SEXUAL SIZE DIMORPHISM, DIET, AND REPRODUCTION IN THE MEXICAN GARTER SNAKE, *THAMNOPHIS EQUES*

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Abstract.—In this study we examined diet, reproduction, and sexual dimorphism in body size of adult *Thamnophis eques*. We measured 307 adult snakes within the hydrologic system of High Lerma. Prey was obtained by forced regurgitation when snakes were collected, and gravid females were housed in the laboratory until parturition. Females had a longer snout-vent length and shorter tails than males, but there was no difference in total length between the two sexes. We found no evidence to support the hypothesis that sexual dimorphism is due to differences in prey size for this species because the sexes did not differ in the type and mass of prey they consumed; however, the size of gravid females was positively related to the number, but not size and weight, of their offspring. Our results suggested that sexual size dimorphism in natural populations of *T. eques* may be determined by fecundity selection rather than the ecological factors associated with the spectrum of available prey sizes. We also discuss possible reasons why the sexes did not differ in total length.

Key Words.—body size; diet; head length; litter size; snout-vent length; tail length

INTRODUCTION

Sex-related differences in size and body proportions have evolved in many animal groups as insects, fishes, amphibians, reptiles and birds, and efforts to understand the ecological and evolutionary significance of sexual dimorphism have focused on adaptive significance and physiological mechanisms (Andersson 1994). Particular interest has been given to the so-called "reverse" size dimorphism (RSD; females larger than males), because in nature the males of most non-mammalian and non-avian species are larger than females (Andersson 1994). Snakes are good subjects for studying RSD because they continue growing after maturation, which leads to great size variability. This variability makes it possible to test the dependence of size on reproductive success. Sexual size dimorphism (SSD) in different viper, elapid, and colubrid species has been reported for snout-vent length (SVL), relative head size, head shape, relative tail size, and mass (Shine 1993; Krause et al. 2003).

Differences between sexes in body and head size and head shape occurs in snakes, which can result in resource partitioning (Houston and Shine 1993; Pearson et al. 2002). Research into the role of SSD in resource dynamics has garnered considerable attention, specifically because SSD may be influenced by dietary intake (Cox et al. 2008; Stahlschmidt et al. 2010). Snakes are gape-limited predators that consume their prey whole, so that head size limits the maximum size of ingestible prey (King 2002; Shetty

and Shine 2002; Vincent et al. 2004). Females that attain a larger head length may be able to consume larger or heavier prey than males (Shine 1991, 1993; Pearson et al. 2002), or live in slightly different microhabitats (Manjarrez and Macías García 1993), which suggests that males and females occupy different ecological niches either to reduce intra-sexual competition for food or because of different food requirements (Shine 1991, 1993; Houston and Shine 1993; Herrel et al. 1999; Pearson et al. 2002).

Sexual dimorphism may also have reproductive advantages (e.g., fecundity selection) because greater clutch sizes and fecundity confer reproductive advantages to larger females over smaller snakes (Seigel and Ford 1987; Shine 1993). Larger females may produce offspring that are in better condition at birth and have a higher probability of survival (Bronikowski 2000; Kissner and Weatherhead 2005). For males, it is advantageous to mature earlier at the expense of smaller size (Bronikowski 2000; Sparkman et al. 2007).

Another sexual difference among snake species is that males have longer tails than females (Shine 1993; Rossman et al. 1996). Males with relatively longer tails tend to have a longer hemipenes and may have higher mating success compared to males with shorter tails (Shine et al. 1999). Usually, the above hypotheses assume sexual dimorphism only for the SVL, tail length, or head length. However, the sum of SVL and tail length may result in there being no dimorphism in total length of some snake species (King 1989).

FIGURE 1. Mexican Garter Snake, *Thamnophis eques*, from Toluca Valley, State of México, México. (Photographed by Javier Manjarrez).

The semi-aquatic colubrid, Mexican Garter Snake (*Thamnophis eques*), is suitable for testing SSD, which can affect intraspecific differences in diet and female reproduction. Our previous study concluded that both sexes have similar head sizes (Manjarrez and Macías García 1993); however our new data suggest there is variation in tail length and head length throughout its distribution in Mexico. *Thamnophis eques* (Fig. 1) is widely distributed over the Mexican Plateau. However, despite the apparent widespread distribution, this species has a constricted ecological distribution and low population densities (Manjarrez 1998). In Mexico, its populations are severely fragmented and isolated due to its habitat requirements, habitat loss, and disturbance (Conant 2003). Many populations of garter snakes show considerable intraspecific variation in habitat or diet (Rossman et al. 1996), but dietary data are particularly scarce for Mexican populations of *T. eques*. Previous studies of Mexican populations have revealed some differences in prey taxa size between males and females, neonates and adults, and between rainy and dry seasons (Sosa 1982; Macías García and Drummond 1988; Drummond and Macías García 1989). At Lake Tecocomulco, Mexico, large snakes of both sexes (> 44.0 cm SVL) feed mainly on aquatic vertebrates (fishes, frogs, and salamander larvae), and small snakes on aquatic invertebrates (earthworms and leeches). There is also seasonal variation in prey that was associated with fluctuations in prey availability (Macías García and Drummond 1988). At Toluca, Mexico, *T. eques* ate tadpoles (*Hyla* sp.), earthworms, mice, and slugs (Manjarrez 1998).

To assess sexual dimorphism in body size in *T. eques,* we examined measured the SVL, tail length, total length, and head length of adult snakes, and analyzed stomach contents and reproductive condition. We tested the hypothesis that females would have greater SVL and HL, and would consume different prey species or larger prey compared to males. We also tested for phenotypic plasticity, exploring the relationship between maternal SVL and the number, weight, and SVL of their offspring.

MATERIALS AND METHODS

We examined 307 adult snakes (> 39 cm SVL; see Manjarrez 1998) captured between 1991 and 2003 in Toluca Valley, within the hydrological system of Lerma River in the State of México (approx. 2000 km^2). We captured snakes by hand while walking within 10 m of streams, rivers, canals, ponds, and lakes, and looking under rocks and other objects. We measured the SVL, tail length (TaL; defined as posterior tip of vent to tip of tail when they were complete), total length (TL), and head length (HL; from the anterior-most tip of the rostral scale to the angle of the jaw; Rossman et al. 1996). We determined sex by the presence or absence of an everted hemipenis. Stomach contents of the snakes were obtained by forced regurgitation when they were collected (Carpenter 1952). We measured the wet mass of each prey item (± 0.01 g) after drying items externally on a paper towel.

To determine the relationship between female body size and reproductive output, we maintained the gravid females in the laboratory until parturition, housing them in 40 L aquaria containing water dishes and clay shelters, under a natural (Toluca) photoperiod, at 20–25° C room temperature, and fed them with live fish. In general, they were kept in captivity from one day to five weeks prior to parturition. We counted neonates at the age of three days, and we weighed (± 0.01 g) and measured (SVL) them. We released all snakes after being processed.

Because the dimensions of tails and heads of snakes, as well as the mass of prey items, vary with body length, we tested for sexual differences used ANCOVA with SVL as a covariate (Warton et al. 2006). For SVL and TL, we used ANOVA or its non-parametric analogue, the Kruskal–Wallis test, depending on the results of tests for normality and homoscedasticity. We used Chi-square (χ^2) to test for sexual differences in the frequency of the snakes that contained prey items. We used the Pearson (r_p) correlation and linear regression to explore the relationship between SVL of gravid females (independent variable) and the number, weight, and SVL of their offspring (dependent variables). We used a standardized major axis (SMA, or reduced major axis) to test the relationship of SVL with TaL and HL for both sexes. We compared slopes of the regression functions obtained for both sexes. In the case of non-significant differences between slopes, we compared intercepts as well as shifts along the common slope. We used a resampling algorithm implemented in the program (S)MATR v. 2 (Warton et al. 2006), which applies the likelihood ratio test statistic to compare slopes, and the Wald test, to compare both elevation and the shift along the common slope, both approximated by the Chi-squared distribution. To satisfy statistical assumptions and facilitate biological

TABLE 1. Mean, standard deviation (SD), minimum (min), maximum (max), sample size (n), and normality test (Kolmogorov–Smirnoff, *K–S*) for biometric traits of male (M) and female (F) adult *Thamnophis eques*. *D* is the critical value for the *K–S* test for normality, and significant results are in bold. Differences in the sample size for different traits were a result of incomplete data for some individuals.

	Sex	Mean	SD	min	max	n	*D*
SVL [cm]	M	51.6	8.1	39.5	78.5	109	0.129
	F	54.5	10.3	39.5	92.0	198	0.080
TaL [mm]	M	130.8	25.8	60.0	190.0	109	0.084
	F	123.8	27.0	50.0	200.0	198	0.067
HL [mm]	M	17.7	3.5	10.8	28.0	105	115.0
	F	19.8	4.8	10.1	40.0	189	108.0

interpretation, we used the natural logarithm transformation for allometric relationships between traits (*sensu* King 2000). We transformed HL and TL with natural logarithms because of the lack of both homoscedasticity and skewed distribution. We performed ANOVA and ANCOVA tests with STATISTICA 8.0 (StatSoft, Tulsa, Oklahoma, USA). We tested all data for normality with XLSTAT 2011 (Addinsoft, New York, New York, USA), presented descriptive statistics as the mean ± 1 SD, and set alpha to 0.05.

RESULTS

We observed significant sexual dimorphism in SVL, which was larger in adult females of *T. eques* than adult males by 5.6% (Table 1; Fig. 2A; *H* = 5.96, *P* = 0.015). Absolute length of tails of adult males were 5.6% longer than tails of females (Table 1; Fig. 2B), but the differences were not significant (Table 1, Fig. 2D; $F_{1, 292}$ = 1.87, *P* = 0.170). However, tails

FIGURE 2. Mean SVL, tail length, head length, and total length of adult *Thamnophis eques*. Least significant difference intervals are represented in the original units, even when data for (C) and (D) were transformed using natural logarithms. The probability in (A; *) refers to the Kruskal–Wallis test for non-transformed data. The probabilities in (C) and (D) refer to the results for the ln-transformed data. ANCOVA with SVL as covariate was performed in (B) and (C), and ANOVA in (D). Numbers of snakes are shown above the error bars (± 1 SD).

TABLE 2. Slope, intercept, coefficient of determination (r^2), and sample size (n) for the standardized major axes of the relationship of tail length (mm) vs. SVL (cm) and head length (mm) vs. SVL (cm) of male and female adult *Thamnophis eques*. Significant results in bold: for all cases *P* < 0.001.

	Tail length vs. SVL		Head length vs. SVL	
Variables	Males	Females	Males	Females
Slope	0.31	0.26	0.43	0.46
Intercept	-3.27	-1.89	-4.57	-5.42
r^2	0.220	0.210	0.509	0.568
n	109	198	105	189

comprised a significantly larger part of TL in males ($F_{1, 304}$ = 14.03, *P* < 0.001; TaL [mm] = 1.49 (SVL) + 53.74 [mm] for males and TaL [mm] = 1.19 (SVL) + 5.86 [mm] for females). Sexual differences were also evident in HL: males had shorter heads (SVL adjusted) than females (Table 1, Fig. 2C; $F_{1,291}$ = 10.37, *P* = 0.001; HL [mm] = 0.31 (SVL) + 1.82 [mm] for males and HL [mm] = 0.35 (SVL) + 0.79 [mm] for females).

We found an isometric relationship between SVL and TaL as well as between SVL and HL (Fig. 3). The distribution of HL for females deviated from normality (Table 1), but this was not critical to the computationally intensive method of regression adjustment and comparison used here (Warton et al. 2006). There was no significant difference observed between the sexes relating to the slopes of the standardized major axes for the relationship between TaL or HL and SVL; there was, however, a significant difference in their intercepts (Table 2; Table 3). Additionally, there was a significant difference between sexes in the shift along the common slope for the relationship between HL and SVL (Table 2; Table 3; Fig. 3).

Males and females did not differ in proportions of prey types consumed (χ^2 = 14.5, df = 9, *P* = 0.100, n = 148 snakes; Table 4) nor in total prey mass for each regurgitation (females: 4.80 ± 1.43 g, n = 34; males: 3.36 ± 1.19 g, n = 49; $F_{1,81}$ = 0.59, *P* = 0.440; Table 4). Sample sizes were insufficient to compare the slopes of the prey size / snake size relationship separately for each type of prey. There was a significant difference in mean SVL of adult snakes consuming each prey type, but mean SVL was similar between sexes (two-factor ANOVA, prey type: $F_{4,142}$ = 4.39, *P* = 0.001; sex: $F_{1,142}$ = 3.06, *P* = 0.080). The largest specimens of *T. eques* consumed rodents (60.5 ± 4.2 cm SVL, range 52.0–64.5, n = 10), earthworms (55.3 ± 2.2 cm, range 48.0–56.0, n = 30), and frogs (54.6 ± 7.0 cm, range 41.5–69, n = 15). Fish (52.9 ± 10.0 cm, range 39.5–85.0, n = 33), tadpoles (51.0 ± 6.5 cm, range 40.0–67.0, n = 43), and leeches (47.8 ± 6.0 cm, range 39.5–61.0, n = 13) were taken by smaller snakes.

The mean number of offspring of the 24 gravid females that gave birth in the laboratory was 12.58 ± 5.9 (3–26 offspring; Fig. 4). The mean mass and size of offspring per litter was 1.96 ± 0.51 g (1.13–3.60 g) and 155.38 ± 16.52 mm SVL (122.33–186.08 mm).
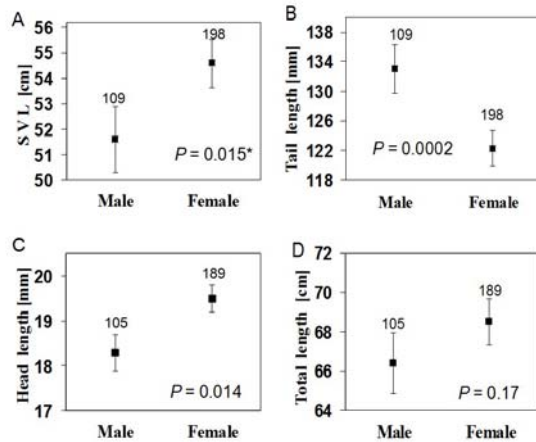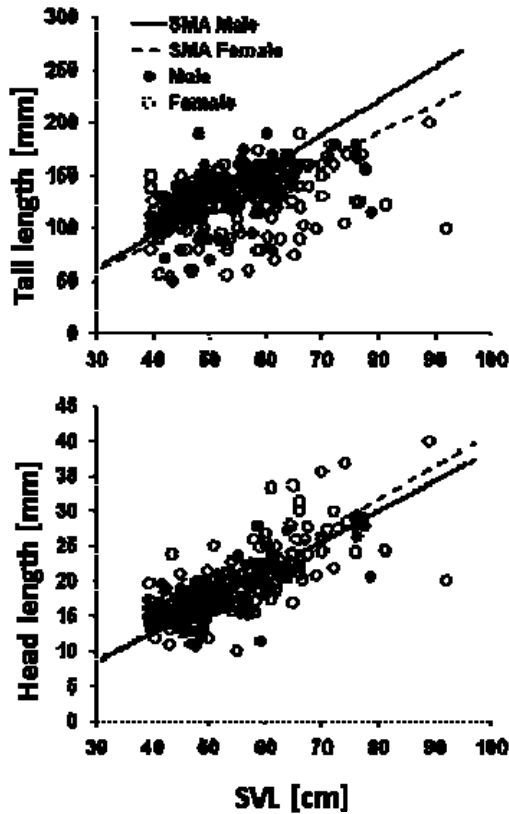
FIGURE 3. Relationship between (A) tail length or (B) head length and SVL of *Thamnophis eques*. We used standardized major axes for the relationship for both sexes. There were no significant differences between sexes in the slopes, but there were significant differences in the intercepts for (A) and (B). There was a significant shift along the common slope in HL (see also Table 3).

TABLE 3. Tests for common slopes and intercepts between sexes for the relationships tail length vs. SVL and head length vs. SVL, as well as the test of shift along the common slope for male and female adult *Thamnophis eques*. Significant results show with an asterisk, CS is the common slope, CE is the common elevation, and n is the sample size.

	Tail length vs. SVL	Head length vs. SVL
CS	0.28	0.45
Test statistic for common slope	3.22	0.73
N	107	194
Intercept males	-1.38	-5.69
Intercept females	-2.90	-4.83
Wald statistic (χ^2) for CE	22.40*	5.47
Wald statistic (χ^2) for shift along CS		12.53

The SVL of gravid females (56.25 ± 9.35 cm; 4.3–8.0 cm) was positively correlated with the number of their offspring (SMA: ln(number of offspring) = 0.052 (SVL) mother - 0.521), but was not correlated to offspring weight ($r_p^2 = 0.001$, n = 24, P = 0.950) or SVL ($r_p^2 = 0.018$, n = 24, P = 0.550). Mean male and female SVL and mass for each litter of neonates did

Table 4. Number of males and females of *Thamnophis eques* that consumed each prey items and prey mass consumed. "Other" includes birds, toads, and crayfish.

	Number of snakes (Proportion)		Mean prey mass in g ± 1 SD	
Items	Males	Females	Males	Females
Fishes	23 (0.26)	20 (0.34)	1.80 ± 1.11	1.47 ± 2.29
Tadpoles	24 (0.27)	9 (0.15)	2.76 ± 2.40	1.71 ± 1.01
Earthworms	23 (0.26)	7 (0.12)	0.27 ± 0.24	0.23 ± 0.16
Frogs	6 (0.07)	9 (0.15)	6.12 ± 8.24	5.60 ± 7.48
Leeches	7 (0.08)	6 (0.10)	1.41 ± 2.28	0.19 ± 0.16
Rodents	5 (0.06)	5 (0.09)	5.19 ± 5.14	7.12 ± 8.57
Other	1 (0.01)	3 (0.05)	--	--

not differ between the sexes (SVL: $F_{1,22}$= 3.71, P = 0.910; mass: $F_{1,22}$= 0.91, P = 0.340).

DISCUSSION

Although adult *T. eques* females had a longer SVL and HL than males, the sexes did not differ in their diet, and we found that larger females had more offspring. These results suggest that sexual size dimorphism in natural populations of *T. eques* may be determined by fecundity selection rather than by the ecological factors associated with the spectrum of available prey sizes. The lack of intersexual differences in the slope of the regression between HL and SVL, and the upward shift in the intercept of the regression line for females together with the shift along the common slope toward larger females (data for larger females do not overlap with the data for larger males), showed that the larger heads of the females are probably an outcome of their larger bodies (SVL) and not of the allometric relationship between these traits.

There are many hypotheses regarding the evolution of SSD (Shine 1993). For example, SSD may evolve through delayed maturation of the larger sex. The delay in reproduction may be compensated by a higher rate of reproduction or, in indeterminate growers, by a longer lifespan (Bronikowski 2008). A longer lifespan, in turn, may lead to a greater abundance of that sex, in our case, females. In this study, we collected more adult female than male *T. eques*, and also 28% of the females were > 65 cm of SVL, versus 9% of males. A third possible mechanism to obtain SSD is faster growth, resulting from the first factor: the physiological properties of the larger sex (Bronikowski 2000).

Some studies (Kozłowski and Uchmański 1987; Kozłowski and Wiegert 1987) describe the life-history traits responsible for SSD: for the same somatic growth rate and initial size, delayed maturity and larger body size are promoted by a high gain in reproductive rate with increasing body size and by a
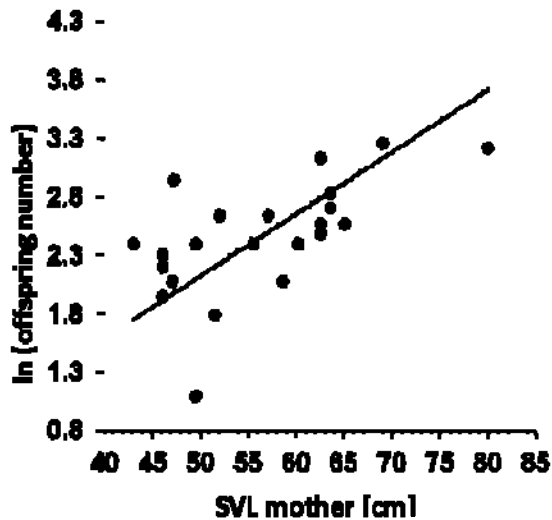
FIGURE 4. Relationship between the SVL of 24 mothers of *Thamnophis eques* and the number of offspring. We used standardized major axes for the relationship: ln(offspring number) = 0.053 SVL – 0.52 (r^2=0.37, P = 0.003).

long life expectancy at maturity (Kozłowski 1989). This phenomenon, together with SVL-dependent litter size in females, is probably responsible for the existence of RSD in *T. eques*. Whether age at maturity is the proximate cause of the RSD (bimaturism resulting from the independent optimization of age at maturity for each sex) can be determined by examining the ages at maturity for both males and females. Indeed, our studies of *T. eques* (over an area of 2,000 km²) and a study of one population next at Toluca City (Manjarrez 1998) showed that neonate males and females do not differ in SVL nor body weight. Similarly, newborn of the sympatric snake over the Mexican Plateau, *T. scalaris*, do not reveal sex-related differences in either SVL or body mass (Manjarrez et al. 2007).

A comparison of the different species of Colubridae shows that for every species considered, females mature later than males independently of size (Parker and Plummer 1987). Currently, we do not have data that would enable an intersexual comparison of early-life growth rates and time of maturation in *T. eques*; however, in the closely related species *T. elegans*, youngsters of both sexes grow and survive at the same rate during the first year of life (Bronikowski 2000). If this is the case for *T. eques*, we would expect females to have delayed maturation.

For the same growth rate, delayed maturity implies a larger body size. In turn, larger females can produce more numerous and/or larger offspring. In snakes, adult body size correlates with traits such as diet and reproductive success (Seigel and Ford 1987). To the best of our knowledge, there are no reports concerning lifetime reproductive success in female *T. eques*. In the closely related *T. atratus*, larger females have a better annual survival rate than smaller males (Lind et al. 2005). In *Nerodia sipedon*, larger neonates and

neonates that are heavier relative to their body length had a higher probability of survival in both the pre-hibernation and hibernation periods, probably because they were able to access a greater range of prey while being vulnerable to fewer predators (Kissner and Weatherhead 2005). Future studies are needed to explore whether both small and large females begin reproductive events at the same age but different size (under this scenario, larger females would produce more offspring than smaller ones) or if small females start reproduction earlier in life than large females, and maybe there is geographic variation in age at first reproduction in females throughout this species. More studies are also required of offspring survival in relation to offspring size, to assess benefit to *T. eques* females of giving birth to larger offspring. Despite the apparent advantages of size and offspring number to larger females, there are additional advantages for females with large body sizes. For example, the offspring of larger females were born earlier and had lower mortality when compared to the offspring of smaller females (Weatherhead et al. 1999).

Although some studies have shown that snake species are sexually dimorphic in both head size and maximum size or item of consumed prey (Bonnet et al. 2000; Pearson et al. 2002; Shetty and Shine 2002; Krause et al. 2003), in *T. eques*, there was dimorphism in head size but not in consumed prey size. This may imply little relevance of HL to feeding (Brown and Weatherhead 1999). However, sexual dimorphism in head traits (i.e., teeth number) and ingested prey shape have rarely been explored and it will be necessary to measure other head and prey dimensions for *T. eques* (i.e., head width) to assess the role of intersexual resource competition in driving sexual dimorphism. Conversely, sexual dimorphism in the HL of *T. eques* may also be the result of non-adaptive processes that do not confer any selective advantage or disadvantage, such as the allometric effects of absolute body size reflected in the dimensions of the head (Shine 1993). Here, we found an isometric relationship between SVL and HL that does not contradict the suggestion that head dimensions reflect body dimensions (Shine 1993).

Males and females of this species do not appear to differ in microhabitat use (Crystian Venegas-Barrera, unpubl. data) or, as was found in the present study, in the size and species composition of prey consumed. This may explain the lack of difference between sexes. Small differences in microhabitat and diet might be revealed by very large sample sizes. Larger body size in *T. eques* adult females could not be explained by sexual differences in diet. Our results supported previous suggestions that the direction of sexual dimorphism in snakes is primarily determined by sexual and fecundity selection (Shine 1993) because the SVL of gravid females was positively related to the number of their offspring in *Thamnophis eques* from one area in Mexico.

LITERATURE CITED

Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey, USA.

Bonnet, X., G. Naulleau, R. Shine, and O. Lourdais. 2000. Reproductive versus ecological advantages to larger body size in female snakes, *Vipera aspis*. Oikos 89:509–518.

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. 2008. The evolution of aging phenotypes in snakes: a review and synthesis with new data. Age 30:169–176.

Brown, G.P., and P.J. Weatherhead. 1999. Demography and sexual size dimorphism in Northern Water Snakes, *Nerodia sipedon*. Canadian Journal of Zoology 77:1358–1366.

Carpenter, C.C. 1952. Comparative ecology of the Common Garter Snake (*Thamnophis s. sirtalis*), the Ribbon Snake (*Thamnophis s. sauritus*), and the Butler`s Garter Snake (*Thamnophis butleri*). Ecological Monographs 22:235–258.

Conant, R. 2003. Observations on garter snakes of the *Thamnophis eques* complex in the lakes of Mexico's transvolcanic belt, with descriptions of new taxa. American Museum Novitates 3406:1–64.

Cox, R.M., M.M. Barrett, and H.B. John-Alder. 2008. Effects of food restriction on growth, energy allocation, and sexual size dimorphism in Yarrow's Spiny Lizard, *Sceloporus jarrovii*. Canadian Journal of Zoology 86:268–276.

Drummond, H., and C. Macías García. 1989. Limitations of a generalist: a field comparison of foraging snakes. Behaviour 108:23–42.

Herrel, A., L. Spithoven, R. Van Damme, and F. de Vree. 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. Functional Ecology 13:289–297.

Houston, D., and R. Shine. 1993. Sexual dimorphism and niche divergence: feeding habits of the Arafura File Snake. Journal of Animal Ecology 62:737–748.

King, R.B. 1989. Sexual dimorphism in snake tail length: Sexual selection, natural selection, or morphological constraint? Biological Journal of the Linnean Society 38:133–154.

King, R.B. 2000. Analyzing the relationship between clutch size and female body size in reptiles. Journal of Herpetology 34:148–150.

King, R.B. 2002. Predicted and observed maximum prey size: Snake size allometry. Functional Ecology 16:766–772.

Kissner, K.J., and P.J. Weatherhead. 2005. Phenotypic effects on survival of neonatal Northern Watersnakes *Nerodia sipedon*. Journal of Animal Ecology 74:259–265.

Kozlowski, J. 1989. Sexual size dimorphism: a life history perspective. Oikos 54:253–255.

Kozłowski, J., and J. Uchmański. 1987. Optimal individual growth and reproduction in perennial species with indeterminate growth. Evolutionary Ecology 1:214–230.

Kozłowski, J., and R.G. Wiegert. 1987. Optimal age and size at maturity in annuals and perennials with determinate growth. Evolutionary Ecology 1:231–244.

Krause, M.A., G.M. Burghardt, and J.C. Gillingham. 2003. Body size plasticity and local variation of relative head and body size sexual dimorphism in Garter Snakes *Thamnophis sirtalis*. Journal of Zoology 261:399–407

Lind, A.J., H.H. Welsh, Jr., and D.A. Tallmon. 2005. Garter snake population dynamics from a 16-year study: Considerations for ecological monitoring. Ecological Applications 15:294–303.

Macías García, C., and H. Drummond. 1988. Seasonal and ontogenetic variation in the diet of the Mexican Garter Snake, *Thamnophis eques*, in Lake Tecocomulco, Hidalgo. Journal of Herpetology 22:129–134.

Manjarrez, J. 1998. Ecology of the Mexican Garter Snake (*Thamnophis eques*) in Toluca, Mexico. Journal of Herpetology 32:464–468.

Manjarrez, J., and C. Macías García. 1993. Variación morfológica intrapoblacional en la culebra de agua *Thamnophis eques*. Boletín de la Sociedad Herpetológica Mexicana 5:1–5.

Manjarrez, J., C.S. Venegas-Barrera, and T. García-Guadarrama. 2007. Ecology of the Mexican Alpine Blotched Garter Snake (*Thamnophis scalaris*). Southwestern Naturalist 52:258–262.

Parker, W.S., and M.V. Plummer. 1987. Population ecology. Pp. 253–301 *In* Snakes: Ecology and Evolutionary Biology. Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). McGraw-Hill, New York, New York, USA.

Pearson, D., R. Shine, and R. How. 2002. Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*). Biological Journal of the Linnean Society 77:113–125.

Rossman, D.A., N.B. Ford, and R.A. Seigel. 1996. The Garter Snakes: Evolution and Ecology. The

University of Oklahoma Press, Norman, Oklahoma, USA.

Seigel, R.A., and N.B. Ford. 1987. Reproductive ecology. Pp. 210–252 *In* Snakes: Ecology and Evolutionary Biology. Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). McGraw-Hill, New York, New York, USA.

Shetty, S., and R. Shine. 2002. Sexual divergence in diets and morphology in Fijian Sea Snakes *Laticauda colubrina* (Laticaudinae). Austral Ecology 27:77–84.

Shine, R. 1991. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. American Naturalist 138:103–122.

Shine, R. 1993. Sexual dimorphism in snakes. Pp. 49–86 *In* Snakes: Ecology and Behavior. Siegel, R.A., and J.T. Collins (Eds.). McGraw-Hill, New York, New York, USA.

Shine, R., M.M. Olsson, I.T. Moore, M.P. Lemaster, and R.T. Mason. 1999. Why do male snakes have longer tails than females? Proceedings of the Royal Society of London B 266:2147–2151.

Sosa, O. 1982. Estudio Preliminar de la Ecología Alimenticia de Tres Especies de Culebras Semiacuáticas del Género *Thamnophis* en los Estados de Zacatecas y Durango, México. B.Sc. Thesis, Universidad Nacional Autónoma de México, México.

Sparkman, A.M., S.J. Arnold, and A.M. Bronikowski. 2007. An empirical test of evolutionary theories for reproductive senescence and reproductive effort in the Garter Snake *Thamnophis elegans*. Proceedings of the Royal Society B. 274:943–950.

Stahlschmidt, Z.R., J.R. Davis, and D.F. DeNardo. 2010. Sexual variation in assimilation efficiency: its link to phenotype and potential role in sexual dimorphism. Journal of Comparative Physiology B 18:383–389.

Vincent, S.E., A. Herrel, and D.J. Irschick. 2004. Sexual dimorphism in head shape and diet in the Cottonmouth Snake (*Agkistrodon piscivorus*). Journal of Zoology 264:53–59.

Warton, D.I., I.J. Wright, D.S. Falster, and M. Westoby. 2006. Bivariate line-fitting methods for allometry. Biological Reviews 81:259–291.

Weatherhead, P.J., G.P. Brown, M.R. Prosser, and K.J. Kissner. 1999. Factors affecting neonate size variation in Northern Water Snakes, *Nerodia sipedon*. Journal of Herpetology 33:577–589.

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