and lower HL and mass (measures showing an overall female size bias). Testing these hypotheses using multiple regressions, we found no overall relationship between sex ratio and the ratio of the four body measurements collectively [$R^2 = 0.09$, $F(4, 9) = 0.21$, NS] or individually (all P 's > 0.05). Thus, unlike scale counts, body and head measurements may not be affected by the relative numbers of males and females present in the embryonic environment.

Discussion

Body and head size variation in garter snakes was examined in neonates born to mothers from ecologically dissimilar habitats on Beaver Island, MI. Wild-caught animals from these sites reveal plasticity of adult body size, with females feeding on a more diverse array of available prey species and growing larger than more diet-restricted females. Sexual size dimorphism of adult body and head sizes has been observed at both sites (Krause *et al.*, 2003). In this study, female and male neonates born to mothers collected at the two sites significantly differed in body and head size. Female neonates from both sites were heavier than males, and males had longer SVLs and TLs than females. Female neonates from both sites had longer HLs and JLs, wider HWs and greater IODs. Overall, JLs and IODs of neonates born to mothers from Miller's marsh were significantly greater than neonates from McCafferty farm. Site differences in neonatal head measurements from the present study may reflect differences in maternal diet, although evidence for this is equivocal.

Maternal effects on the morphology of neonatal garter snake morphology are potentially strong (King *et al.*, 2001). In this study, maternal body size was not significantly related to litter size and absolute body size measures (SVL and mass) of the neonates. Maternal body size frequently predicts litter size (Ford & Seigel, 1989), but other factors, such as age, are more reliable predictors for some populations of garter snakes (Bronikowski & Arnold, 1999). In addition, there were relatively few stomach contents found in adults sampled in the 2-year period of this study (see Krause *et al.*, 2003). The relationships between maternal body size and litter and neonate size may vary with resource availability (see Bronikowski & Arnold, 1999 for data on *Thamnophis elegans*). Thus, resource levels may account for the weak or non-significant relationships between maternal size, litter size, and neonatal SVL and mass. However, using an alternative measure, the condition index, we found a relationship between maternal condition and neonatal SVL. Body and head measurements all varied among litters.

The sex and litter effects reported here, and those of King *et al.* (1999), are not consistent with all studies of neonatal morphology in *T. sirtalis*. Arnold & Peterson (1989) report no sexual size dimorphism or significant litter differences in body size, HL, HW and eye diameter in neonatal *T. sirtalis*.

The discrepancies in these studies may reflect geographic variation in neonatal morphology, but differences in sample sizes or maternal effects may be a contributing factor. The sample size of Arnold & Peterson (1989) was relatively low (nine litters, 65 snakes) in comparison with ours (33 litters, 286 snakes) and King *et al.*'s (27 litters, 407 snakes). Regardless, litter differences in neonatal morphology may have important ecological and evolutionary implications (King, 1997). Further studies on the contributions of maternal, genetic, and early environmental influences on morphology and growth are needed (see King *et al.*, 2001).

Diet-induced variation in body size is relatively widespread in snakes, although genetic factors are known to account for geographic variation of morphological traits in snakes, as well as in other taxa (Madsen & Shine, 1993; Bronikowski, 2000). Phenotypic plasticity of body and head sizes has been found in many species of snakes, possibly in response to dietary variation (Madsen & Shine, 1993). For example, European adders feeding on larger prey have, on average, larger heads (Forsman & Lindell, 1991a,b). Thus, phenotypic plasticity accounts for some of the head and body size variation found in snakes. In addition to geographic and genetic factors, sex determines the extent to which body and head sizes differ in snakes.

The majority of studies examining sexual size dimorphism in snake body and head sizes have used adult snakes. Limited emphasis has been placed on understanding the ontogenetic origins and processes that give rise to adult sexual size dimorphism (see Shine & Crews, 1988; King, 1997). Sexual size dimorphism of neonatal snakes is fairly widespread, and has previously been reported for *T. sirtalis* (Shine, 1993; King *et al.*, 1999). The prenatal origins of sex differences in body and head size suggest that the fitness-related effects of sexual dimorphism may exist in very early development. Unexpectedly, newborn males in our study had greater SVLs than females. The male-biased difference in SVL at birth reverses, as females are the longer sex in this population and species. Female neonates were significantly heavier than males, which may be due to a greater maternal investment of nutrients in female offspring. Further research could examine whether there are sex differences in survival in neonatal *T. sirtalis* and whether any differences relate to birth weight and length.

Several possible explanations for adult head size dimorphism in snakes have been proposed. Crews *et al.* (1985) and Shine & Crews (1988) found that male *T. sirtalis* have smaller heads than females because higher androgen levels inhibit male growth. Lerner & Mason (2001) found no difference in body mass and SVL in neonatal *T. sirtalis* just after parturition. Androgen-mediated size differences, with females the larger sex, were apparent by around 20 weeks of age. As with many species, estradiol 17 β levels enhance female growth in garter snakes and testosterone inhibits growth rates (Lerner & Mason, 2001). This finding offers a proximate mechanism for sexual size dimorphism of head size and raises the possibility that sexual selection accounts for sexual size dimorphism in garter snake head sizes. However, if female mate

choice exists in garter snakes, it appears to have little to do with male head size. Also, male garter snakes are not noticeably aggressive toward one another during their attempts to mate with females, a behavior correlated with larger male body size (Schuett & Gillingham, 1989).

An alternative hypothesis is that sexually dimorphic head and body sizes may relate to differential utilization of food (Selander, 1966). For snakes, there is some support for this hypothesis (Shine, 1986). Sex-based resource partitioning in snakes has been documented in Arafura file snakes (Houston & Shine, 1993). Females of this species tend to eat single, large prey items, while males consume several small prey items. Adults of this species show female-biased sexual size dimorphism in length, shape, and relative head size and shape. Adult female garter snakes also take larger prey than do males (White & Kolb, 1974; Fitch, 1982). It is possible that male garter snakes are more likely to pursue burrowing prey such as worms, which could be better accomplished with a relatively small head.

Sex differences in neonatal diets are difficult to determine at present given the paucity of field data available. Lind & Welsh (1994) compared the foraging behavior and diets of neonatal and adult *Thamnophis atratus*. Juveniles and neonates in Lind and Welsh's study foraged along stream margins and consumed smaller prey than adult snakes foraging in a wider variety of habitats. In nature, neonatal garter snakes of both sexes probably consume very small prey (worms, larval amphibians) simply because they are constrained by their small heads. At present, field data on the diets of very young snakes of both sexes are needed, as well as detailed laboratory studies comparing prey-swallowing performance in male and female snakes with head size dimorphism (Forsman & Lindell, 1991a,b).

Alternatively, sex differences in garter snake head size may be an incidental effect of androgen levels. However, this is unlikely as males of many species of snakes have larger heads than females, and there are populations of *T. sirtalis* in which head sizes do not differ between the sexes (Shine & Crews, 1988). Furthermore, male neonates from this study actually had greater SVLs than did females, but had smaller relative head sizes. In this case, it appears that the inhibitory growth effect of testosterone does not affect all measures equally. It is presently unknown whether sexual size dimorphism of adult garter snake head sizes has fitness consequences, or even whether head size dimorphism is correlated with ecological factors such as food resource partitioning. The presence of sexual size dimorphism in neonatal *T. sirtalis* suggests an ecologically important role early in life. Further research examining the relationship between head and body size at birth, and actual behavior and survival, is needed.

We studied a single, widespread generalist species, and emphasized a developmental perspective on sexual size dimorphism. Comparative studies are needed to further our understanding of the evolution and plasticity of sexual size dimorphism (see Fairbairn, 1997). Furthermore, such studies will inform us about possible relationships between sex-

ual size dimorphism and ecological variables such as diet and feeding niche.

Acknowledgements

We thank Jim Gillingham for support while at the Beaver Island Biological Station. John Placyk and Paul Andreadis provided valuable comments on the manuscript and statistical advice. We also thank Madonna McCafferty for access to the McCafferty Farm Field site. This work was supported by a University of Tennessee S.A.R.I.F. award and an alumni dissertation support grant.

References

- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Arnold, S.J. & Peterson, C.R. (1989). A test for temperature effects on the ontogeny of shape in the garter snake *Thamnophis sirtalis*. *Physiol. Zool.* **62**, 1316–1333.
- Bronikowski, A.M. (2000). Experimental evidence for the adaptive evolution of growth rate in the garter snake *Thamnophis elegans*. *Evolution* **54**, 1760–1767.
- Bronikowski, A.M. & Arnold, S.J. (1999). The evolutionary ecology of life history variation in the garter snake *Thamnophis elegans*. *Ecology* **80**, 2314–2325.
- Burghardt, G.M. & Schwartz, J.M. (1999). Geographic variations on methodological themes in comparative ethology: a natricine snake perspective. In *Geographic variation in behavior: perspectives on evolutionary mechanisms*: 69–94. Foster, S.A. & Endler, J.A. (Eds). Oxford: Oxford University Press.
- Conant, R. & Collins, J.T. (1991). *A field guide to reptiles and amphibians of eastern and central North America*. 3rd edn. Boston: Houghton Mifflin.
- Crews, D., Diamond, M., Whittier, J. & Mason, R. (1985). Small male body size in garter snakes depends on testes. *Am. J. Physiol.* **249**, R62–R66.
- Fairbairn, D.J. (1997). Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annu. Rev. Ecol. Syst.* **28**, 659–687.
- Fitch, H.S. (1965). An ecological study of the garter snake, *Thamnophis sirtalis*. *Univ. Kan. Pub. Mus. Nat. Hist.* **15**, 493–564.
- Fitch, H.S. (1982). Resources of a snake community in prairie-woodland habitat in northeastern Kansas. In *Herpetological communities*: 83–97. Scott, N.J. (Ed.). Washington, DC: US Fish and Wildlife Services.
- Ford, N.B. & Seigel, R.A. (1989). Relationships among body size, clutch size, and egg size in three species of oviparous snakes. *Herpetologica* **45**, 75–83.
- Forsman, A. (1996). An experimental test for food effects on head size allometry in juvenile snakes. *Evolution* **50**, 2536–2542.

- Forsman, A. & Lindell, L.E. (1991a). Trade-off between growth and energy storage in male *Vipera berus* (L.) under different prey densities. *Funct. Ecol.* **5**, 717–723.
- Forsman, A. & Lindell, L.E. (1991b). The advantage of a big head: swallowing performance in adders, *Vipera berus*. *Funct. Ecol.* **7**, 183–189.
- Garner, T.W.J., Gregory, P.T., McCracken, G.F., Burghardt, G.M., Koop, B.F., McLain, S.E. & Nelson, R.J. (2002). Geographic variation of multiple paternity in the common garter snake (*Thamnophis sirtalis*). *Copeia* **2002**, 15–23.
- Gillingham, J.C. (1980). Communication and combat behavior of the black rat snake (*Elaphe obsoleta*). *Herpetologica* **36**, 120–127.
- Gregory, P.T. & Prelypchan, C.J. (1994). Analysis of variance of first-year growth in captive garter snakes (*Thamnophis elegans*) by family and sex. *J. Zool. (Lond.)* **232**, 313–322.
- Grudzien, T.A., Huebner, B.J., Cvetkovic, A. & Joswiak, G.R. (1992). Multivariate analysis of head shape in *Thamnophis s. sirtalis* (Serpentes: Colubridae) among island and mainland populations from northeastern Lake Michigan. *Am. Mid. Nat.* **127**, 339–347.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* **6**, 65–70.
- Houston, D. & Shine, R. (1993). Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *J. Anim. Ecol.* **62**, 737–748.
- King, R.B. (1997). Variation in brown snake (*Storeria dekayi*) morphology and scalation: sex, family, and microgeographic differences. *J. Herpetol.* **31**, 335–346.
- King, R.B., Bittner, T.D., Queral-Regil, A. & Cline, J.H. (1999). Sexual size dimorphism in neonate and adult snakes. *J. Zool. (Lond.)* **247**, 19–28.
- King, R.B., Milstead, W.B., Gibbs, H.L., Prosser, M.R., Burghardt, G.M. & McCracken, G.F. (2001). Application of microsatellite DNA markers to discriminate between maternal and genetic effects on scalation and behavior in multiply-sired garter snake litters. *Can. J. Zool.* **79**, 121–128.
- Krause, M.A. (2000). *Plasticity of morphology, chemoreception, and predatory behavior in garter snakes (Thamnophis sirtalis)*. PhD thesis, University of Tennessee, Knoxville.
- Krause, M.A., Burghardt, G.M. & Gillingham, J.C. (2003). Body size plasticity and local variation of relative head and body size sexual dimorphism of garter snakes (*Thamnophis sirtalis*). *J. Zool. (Lond.)* **261**, 399–407.
- Lerner, D.T. & Mason, R.T. (2001). The influence of sex steroids in the sexual size dimorphism in the red-spotted garter snake, *Thamnophis sirtalis concinnus*. *Gen. Comp. Endocr.* **124**, 218–225.
- Lind, A.J. & Welsh, H.H. (1994). Ontogenetic changes in foraging behavior and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. *Anim. Behav.* **48**, 1261–1273.
- Madsen, T. & Shine, R. (1993). Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution* **47**, 321–325.
- Osycka, N.M. & Arnold, S.J. (2000). The developmental effect of sex ratio on a sexually dimorphic scale count in the garter snake *Thamnophis elegans*. *J. Herpetol.* **34**, 1–5.
- Pearson, D., Shine, R. & Williams, A. (2002). Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia* **131**, 418–426.
- Placyk, J.S. (2006). *Geographic variation in the behavior, morphology, and life history of Michigan common gartersnake, Thamnophis sirtalis, populations: the role of historical processes, evolutionary change, and phenotypic plasticity*. PhD thesis, University of Tennessee, Knoxville.
- 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.
- Rivas, J.A. (2000). *Life history of the green anaconda (Eunectes murinus) with emphasis on its reproductive biology*. PhD thesis, University of Tennessee, Knoxville.
- Rivas, J.A. & Burghardt, G.M. (2005). Snake mating systems, behavior, and evolution: the revisionary implications of recent findings. *J. Comp. Psychol.* **119**, 447–454.
- Schuett, G.W. & Gillingham, J.C. (1989). Male–male agonistic behavior of the copperhead *Agkistrodon contortrix*. *Amphibia-Reptilia* **10**, 243–266.
- Schuett, G.W., Hardy, D.L., Early, R.L. & Greene, H.W. (2005). Does prey size induce head skeleton phenotypic plasticity during early ontogeny in the snake *boa constrictor*? *J. Zool. (Lond.)* **267**, 363–369.
- Seigel, R.A. & Ford, N.B. (1987). Reproductive ecology. In *Snakes; ecology and evolutionary biology*: 210–252. Seigel, R.A., Collins, J.T. & Novack, S.S. (Eds). New York: Macmillan.
- Selander, R.K. (1966). Sexual dimorphism and differential niche utilization in birds. *Condor* **68**, 113–151.
- Shine, R. (1986). Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia* **69**, 260–267.
- Shine, R. (1993). Sexual dimorphism in snakes. In *Snakes: ecology and behavior*: 49–86. Seigel, R.A. & Collins, J.T. (Eds). New York: McGraw-Hill.
- 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., Olsson, M.M., Moore, I.T., LeMaster, M.P. & Mason, R.T. (1999). Why do male snakes have longer tails than females? *Proc. Roy. Soc. Lond. B* **266**, 2147–2151.
- Slatkin, M. (1984). Ecological causes of sexual dimorphism. *Evolution* **38**, 622–630.

- Székely, T., Freckleton, R.P. & Reynolds, J.D. (2004). Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *PNAS*, **101**, 12224–12227.
- Vincent, S.E., Herrel, A. & Irschick, D.J. (2004). Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). *J. Zool. (Lond.)* **264**, 53–59.
- White, M. & Kolb, J. (1974). A preliminary study of *Thamnophis* near Sagehen Creek, California. *Copeia* **1974**, 126–136.
- Wikelski, M. & Trillmich, F. (1997). Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution* **51**, 922–936.