Evidence for Phenotypic Plasticity in Snake Body Size and Relative Head Dimensions in Response to Amount and Size of Prey

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To test whether variation in body size and relative head dimensions may be a phenotypically plastic response to feeding experience in snakes, we assigned neonate water snakes, *Nerodia sipedon*, from four litters (n = 48) to two feeding treatment groups. One group was offered one large minnow twice weekly; the other group was offered two small minnows twice weekly. Body size (snout–vent length, mass) and head dimensions (head length, head width, jaw length, interocular distance) were measured at the beginning of the experiment and upon completion of the experiment 20 weeks later. Repeated-measures multivariate analysis of variance revealed significant effects of feeding treatment, sex, and family on change in body size. Repeated-measures MANCOVA (with body length as covariate) also revealed a significant effect due to family on change in head dimensions. The multivariate effect of feeding treatment on head dimensions approached statistical significance ($P = 0.102$); the univariate effect of feeding treatment was significant for jaw length ($P = 0.010$). Females increased in body size more than males did, and snakes offered large fish increased in body size and jaw length more than snakes offered small fish. These results suggest that body size and jaw length respond plastically to amount and size of prey.

SEXUAL dimorphism and geographic variation in body size and head dimensions have been documented in many snake species (e.g., Benton, 1980; Fitch, 1981; King, 1989). Sexual dimorphism in body size may evolve by means of sexual selection (Darwin, 1871; Shine, 1993; Reynolds and Harvey, 1994). For example, males tend to be the larger sex in snake species in which male-male combat occurs, whereas females are usually the larger sex in species lacking male combat (Shine, 1978). However, sexual selection is unlikely to explain sexual dimorphism in head dimensions: unlike some lizards, snakes do not bite during combat, nor do they use their heads in elaborate visual displays. An ultimate explanation for sex differences in head dimensions may be that preexisting differences in body size (perhaps resulting from sexual selection) allow each sex to use different prey types, and subsequently experience different selection pressures on head dimensions (Slatkin, 1984; Shine, 1986; Camilleri and Shine, 1990). Geographic variation in body size and head dimensions is most often associated with variation in the size of available prey (e.g., *Notechis ater*, Barnett and Schwaner, 1985; *Vipera berus*, Forsman, 1991; *Natrix natrix*, Madsen and Shine, 1993). Typically, snakes are larger and have relatively larger heads where prey are large (e.g., Forsman, 1991). Because older snakes tend to be larger, demographic differences may also contribute to geographic variation in body size (King, 1989).

Phenotypically plastic responses to ecological variables such as prey size and availability may result in differences in body size and in trophic structures. For example, differences in body size between insular and mainland populations of the European grass snake (*N. natrix*) appear to be phenotypically plastic responses to differential food availability (Madsen and Shine, 1993). Diet-induced phenotypic plasticity of trophic structures has been documented in fishes (e.g., Meyer, 1987; Day et al., 1994; Robinson and Wilson, 1995) and mammals (e.g., Moore, 1965; Myers et al., 1996). However, we know of only a single study that has tested for phenotypically plastic responses of head dimensions in reptiles. Forsman (1996) reared captive adders (*V. berus*) on two feeding regimes (one mouse every fifth day vs one mouse weekly) and found that feeding frequency had an effect on growth rate in body size but not on relative head length. However, prey size was similar between treatments (mean prey mass = 2.7 g vs 2.3 g, respectively). Thus, Forman's experiment is primarily a test for phenotypic plasticity of head size in response to feeding frequency (and hence growth rate) and not prey size. Similarly, Arnold and Peterson (1989) demonstrated that relative head size was unaffected by growth rate in garter snakes (*Thamnophis sirtalis*) raised under three different temperature regimes.

To test for phenotypic plasticity in relative head dimensions in response to prey size, we raised newborn northern water snakes (*Nerodia*

sipedon) on two feeding regimes: one large prey per feeding and two small prey per feeding. Male and female siblings from four litters were assigned to treatments at random in a factorial design. Thus, our design allows for tests of the effect of prey size on body size and relative head dimensions while controlling for differences between the sexes and among litters.

MATERIALS AND METHODS

We collected four gravid female *N. sipedon* in Ottawa County, Ohio, on 8 August 1995, and maintained them in the laboratory until parturition between 21 August and 8 September 1995. Females were kept in individual cages and offered food and water ad libitum during gestation. Neonates (n = 48; 6–17 per litter) were housed in individual cages (33 × 18 × 10 cm) lined with paper towels and provided water ad libitum. The room in which snakes were housed was maintained at 26–28 C with a 12:12 L:D photoperiod.

Snakes were assigned to one of two food size treatment groups at random within sexes within families. Snakes in the LARGE treatment group were offered one large fish per feeding (range = 1.6–3.0 g); snakes assigned to the SMALL treatment group were offered two small fish per feeding (range = 0.5–1.2 g per fish). Both groups were offered food twice per week. Number of fish consumed (0, 1, or 2) was scored after 24 h. Number and size of fish were selected so that all snakes were offered approximately the same mass of food at each feeding. However, because of variation in size of fish available (*Pimephales promelas*, obtained from a local bait retailer) and in number of fish consumed, snakes in the SMALL treatment group ingested less prey biomass than did snakes in the LARGE treatment group (see Results).

Snakes were weighed and measured 48 h prior to the onset of the experiment and again 20 weeks later upon completion of the experiment. 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 millimeter by extending the snake along a ruler. Head dimensions were measured to the nearest 0.01 mm with digital calipers. Head length (HL) was defined as the distance from the posteriormost point of the parietal scales to the tip of the rostral scale. Head width (HW) was measured at the hinges of the jaws. Jaw length (JL) was measured from the posterior edge of the posteriormost labial scale to the tip of the rostral on the right side of the head. Interocular distance (IO) was defined as the distance between the outermost edges of the supraocular scales, above the eyes. Body length (BL) was calculated by subtracting HL from SVL. Snakes were 18–36 days old at the start of the experiment. Prior to the start of the experiment, each snake had been fed one to three times. After completion of the experiment, 12 individuals were selected at random and measured twice to determine repeatability of morphological measurements by analysis of variance (Lessells and Boag, 1987). Repeatability is an estimate of the between-subjects component of variance (Sokal and Rohlf, 1995).

Repeated-measures multivariate analysis of variance was used to test for effects of sex, litter, and prey size on snake body size. All measurements were natural-log transformed to meet the assumption of homoscedasticity in analyses of variance and covariance. Initial and final SVL and initial and final mass were dependent variables; sex, litter, and treatment were between-subjects factors; and time of measurement (initial and final) was a within-subjects factor. In this analysis, a significant between-subjects effect indicates a difference in size over the entire course of the experiment. Such a difference could be the result of a difference in size at the beginning of the experiment, a difference in growth over the 20 weeks, or both. A significant within-subjects effect (e.g., treatment-by-time) is a more interesting result because it indicates an unambiguous difference in growth over the course of the experiment. Repeated-measures multivariate analysis of covariance was used to test for effects of sex, litter, or prey size on relative head dimensions over the 20 weeks of the experiment. Initial head dimensions (with initial BL as a covariate) and final head dimensions (with final BL as a covariate) were dependent variables; sex, litter, and treatment were between-subjects factors; and time was a within-subjects factor. By using initial and final BL as covariates for initial and final head dimensions, we statistically removed the effect of changes in body length on changes in head dimensions over the course of our experiment. Thus, a significant within-subjects effect in this analysis (e.g., treatment-by-time) indicates an unambiguous difference in size-independent growth in head dimensions.

Small litter size (there were no females in the SMALL treatment for one litter) precluded testing the litter-by-sex-by-treatment interaction. However, this interaction was nonsignificant when tested using data from the three other litters ($F_{4,60} = 0.0856$, $P = 0.615$ for body size; $F_{8,54} = 0.3342$, $P = 0.238$ for head dimensions). In addition, to maximize statistical power for de-

TABLE 1. ADJUSTED MEAN BODY SIZE AND MEAN RELATIVE HEAD DIMENSIONS FOR MALE AND FEMALE SNAKES IN THE LARGE AND SMALL TREATMENT GROUPS AT THE BEGINNING AND AT THE END OF THE EXPERIMENT (20 WEEKS). Snout-to-vent length (mm) and mass (g) were adjusted for litter differences (using the P-means option of MANOVA in SPSS 6.1). Head dimensions (mm) were adjusted for body length and litter differences and, thus, represent the expected head dimensions of snakes of average body length at the start (males: 190.65 mm; females: 193.10 mm) and at the end (males: 307.52 mm; females: 337.54 mm) of the experiment.

Sex	Prey size	n	SVL (adj.)		Mass (adj.)		HL (adj.)		HW (adj.)		JL (adj.)		IO (adj.)	
			Start	End	Start	End	Start	End	Start	End	Start	End	Start	End
Male	Small	10	189.73	294.47	4.98	14.19	10.51	12.54	6.15	6.75	10.19	12.69	4.98	5.76
	Large	8	191.57	320.56	5.18	18.78	10.60	12.65	6.31	7.06	9.87	13.09	5.02	5.76
Female	Small	15	193.27	324.77	5.48	18.00	10.83	12.92	6.48	6.83	10.54	13.49	5.18	6.00
	Large	15	192.93	350.31	5.27	23.51	10.73	13.06	6.25	7.14	10.40	13.55	5.24	6.15

tecting treatment and sex effects, litters were treated as blocks and litter-by-sex and litter-by-treatment interactions were not tested. Pillai's trace was used for significance testing in multivariate analyses with $\alpha = 0.05$. Analyses were carried out using SPSS for Windows, version 6.1 (M. J. Norusis, 1993, unpubl.).

RESULTS

Snakes averaged 192.2 ± 11.8 mm SVL (mean $\pm$ SD) and 5.33 ± 1.11 g at the start of the experiment and increased to a mean of 327.7 ± 34.8 mm SVL and 19.52 ± 6.05 g at 20 weeks; head dimensions increased proportionately (Table 1). Repeatability of morphological measurements was generally high (SVL: 0.99; mass: 0.99; HL: 0.97; HW: 0.77; JL: 0.80; IO: 0.68), indicating that, for example, only 1% of the variability in SVL may be attributed to measurement error.

There were significant between-subjects and within-subjects effects of litter, sex, and treatment on body size (Table 2A). The within-subjects effects indicate that members of different litters grew at different rates, females grew faster than males, and snakes in the LARGE treatment group grew faster than snakes in the SMALL treatment group. A three-way ANOVA revealed significant differences in the proportion of fish consumed over the entire course of the experiment among litters ($F_{3,39} = 3.43$, $P = 0.026$), between males and females ($F_{1,39} = 4.96$, $P = 0.032$), and between treatment groups ($F_{1,39} = 20.33$, $P < 0.001$; all interactions were nonsignificant at $P > 0.05$). Snakes in the SMALL treatment frequently ate only one of the two fish offered each feeding, consuming a mean of 38 fish per snake over the course of the 20 weeks. Snakes in the LARGE treatment ate a smaller number of fish, consuming a mean of 34 fish per snake over the course of 20 weeks; however, since these fish were larger, snakes in

the LARGE treatment group consumed approximately twice the prey mass of snakes in the SMALL treatment. Male snakes consumed a mean of 34 fish per snake, whereas females consumed a mean of 37 fish per snakes over the course of 20 weeks. Thus, the significant between-subjects and within-subjects effects of litter, sex, and treatment on body size (described above) could be attributed to differences in total biomass consumed.

Head dimensions covaried positively with BL (Table 2B). There were significant between-subjects effects of litter and sex and a significant within-subjects effect of litter on head dimensions. There was a significant within-subjects effect of time on head dimensions, reflecting a decrease in head dimensions relative to SVL over the course of the experiment (e.g., JL decreased from about 5% of SVL at the beginning of the experiment to about 4% of SVL at the end of the experiment).

Diet-induced plasticity in head dimensions, reflected in the within-subjects effect of treatment, approached significance ($P = 0.102$, Table 2B). Our test for the treatment-by-time interaction effect on head dimensions had only moderate power: with $\alpha = 0.05$, there was a 44% chance of committing a type II error and falsely concluding that treatment had no effect on growth in head dimensions; increasing α to 0.1 reduced this risk to 31%. In addition, partial correlations among head dimensions (controlling for BL, litter, sex, and treatment), although mostly significant, were only of moderate magnitude, ranging from 0.29–0.47. For these reasons, we also conducted univariate analyses of the four measurements of head size. Consistent with our multivariate results, there was a significant litter-by-time effect on HW and JL (Table 3). In addition, there was a significant treatment-by-time effect on JL (Table 3): snakes in the LARGE treatment group had longer jaws

TABLE 2. RESULTS OF REPEATED MEASURES MULTIVARIATE ANALYSIS OF VARIANCE AND COVARIANCE TESTING FOR DIFFERENCES IN BODY SIZE (A), AND RELATIVE HEAD DIMENSIONS (B). In (B) body length was used as a covariate to control for differences in body size among snakes (see text). Statistically significant effects are shown in bold.

Source of variation	Pillai's trace	F	df	P
(A) Body size				
Between-subjects				
Litter	1.08	15.98	6, 82	**< 0.001**
Sex	0.21	5.14	2, 40	**0.010**
Treatment	0.19	4.63	2, 40	**0.016**
Sex-by-treatment	0.34	0.69	2, 40	0.505
Within-subjects				
Time	0.99	1466.97	2, 40	**< 0.001**
Litter-by-time	0.30	2.43	6, 82	**0.033**
Sex-by-time	0.31	9.11	2, 40	**0.001**
Treatment-by-time	0.43	15.27	2, 40	**< 0.001**
Sex-by-treatment-by-time	0.04	0.87	2, 40	0.425
(B) Head size				
Between-subjects				
Covariate (BL)	0.63	15.58	4, 37	**< 0.001**
Litter	0.53	2.13	12, 117	**0.020**
Sex	0.44	7.36	4, 37	**< 0.001**
Treatment	0.07	0.70	4, 37	0.597
Sex-by-treatment	0.05	0.46	4, 37	0.764
Within-subjects				
Covariate (BL)	0.41	6.34	4, 37	**0.001**
Time	0.23	2.82	4, 37	**0.039**
Litter-by-time	0.83	3.74	12, 117	**< 0.001**
Sex-by-time	0.09	0.86	4, 37	0.495
Treatment-by-time	0.18	2.09	4, 37	0.102
Sex-by-treatment-by-time	0.13	1.38	4, 37	0.260

TABLE 3. RESULTS OF REPEATED-MEASURES UNIVARIATE ANALYSIS OF COVARIANCE (WITH BODY LENGTH AS THE COVARIATE) FOR THE INDIVIDUAL HEAD DIMENSIONS (ONLY P-VALUES ARE SHOWN). STATISTICALLY SIGNIFICANT EFFECTS ARE SHOWN IN BOLD.

Source of variation	df	Head length	Head width	Jaw length	Interocular
Between-subjects					
Covariate (BL)	1, 40	**< 0.001**	**0.001**	**< 0.001**	0.181
Litter	3, 40	**0.050**	**0.011**	0.361	0.294
Sex	1, 40	**0.002**	0.352	**< 0.001**	**< 0.001**
Treatment	1, 40	0.929	0.252	0.692	0.400
Sex-by-treatment	1, 40	0.424	0.238	0.734	0.649
Within-subjects					
Covariate (BL)	1, 40	**< 0.001**	**0.029**	**0.032**	0.197
Time	1, 40	0.868	0.170	0.060	0.582
Litter-by-time	3, 40	0.174	**< 0.001**	**0.025**	0.193
Sex-by-time	1, 40	0.168	0.581	0.638	0.520
Treatment-by-time	1, 40	0.129	0.161	**0.010**	0.841
Sex-by-treatment-by-time	1, 40	0.503	0.370	0.167	0.507

(controlling for BL) than did snakes in the SMALL treatment group (see Table 1). This effect remained significant even after Bonferroni adjustment of α-levels for the fact that four separate analyses (on HL, HW, JL, and IO) were conducted (Sokal and Rohlf, 1995).

DISCUSSION

This study revealed a significant effect of prey size and amount of food ingested on growth in snake body size and relative head dimensions, suggesting that phenotypic plasticity in these traits may contribute to patterns of morphological variation observed in nature. Although phenotypically plastic responses of the jaw and skull have been documented for other taxa (e.g., Wimberger, 1991; Day et al., 1994; Myers et al., 1996), few experiments have tested for a phenotypically plastic response of the trophic apparatus to feeding regime in snakes. Forsman (1996) found that adders (*V. berus*) raised on high versus low food levels grew at different rates. However, he found no effect of treatment on relative head dimensions of snakes of the same age, nor on the growth trajectories of relative head size. A key difference between our experiment and Forsman's is that we assigned snakes to treatments differing in prey size, whereas Forsman assigned snakes to treatments differing mostly in feeding frequency. In the present study, snakes in the large fish treatment group had significantly higher growth rates for relative jaw length (growth in JL controlling for growth in BL) than did snakes in the small fish treatment group. Increased mechanical stress on the mandibular unit during swallowing of large prey may explain the plastic response of the jaw to the LARGE fish treatment (Rubin and Lanyon, 1984; Emerson and Bramble, 1993). Elongation of the jaw relative to body length may allow snakes to ingest larger prey (Pough and Groves, 1983; Forsman and Lindell, 1993). Therefore, phenotypic plasticity in jaw length may be adaptive when prey size varies spatially or temporally (Travis, 1994). An experiment comparing swallowing performance of diet-induced morphotypes may help answer this question. Since snakes in the LARGE treatment group in our experiment ate more biomass than did snakes in the SMALL treatment group, the effect of prey size on relative head dimensions is potentially confounded by the differences in the amount of food consumed. However, the lack of an effect of growth rate on relative head dimensions in *T. sirtalis* and *V. berus* (Arnold and Peterson, 1989; Forsman, 1996) suggest that prey size (not total prey biomass) is responsible for the observed plasticity in jaw length.

Growth in body size also showed a phenotypically plastic response to treatment: snakes in the large fish treatment group showed a greater increase in body size than did snakes in the small fish treatment group. Comparable results were obtained by Madsen and Shine (1993), who found that island and mainland *N. natrix* grew at similar rates when fed the same amounts of food, suggesting that body size differences in nature (island snakes are smaller than mainland snakes) are a phenotypically plastic response to prey availability. Differences among litters in growth rate may reflect inherited differences in patterns of nutrient assimilation or satiation. As in this study, differences in growth rate among litters of *Thamnophis elegans* were associated with differences in number of fish eaten (Gregory and Prelypchan, 1994). Differences between males and females in growth rate may also reflect differences in satiation patterns or assimilation efficiencies (Shine, 1993). In this study, male snakes ate a significantly lower proportion of fish than did female snakes. Sex differences in growth rate have been attributed to inhibitory effects of androgens on body growth in male *T. sirtalis* (Crews et al., 1985; Shine and Crews, 1988). However, no difference in growth rate was found between male and female *T. elegans* (Gregory and Prelypchan, 1994).

In this experiment, the effects of prey size on head dimensions were not clear cut (the multivariate analyses only approached statistical significance, whereas the univariate analysis suggests prey size had a significant effect on relative jaw length). Furthermore, the effect of prey size on relative head dimensions may be confounded with differences in total prey mass consumed. Regardless, our results suggest that phenotypic plasticity may contribute to patterns of geographic variation and sexual dimorphism observed in nature. Previous studies have demonstrated that differences in body size (Schwaner, 1985; Shine, 1987) and head shape (Forsman, 1991; Grudzien et al., 1992) between island and mainland snake populations correlate with differences in prey availability between sites and that sexual dimorphism in body size and head dimensions may result in different patterns of resource use by males and females (Shine, 1986). However, it is unknown what role phenotypic plasticity plays in determining patterns of sexual and geographic variation. Future studies must consider the degree to which variation in snake head dimensions is influenced by genetic differences versus plastic responses to

prey characteristics. The possibility that phenotypic plasticity contributes to sexual and geographic variation contrasts with the conclusions of Forsman (1996) and Forsman and Shine (1997) and suggests that further experiments such as ours, coupled with "common garden" experiments (e.g., Madsen and Shine, 1993), and heritability estimates (King, 1997) may help distinguish between these alternatives.

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