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Sexual dimorphism in neonate and adult snakes

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Abstract

Sex differences in body size and head dimensions are widespread in adult snakes, but because data are scarce for neonates, it is unclear whether differences are present from birth or arise post-natally. Here we analyse patterns of sexual dimorphism in neonates and adults of four species of natricine snakes, *Nerodia sipedon, Storeria dekayi, Thamnophis radix,* and *T. sirtalis*. Two measures of body size (snout–vent length, mass), four measures of head morphology (head length, head width, jaw length, and interocular distance), and tail length were obtained from wild-caught adults and from offspring born to wild-caught females. Among neonates, significant sexual dimorphism was found in body size for *S. dekayi* and *T. sirtalis,* in head dimensions for *S. dekayi, T. radix,* and *T. sirtalis*, and in tail length for all four species. Among adults, significant sexual dimorphism was found in body size, head dimensions, and tail length for all four species. The degree of sexual dimorphism in body size among adults greatly exceeded that among neonates. In contrast, the degree of sexual dimorphism in head dimensions was similar between neonates and adults. The presence of significant sexual dimorphism among neonates suggests that hypotheses regarding the evolutionary significance of sexual dimorphism in snakes should consider newborns as well as adults.

Key words: sexual dimorphism, snakes, body size, head dimensions, tail length

INTRODUCTION

Efforts to understand the ecological and evolutionary significance of sexual dimorphism have focused on processes occurring at many different levels of biological organization (e.g. Short & Balaban, 1994). Among these, investigations of the ontogeny of sexual dimorphism have sometimes served as useful guides for hypotheses and further investigation (e.g. Vitt & Cooper, 1985; Cooper & Vitt, 1989; Mouton & van Wyk, 1993; Beaupre, Duvall & O'Leile, 1998). Three general ontogenetic patterns are possible. Sexual dimorphism may be present among adults but lacking among neonates. In this case, analyses aimed at understanding evolutionary processes and ecological implications might reasonably focus on adults. Alternatively, the direction and degree of sexual dimorphism seen in adults may be similar to that seen in neonates. In this case, analyses that focus on neonates as well as adults are warranted and the possibility that sexual dimorphism in adults is simply a developmental consequence of dimorphism in neonates bears consideration. Finally, the direction or degree of sexual dimorphism may differ between neonates and adults. Here again, analyses that focus on neonates as well as adults are warranted and the possibility that the consequences of dimorphism in neonates differ from those in adults bears consideration. In addition, the developmental processes responsible for adult sexual dimorphism likely differ among these alternatives. In cases where the degree and direction of dimorphism differs between neonates and adults, post-natal ontogenetic processes (e.g. differential survival, growth rates, or age at sexual maturity) are of special interest; in cases where dimorphism is present at birth, pre-natal processes are also of interest. Among snakes, sexual dimorphism in body size, head dimensions, and tail length is well known (e.g. Fitch, 1981; King, 1989; Shine, 1991, 1993, 1994) but data come largely from adults. Likewise, analyses of the evolutionary processes influencing degree of dimorphism (e.g. effect of mating system on selection for male and female body size; Shine, 1978) and the ecological implications of sexual dimorphism (e.g. degree of diet overlap; Shine, 1991) have focused primarily on adults. Fewer data are available on patterns of sexual dimorphism in neonates.

In this paper we describe patterns of sexual dimorphism in neonates of four species of natricine snakes and compare these with patterns seen in adults. Our analysis of sexual dimorphism among neonates is

of further interest because those data that are available have often been analysed without taking family membership into account. Family differences in neonate morphology can be highly significant (see Results) and analyses that fail to account for these differences can lead to erroneous conclusions. When neonates born to different females are pooled for analysis, significant sex differences may be masked by differences among families. Alternatively, sex differences may be inferred when none are present because of differences in morphology and sex ratio among families. Several methods are available that account for family membership when testing for sexual dimorphism in neonates. One approach is to compare males and females within each family separately (e.g. Seigel, 1992: table 4). A drawback is that significant differences may be overlooked because of small family sizes and hence low statistical power. Another approach is to compute male and female means within families and test for significant sexual dimorphism across families using paired *t*-tests (e.g. Weatherhead *et al.*, 1995). This method has the drawback of requiring a larger number of families than might be available in many cases. A third approach, employed here, is to use factorial analyses (analysis of variance or covariance) to test explicitly for both sex and family effects on morphology (e.g. Seigel, 1992; King, 1997). One advantage of this approach is that significant family differences may be of interest because they may reflect underlying genetic variation in morphology (Brodie & Garland, 1993; King, 1997). Another advantage is that it is possible to test for family-by-sex interaction effects on morphology. Such interactions might be present if, for example, females differing in size or condition allocate energy differentially to male and female offspring (e.g. Shine & Bull, 1977; Dunlap & Lang, 1990). In addition, by using multivariate analyses, sets of correlated characters (e.g. head length and head width) can be tested simultaneously and significant sources of variation may be detected that would be overlooked by univariate analysis (Stevens, 1992). Multivariate analysis also avoids the problem of an inflated probability of Type I error that results from conducting multiple univariate tests (Stevens, 1992).

METHODS

Data on neonate and adult morphology were collected for 4 species of live-bearing natricine snakes (Serpentes: Colubridae): *Nerodia sipedon, Storeria dekayi, Thamnophis radix,* and *T. sirtalis*. Data on neonates were obtained from young born in captivity to wild-caught females. Gravid females were collected from the wild in mid- to late-summer and maintained in captivity until parturition. Four *N. sipedon* females were collected from a single study site in Ottawa County, Ohio in 1995. Twenty-five *S. dekayi* females were collected from 3 study sites (4–17 females per site) in Ottawa County, Ohio and Essex County, Ontario in 1990. Twenty-seven *T. sirtalis* females were collected from 5 study sites (2–9 females per site) in Ottawa County, Ohio in 1994, 1995, and 1996. Six *T. radix* females were collected from a single study site in DeKalb County, Illinois in 1995 and 1996. Females were housed individually, fed fish (*N. sipedon*) or earthworms (other species) 2–3 times a week, and provided water *ad libitum* during gestation. Offspring of *N. sipedon* ($n = 50$), *T. sirtalis* ($n = 407$), and *T. radix* ($n = 71$) were classified by sex, weighed, and measured within 48 h of birth. Subsequently, these offspring were used in investigations of the proximate mechanisms influencing behavioural and morphological variation during ontogeny (King & Turmo, 1997; Queral-Regil & King, 1998). Offspring of *S. dekayi* were weighed and measured for snout–vent length and total length within 48 h of birth and preserved ($n = 343$). Other variables (see below) were measured at a later date for up to 3 males and 3 females randomly selected from each family ($n = 145$).

Data on adult snakes came from individuals collected at the same study sites from which gravid females were collected (*S. dekayi*, *T. radix*, *T. sirtalis)* or from nearby study sites (*N. sipedon*). Mothers of captive born litters were included with other adults except for *N. sipedon*. Adult *N. sipedon*, *T. radix*, and *T. sirtalis* were captured, measured, and released. Adult *S. dekayi* were killed, eviscerated to obtain tissues for use in an analysis of genetic differentiation (R. King & R. Lawson, pers. obs.), and measured following preservation. Body mass was measured for only a subset of adult *S. dekayi* and so was omitted from analysis. Sample sizes for *N. sipedon* were 102 males and 50 females from 4 localities (South Bass Island, Middle Bass Island, North Bass Island, Kelleys Island); for *S. dekayi*: 58 males and 47 females from 3 localities (Pelee Island, North Bass Island, East Harbor); for *T. radix*: 33 males and 31 females from 1 locality; and for *T. sirtalis:* 55 males and 133 females from 4 localities (Winous Point, East Harbor, Middle Bass Island, Rattlesnake Island). Study sites from which *N. sipedon, S. dekayi,* and *T. sirtalis* were collected were separated by a maximum of 28.3 km. Neonate and adult *N. sipedon* differ in subspecies designation (*N. s. sipedon* and *N. s. insularum*, respectively), but these subspecies are not known to differ in characters other than colour pattern (Conant & Clay, 1937). *S. dekayi* included here represent neonates and a subset of the adults analysed previously (King, 1997).

Mass was determined on an electronic balance to the nearest 0.01 g. Snout–vent length (SVL) and total length (TL) were measured to the nearest mm by extending snakes along a ruler. Tail length was calculated by subtracting SVL from TL. Head dimensions were measured to the nearest 0.01 mm using digital callipers. Head length (HL) was measured from the posterior-most point of the parietal scales to the tip of the rostrum. Head width (HW) was measured at the widest point of the head. Jaw length (JL) was measured from the posterior edge of the posterior-most upper labial scale to the tip of the rostrum. Interocular distance (IO) was measured between the outermost edges of the

supraocular scales. An illuminated magnifier or dissecting microscope was used to aid in head measurements. Repeatability (Lessells & Boag, 1987) was computed for each variable from analysis of variance of replicate measurements of 12 *N. sipedon* neonates, 14 *S. dekayi* neonates, and 14 *S. dekayi* adults. Repeatability was generally high, exceeding 0.80 for all characters except HW and IO in *N. sipedon*, for which repeatability was 0.77 and 0.68, respectively.

Except as noted below, 2-factor mixed-model analysis of covariance (ANCOVA), multivariate analysis of variance (MANOVA), and multivariate analysis of covariance (MANCOVA) were used to test for sex and family differences in neonate morphology within each species. In all analyses, sex was treated as a fixed effect and family was treated as a random effect (we wished to draw inferences about the population of which the families included in our analysis represented a random sample). All variables were transformed by computing natural logarithms. This transformation served to improve homogeneity of variances and normality of error terms in all analyses and to linearize variate–covariate relationships and eliminate scale dependence of error terms in analyses of covariance. Three analyses were performed for each species: (1) a multivariate analysis of body size as reflected in SVL and mass, (2) a multivariate analysis of head dimensions with SVL as a covariate, and (3) a univariate analysis of tail length with SVL as a covariate. Including SVL as a covariate in the latter 2 analyses allows us to test for differences in head dimensions and tail length among families and between sexes while controlling for differences in body size. Analyses of covariance were preceded by tests confirming equality of slopes among cells (not shown). Full factorial analyses (including the sex-by-family interaction) were conducted for *S. dekayi* (body size, head dimensions, and tail length) and *T. sirtalis* (body size only). For head dimensions and tail length in *T. sirtalis*, there was significant heterogeneity among cells in the slope of the relationship between dependent variables and SVL; therefore, in this species mean head dimensions, mean tail length, and mean SVL were computed separately for males and females within each family and these means were analysed using MANCOVA (head dimensions) and ANCOVA (tail length) with sex as a factor and mean SVL as a covariate. Because the number of families was small for *N. sipedon* and *T. radix*, families were treated as blocks and the sex-by-family interaction was not tested in these species. (Denominator degrees of freedom for the fixed effect (e.g. sex) in a full factorial mixed-model ANOVA is determined by number of levels of the random effect (e.g. family). Consequently, testing the significance of sex using a full-factorial model would have little power for *N. sipedon* and *T. radix* (e.g. Zar, 1996: table 12.3).) The sex-by-family interaction was not significant for *S. dekayi* or *T. sirtalis* (see Results), suggesting that omitting it for the other species had no effect on our conclusions. Only live-born young were included and only families consisting of at least 2 offspring of each sex were analysed for *N. sipedon*, *T. radix*, and *T. sirtalis*. For *S. dekayi*, both live-born and still-born young were included; all families had at least 2 offspring of each sex except for 1 family with only 1 male. Neonates were born to females collected at 3 and 5 study sites for *S. dekayi* and *T. sirtalis,* respectively. As a consequence, family differences in offspring morphology may be inflated by differences among sites. Because our primary interest is in testing for sex differences in neonate morphology, possible site effects on neonate morphology were not tested (small sample sizes from some sites generally preclude formal tests for site effects on neonate morphology).

One-factor MANOVA, MANCOVA, and ANCOVA were used to test for sex differences in adult morphology in *T. radix*. Two-factor MANOVA, MANCOVA, and ANCOVA were used to test for sex and site differences in adult morphology in the other species. As with neonates, data on adults were transformed by computing natural logarithms and 3 analyses were performed for each species: (1) a multivariate analysis of body size (mass was not measured for adult *S. dekayi* so a univariate analysis of SVL was used to test for sex and site effects on body size), (2) a multivariate analysis of head dimensions with SVL as a covariate, and (3) a univariate analysis of tail length with SVL as a covariate. Analyses of covariance were preceded by tests confirming equality of slopes among cells (not shown). Size at adulthood was determined from size–frequency distributions and reproductive data for each species. Estimated size at adulthood was 430 mm and 590 mm SVL for male and female *N. sipedon* (King, 1986, and references therein; Weatherhead *et al.*, 1995), 160 mm and 230 mm SVL for male and female *S. dekayi* (King, 1993; 1997), 325 mm and 380 mm SVL for male and female *T. radix* (J. Cline & R. B. King, pers. obs.), and 360 mm and 460 mm SVL for male and female *T. sirtalis* (King, 1988, and references therein) (size–frequency histograms for *N. sipedon*, *S. dekayi*, and *T. sirtalis* can be found in King, 1986, 1997, and 1988, respectively).

SPSS 6.1 statistical software was used for all analyses. In multivariate analyses, Pillai's trace was used for significance testing. In all analyses, type III sums of squares were used and P values <0.05 were considered significant.

Indices of sexual dimorphism were calculated for each morphological trait for neonates and adults of each species. For SVL and mass, this index was computed as female mean/male mean (means back-transformed from natural logarithms). For head dimensions and tail length, indices of sexual dimorphism were calculated as follows. Regression equations relating female head dimensions and tail length to female SVL were obtained and used to compute expected head dimensions and tail length for a female with an SVL equal to the mean male SVL (using natural log transforms of all variables). These 'adjusted female' measurements were then divided by the corresponding means for males (both back-transformed from natural logarithms) to give an index of sexual dimorphism (following Shine, 1991).

Table 1. Means of morphological variables in neonatal and adult snakes (back-transformed from natural logarithms; mass in g, other variables in mm). Sexual dimorphism in SVL and mass was quantified by dividing mean female morphology by mean male morphology; sexual dimorphism in head dimensions and tail length was quantified by dividing 'adjusted female' morphology (the expected morphology of a female with SVL equal to mean male SVL) by mean male morphology

Species	Age class (sample size)	Sex	Snout–vent length	Mass	Head length	Head width	Jaw length	Inter-ocular	Tail length
Nerodia sipedon	Neonates	Male	178.9	4.78	10.6	6.3	10.0	5.2	59.6
	(n = 50 in	Female	180.5	5.02	10.8	6.5	10.3	5.3	52.0
	4 families)	'Adjusted female'			10.8	6.5	10.3	5.3	51.7
		Sexual dimorphism	1.01	1.05	1.02	1.03	1.03	1.02	0.87
	Adults	Male	686.9	164.58	21.3	15.3	24.0	9.2	210.2
	(n = 152)	Female	891.5	427.07	26.4	20.7	31.3	11.5	227.6
		'Adjusted female'			21.8	15.5	25.0	9.2	191.6
		Sexual dimorphism	1.30	2.59	1.02	1.01	1.04	1.00	0.91
Storeria dekayi	Neonates	Male	74.8	0.33	6.2	4.0	5.8	3.3	24.6
	(n = 145 in	Female	77.1	0.33	6.2	4.0	5.7	3.3	21.8
	25 families)	'Adjusted female'			6.1	4.0	5.7	3.2	21.3
		Sexual dimorphism	1.03	1.00	0.98	0.99	0.97	0.99	0.87
	Adults	Male	208.6	–	8.9	6.3	8.4	4.6	68.0
	(n = 105)	Female	266.8	–	9.3	7.1	9.4	4.7	67.7
		'Adjusted female'			8.2	6.3	8.3	4.2	53.5
		Sexual dimorphism	1.28	–	0.93	0.99	0.99	0.91	0.79
Thamnophis radix	Neonates	Male	130.5	1.37	8.8	5.3	8.5	4.2	40.0
	(n = 71 in	Female	132.8	1.39	9.0	5.4	8.8	4.3	37.6
	6 families)	'Adjusted female'			9.0	5.4	8.8	4.3	36.8
		Sexual dimorphism	1.02	1.02	1.02	1.02	1.04	1.01	0.92
	Adults	Male	407.7	34.11	14.0	9.8	14.5	6.8	117.6
	(n = 64)	Female	463.6	67.80	15.3	11.8	16.7	7.2	116.6
		'Adjusted female'			13.0	10.5	14.7	6.7	105.7
		Sexual dimorphism	1.14	1.99	0.93	1.08	1.01	0.99	0.90
Thamnophis sirtalis	Neonates	Male	138.4	1.57	9.3	5.6	9.4	4.5	41.2
	(n = 407 in	Female	136.6	1.57	9.5	5.8	9.6	4.6	36.8
	27 families)	'Adjusted female'			9.5	5.8	9.7	4.6	37.3
		Sexual dimorphism	0.99	1.00	1.02	1.03	1.03	1.03	0.91
	Adults	Male	450.8	46.47	16.1	11.4	17.6	7.4	135.8
	(n = 188)	Female	542.3	99.60	18.6	14.2	21.4	8.4	132.8
		'Adjusted female'			15.8	11.9	17.9	7.3	117.9
		Sexual dimorphism	1.20	2.14	0.99	1.04	1.02	0.99	0.87

RESULTS

Nerodia sipedon, S. dekayi, T. radix, and *T. sirtalis* differed markedly in size: mean neonate SVL of *S. dekayi* was less than half that of neonate *N. sipedon* and mean adult SVL of *S. dekayi* was less than one-third that of adult *N. sipedon* (Table 1). Differences in mass were even more extreme. Among neonates, significant family differences in body size, head dimensions, and tail length were present in all species (Table 2; family effects on head dimensions and tail length in *T. sirtalis* were reflected in significant heterogeneity among cells in the slope of the relationship between dependent variables and SVL as noted in Methods). Among adults, significant site differences in body size and head dimensions were present in *N. sipedon, S. dekayi,* and *T. sirtalis*, the three species for which multiple sites were sampled (Table 2). Significant site differences in tail length were present in *T. sirtalis* (Table 2). In addition, head dimensions and tail length covaried with SVL in neonates and adults of all four species (Table 2).

Among neonates, significant sex differences in body size were found in *S. dekayi* and *T. sirtalis* (Table 2); females exceeded males in SVL in *S. dekayi* whereas males exceeded females in SVL in *T. sirtalis* (Table 1). Significant sex differences in head dimensions (controlling for SVL) were found in *S. dekayi, T. radix,* and *T. sirtalis* (Table 2). In *S. dekayi*, males exceeded females in head dimensions whereas in *T. radix* and *T. sirtalis*, females exceeded males (Table 1). Sex differences in head dimensions of *N. sipedon* approached significance (P = 0.091). Significant sex differences in tail length (controlling for SVL) were found in all four species (Table 2) with males consistently exceeding females (Table 1).

Among adults, significant sex differences in body size were found in all four species (Table 2) with females consistently exceeding males (Table 1). Significant sex differences in head dimensions (controlling for SVL) were found in all four species (Table 2). In *N. sipedon*, females exceeded males in head dimensions whereas in *S. dekayi*, males exceeded females. In *T. radix* and *T. sirtalis*, males exceeded females in head length and interocular distance but females exceeded males in head width and jaw length (Table 1). Significant sex differences in tail length (controlling for SVL) were found in all four species (Table 2), with males consistently exceeding females (Table 1).

Table 2. Tests for sex effects on neonatal and adult snake morphology. Shown are *P* values from multivariate analysis of variance (body size), multivariate analysis of covariance (head dimensions), and univariate analysis of covariance (tail length). Measures of body size include SVL and mass. Measures of head dimensions include head length, head width, jaw length, and interocular distance. *P* values less than 0.05 are shown in bold. Mass was not available for adult *Storeria dekayi* so the body size analysis for this species refers to a univariate analysis of variance

Species	Age class	Source	Body size	Head dimensions	Tail length
Nerodia sipedon	Neonates	Covariate		**<0.001**	**<0.001**
		Sex	0.597	0.091	**<0.001**
		Family	**<0.001**	**0.019**	**0.033**
	Adults	Covariate		**<0.001**	**<0.001**
		Sex	**<0.001**	**0.015**	**0.019**
		Site	**0.020**	**0.003**	0.185
		Sex-by-site	**0.014**	0.218	0.980
Storeria dekayi	Neonates	Covariate		**0.008**	**<0.001**
		Sex	**<0.001**	**0.006**	**<0.001**
		Family	**<0.001**	**<0.001**	**0.004**
		Sex-by-family	0.338	0.788	0.819
	Adults	Covariate		**<0.001**	**<0.001**
		Sex	**<0.001**	**<0.001**	**<0.001**
		Site	**0.004**	**<0.001**	0.192
		Sex-by-site	0.133	0.398	0.964
Thamnophis radix	Neonates	Covariate		**0.026**	**<0.001**
		Sex	0.154	**<0.001**	**<0.001**
		Family	**<0.001**	**<0.001**	**0.004**
	Adults	Covariate		**<0.001**	**<0.001**
		Sex	**<0.001**	**<0.001**	**<0.001**
Thamnophis sirtalis	Neonates	Covariate		**<0.001**	**<0.001**
		Sex	**0.016**	**<0.001**	**<0.001**
		Family	**<0.001**		
		Sex by family	0.061		
	Adults	Covariate		**<0.001**	**0.003**
		Sex	**<0.001**	**<0.001**	0.051
		Site	**<0.001**	**0.001**	**0.036**
		Sex-by-site	0.076	0.610	0.769

Among neonates, the degree of sexual dimorphism was low for body size and head dimensions (indices of sexual dimorphism were close to 1; Table 1), but somewhat greater for tail length (index of sexual dimorphism = 0.87–0.92; Table 1). As in neonates, the degree of sexual dimorphism was low for head dimensions and somewhat greater for tail length in adults; in contrast, the degree of sexual dimorphism in body size of adults was large (Table 1).

DISCUSSION

Among the neonate natricine snakes included in this study, significant sexual dimorphism was found in body size (two of four species), head dimensions (three of four species), and tail length (four of four species). Importantly, sex differences were found via analyses that accounted for potential differences in morphology among families. Somewhat different results may be obtained if family membership is ignored. For example, differences in SVL between male and female *S. dekayi* neonates only approached significance when analysed using a one-factor ANOVA ($F_{1,143} = 3.73$, $P = 0.055$), but were highly significant when family membership was included as a factor ($P < 0.001$, Table 2). Further evidence of the value of incorporating family membership into analyses such as ours is seen in the highly significant differences in neonate body size, head dimensions, and tail length that were found among families in all four species. This variation among families probably has at least two sources. One of these is the common pre-natal environment shared by siblings: both female size and number of offspring can influence neonate body size in snakes (e.g. King, 1993). The other is genetic: variation among families in at least some morphological characters (e.g. head length and tail length in *S. dekayi*; King, 1997) can be attributed to differences in genotype.

Among adults, significant sexual dimorphism was found in body size, head dimensions, and tail length of all four snake species included in this study. For body size, sexual dimorphism was most apparent in mass with adult females outweighing adult males by a factor of two or more (Table 1). Part of this difference in male and female body mass is likely due to the inclusion of gravid females in our analysis. However, univariate analyses (not shown) reveal significant sex differences in adult SVL in all four species, indicating that males and females truly differ in overall body size (Table 1, Fig. 1). Although sexual dimorphism in adult snakes is well known (e.g. Fitch, 1981; King, 1989; Shine, 1991, 1993, 1994), the availability of data on both neonates and adults allows us to describe ontogenetic changes in

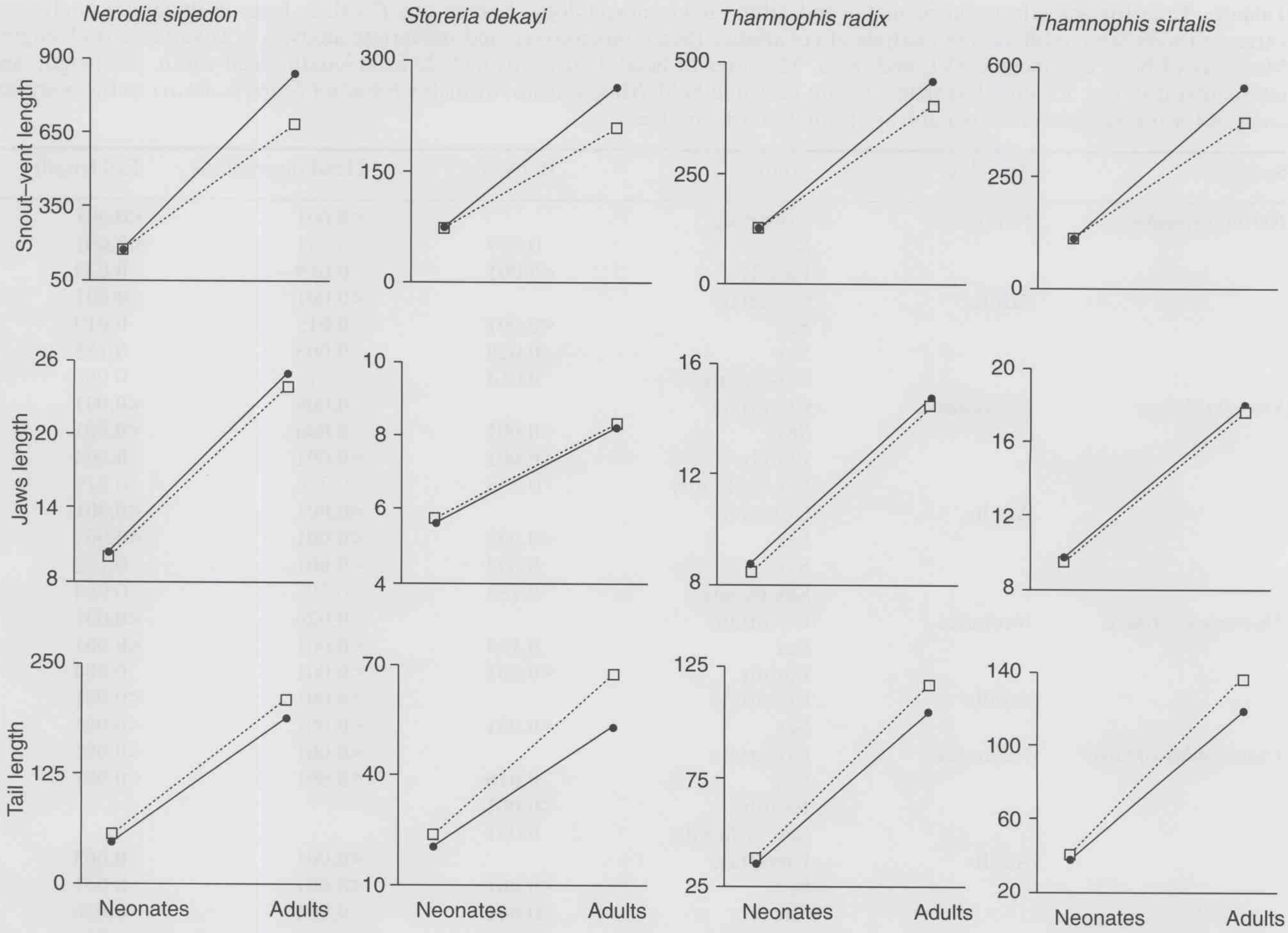

Fig. 1. Ontogenetic patterns of sexual dimorphism in four natricine snakes. Males, dotted lines and squares; females, solid lines and dots. In this figure sexual dimorphism in body size is characterized by SVL and sexual dimorphism in head dimensions by jaw length. For SVL, means of neonate and adult males and females (back-transformed from natural logarithms) are plotted. For jaw length and tail length, means of neonate and adult males and 'adjusted female' values are plotted, thus controlling for differences in body size between males and females. All measurements are in mm. Numerical values can be found in Table 1. Because adult males and females may differ in age (see text), lines do not represent growth trajectories.

sexual dimorphism for the four species included here. Interestingly, different patterns of ontogeny distinguish sexual dimorphism in body size, head dimensions, and tail length but these patterns appear relatively consistent among species (Table 1, Fig. 1). Sexual dimorphism in body size, though sometimes statistically significant, is slight among neonates but increases dramatically by adulthood. For example, the degree of sexual dimorphism in SVL increases by 0.12 in *T. radix* and 0.29 in *N. sipedon* in going from neonates to adults (Table 1). Sexual dimorphism in head dimensions is also slight (though statistically significant) among neonates and remains relatively unchanged in magnitude as snakes mature. For example, the maximum change in our index of sexual dimorphism in jaw length in going from neonates to adults is just 0.03 (in *T. radix*) (Table 1, Fig. 1). Sexual dimorphism in tail length is more evident among neonates than is sexual dimorphism in body size or head dimensions. Modest changes in the degree of sexual dimorphism in tail length occur as snakes mature with a maximum change in our index of sexual dimorphism in tail length of 0.08 in going from neonates to adults (in *S. dekayi*) (Table 1, Fig. 1).

The dramatic ontogenetic increase in sexual dimorphism in body size may have several proximate causes, including differences in growth rate, age at maturity, and adult survivorship (Shine, 1993; Stamps, 1993). Sex differences in growth rate and age at maturity occur in many snakes (Andrews, 1982) and likely relate to sex differences in the fitness consequences of body size. Fecundity generally increases with increasing female body size in snakes (Seigel & Ford, 1987), while in species that do not exhibit male combat (including the four species in this study), mating success appears unrelated to male body size (Shine, 1993, 1994; but see Luiselli, 1996). As a consequence, delayed sexual maturity and accelerated growth rates in females relative to males may be favoured and could contribute to the sex differences in body size seen among adults. Differences in food assimilation efficiencies and energy allocation patterns apparently contribute to sex differences in growth in water snakes (Scudder-Davis & Burghardt,

Table 3. Sexual dimorphism in neonatal and adult snakes for body size and head dimensions. For neonates, the larger sex is indicated for species in which there is a statistically significant sex difference. Whether statistical analysis accounted for family differences in morphology is indicated in the column 'Family effect included?' For adults, the direction of sexual dimorphism is indicated but is frequently not based on statistical tests. A dash indicates missing data

Species	No. of offspring	No. of families	Family effect included?	Larger sex		Reference
				Neonates	Adults	
Body size						
Acrochordidae						
Acrochordus arafurae	37	2	no	females	females	Shine, 1986
Elapidae						
Acanthophis antarcticus	42	2	no	females	females[a]	Johnston, 1987
Notechis scutatus	22	2	no	=	males[a]	Shine & Bull, 1977
Viperidae						
Bothrops asper	305	43	no	females	females	Solórzano & Cerdas, 1989
Crotalus viridis	143	14	no	=	males	Macartney & Gregory, 1988
Porthidium picadoi	59	2	no	=	=	Solórzano, 1990
Sistrurus miliarius	145	27	no	=	=	Bishop, Farrell & May, 1996
Trimeresurus flavoviridis	201	62	no	males	males[b]	Nishimura & Kamura, 1993
Vipera berus	228	38	no	=	females[b]	Madsen & Shine, 1992
	117	17	no	=		Madsen & Shine, 1992
Colubridae						
Carphophis vermis	22	–	no	females	females	Clark, 1970
Coronella austriaca	122	28	no	=	females[b]	Luiselli, Capula & Shine, 1996
Diadophis punctatus	83	21	no	females	females	Fitch, 1975
Elaphe obsoleta	45	4	yes	=	males[a]	Clark & Pendleton, 1995
Nerodia sipedon	318	14	yes	females	females	Weatherhead *et al.*, 1995
	50	4	yes	=	females	This study
Opheodrys aestivus	141	40	no	=	females[b]	Plummer, 1984
Regina grahamii	54	4	yes	males	females	Seigel, 1992
R. septemvittata	128	10	no	=	females	Branson & Baker, 1974
Seminatrix pygaea	20	3	no	=	females[a]	Seigel, Loraine & Gibbons, 1995
Storeria dekayi	343	25	yes	females	females	This study
Thamnophis butleri	41	2	no	males	=[a]	Lyman-Henly & Burghardt, 1995
T. elegans	57	6	no	=	females	Gregory & Prelypchan, 1994
T. radix	71	6	yes	=	females	This study
T. sirtalis	202	8	no	=	females	Crews *et al.*, 1985
	182	14	no	=	females	Gregory, 1977
	67	2	no	=		Lyman-Henly & Burghardt, 1995
	65	9	no	=		Arnold & Peterson, 1989
	407	27	yes	males	females	This study
Tropidoclonion lineatum	14	1	–	=	females[a]	Funk & Tucker, 1978
Head dimensions						
Acrochordidae						
Acrochordus arafurae	37	2	no	females	females	Shine, 1986
Elapidae						
Pseudechis porphyriacus	–	–	–	males	males[a]	Shine, 1991
Viperidae						
Sistrurus miliarius	145	27	no	=	=	Bishop *et al.*, 1996
Trimeresurus flavoviridis	67	62	no	males		Nishimura & Kamura, 1993
Colubridae						
Nerodia erythrogaster	–	–	–	females	females[a]	Shine, 1991
N. rhombifera	–	–	–	females	females[a]	Shine, 1991
N. sipedon	50	4	yes	=	females	This study
Storeria dekayi	145	25	yes	males	males	This study
Thamnophis radix	71	6	yes	females	males/females[c]	This study
T. sirtalis	65	9	no	=	females[a]	Arnold & Peterson, 1989
	24	1	–	females		Shine & Crews, 1988
	121	–	no	females		Shine & Crews, 1988
	407	27	yes	females	males/females[c]	This study
Tropidoclonion lineatum[d]	14	1	–	=	males	Funk & Tucker, 1978

[a] Data on direction of sexual dimorphism in adults comes from Shine (1991: table 1).
[b] Data on direction of sexual dimorphism in adults comes from Shine (1994: appendix 1).
[c] Direction of sexual dimorphism varies among characters (see text).
[d] Data from original source analysed by us for this table.

1996). However, as Shine's (1993) review makes clear, details of the proximate mechanisms and fitness consequences of body size dimorphism in snakes are known for remarkably few species.

In contrast to sexual dimorphism in body size, we found that sexual dimorphism in head dimensions changes little with ontogeny. This result suggests that an understanding of proximate mechanisms of sexual dimorphism in these characters might profitably focus on neonates. Experiments by Shine & Crews (1988) with *T. sirtalis* suggest that the post-natal maintenance of sexual dimorphism in head dimensions is due to an inhibitory effect of testosterone on growth in relative head dimensions in males: castrated males developed longer jaws than did intact males or castrated males that received testosterone-containing implants. The presence of sexual dimorphism in relative head dimensions among neonates suggests that this effect of testosterone may begin during pre-natal development. Diet-induced phenotypic plasticity may also contribute to individual and sex differences in head morphology (Queral-Regil & King, 1998; but see Forsman, 1996*b*).

Efforts to understand the fitness consequences of sexual dimorphism in head dimensions might also profitably focus on neonates. Because snakes swallow their prey whole, gape size (and thus head dimensions) sets an upper limit on prey size (Arnold, 1993; Forsman & Lindell, 1993). This limitation may be especially significant to neonates which, because of small overall body size, are already severely limited in size of prey they can subdue and swallow. As a consequence, neonates might be expected to experience stronger selection on those characters determining swallowing capacity than are adults (Forsman, 1996*a*). The fact that head dimensions show negative allometry in relation to body size (e.g. in *S. dekayi*, jaw length decreases from 7.4% of SVL in neonatal females to 3.5% of SVL in adult females, Table 1) may reflect the greater functional significance of gape size to neonates. Given this functional significance, why relative head dimensions should differ between male and female neonates remains unclear. One possibility is that statistical significance does not reflect biological significance. For example, sexual dimorphism in relative jaw length may have little impact on swallowing performance and might arise as an indirect consequence of selection favouring different adult body sizes in males and females; inhibition of growth in males by testosterone may provide a simple proximate mechanism to achieve this difference in body size but might also produce dimorphism in other traits (King, 1997). Detailed studies of swallowing performance, feeding ecology, and morphology of young snakes would be useful in understanding the fitness consequences of head dimorphism.

In contrast to the snakes included in this study, some lizards show a marked increase in sexual dimorphism in head dimensions with ontogeny (e.g. Vitt & Cooper, 1985; Cooper & Vitt, 1989; Mouton & van Wyk, 1993). Much of this divergence in lizard head dimensions occurs with the onset of sexual maturity and involves both an increase in head growth in males relative to juveniles and a decrease in head growth in females relative to juveniles. This pattern apparently reflects sexual selection for increased head size in males, which are territorial and interact aggressively, and natural selection for increased body size (and hence reproductive output) in females. Neither of these processes appear to contribute to head dimorphism in the snakes we studied. Males do not interact aggressively and, with the exception of *S. dekayi*, relative head dimensions of adult females exceed those of adult males. Data on the ontogeny of head dimorphism in snakes that do exhibit aggressive male–male interactions would be of interest. However, a qualitative examination of data compiled by Shine suggests that there is no association between the direction of head dimorphism in adult snakes (Shine, 1991: table 1) and the presence or absence of male combat (Shine, 1994: appendix 1).

Tail length shows a greater degree of sexual dimorphism among neonates of the species we studied than does body size or head dimensions. Dimorphism in tail length is associated with differences in numbers of subcaudal scales and tail vertebrae (e.g. King, 1997). Among species of snakes, patterns of tail length dimorphism are consistent with two hypotheses; the morphological constraint hypothesis, which posits that minimum tail length in males is constrained by the presence of male reproductive structures, and the female reproductive output hypothesis, which posits that females have relatively shorter tails because of natural selection for increased reproductive capacity (King, 1988; Shine, 1993). Under the latter hypothesis, females might be expected to devote greater energy to increases in body size and less energy to increases in tail length. Hence, the degree of tail length dimorphism should increase ontogenetically (King, 1988). Interestingly, Scudder-Davis & Burghardt (1996) have demonstrated just such an allocation pattern in a growth study of three species of water snakes. Our results provide additional support for sex differences in tail length ontogeny in that we found modest ontogenetic increases in tail dimorphism in three of the four species included in our analysis (Table 1, Fig. 1). Further evidence of such sex differences are found in Klauber's analysis of the relationship between tail length and total length: allometric coefficients of males exceed those of females in 14 of 17 species (Klauber, 1943: table 12).

Patterns of sexual dimorphism have been described for neonates of a variety of snake species but in relatively few studies has family membership been included in statistical analyses (Table 3). Thus, while significant sexual dimorphism in body size or head dimensions is apparent among neonates from about half these studies, we urge caution in interpreting these results. Keeping this caveat in mind, two general patterns emerge from our review of sexual dimorphism in neonate and adult snakes (Table 3). One common pattern is for sexual dimorphism to be present in the same direction in both neonates and adults. The other pattern is for sexual dimorphism to be absent among neonates but present among adults. In only rare instances does sexual

dimorphism appear to be present among neonates but not adults (e.g. body size in *Thamnophis butleri*; Table 3) or to be present in opposite directions in neonates and adults (e.g. body size in *Regina grahamii* and *T. sirtalis*, some head dimensions in *T. radix* and *T. sirtalis*; Table 3). Our review also reveals evidence that sexual dimorphism in neonates may be present in some populations but not others (e.g. body size in *Nerodia sipedon*, body size and head dimensions in *T. sirtalis*; Table 3). Unfortunately, data on sexual dimorphism among neonates are lacking for many species and those data that are available are biased toward temperate-zone colubrids and toward species in which females are larger as adults. Data from other taxonomic groups and from species showing other patterns of dimorphism among adults are needed.

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