J. Zool., Lond. (2005) **267**, 363–369 © 2005 The Zoological Society of London Printed in the United Kingdom doi:10.1017/S0952836905007624

Does prey size induce head skeleton phenotypic plasticity during early ontogeny in the snake *Boa constrictor*?

Gordon W. Schuett[1,2]*, David L. Hardy Sr[1], Ryan L. Earley[2] and Harry W. Greene[3]

[1] Department of Integrated Natural Sciences, Arizona State University West, P.O. Box 37100, Phoenix, AZ 85069-7100, U.S.A.
[2] Center for Behavioral Neuroscience, Georgia State University, 33 Gilmer Street, Atlanta, GA 30303-3088, U.S.A.
[3] Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853-2701, U.S.A.

(Accepted 1 March 2005)

Abstract

Diet was manipulated in juveniles of the snake *Boa constrictor* (Serpentes: Boidae) to test the hypothesis of whether prey size induces phenotypic plasticity of the head skeleton. Additionally, the onset of sexual size dimorphisms (SSDs) was determined under a feeding schedule where total prey mass consumed by snakes was held constant. Twenty-three neonatal *B. constrictor* from a single-sired litter were placed into two treatment groups but maintained under identical environmental conditions. Group 1 (small-food treatment) was fed weanling mice throughout the entire study; group 2 (large-food treatment) was fed weanling mice, followed by rats of increasing size as the size of the snakes increased. At the termination of the study, group 1 consumed more meals but both groups consumed an equivalent mass of rodents. The snakes were measured twice during the study (5 weeks and 58 weeks). All measurements were obtained while the snakes were under general anaesthesia. Linear measurements of the head skeleton (premaxilla–basioccipital (rostrum–occipital) length, ROL; mandible length, ML) were derived from radiographs. The remaining measurements were snout–vent length (SVL), body length (BL), tail length (TL), and body mass (BM). Treatment effects between groups were equivalent, with the exception of BM and TL (group 1 > group 2), and interactions between main effects were not statistically significant. Between-group differences in ROL and ML were not significant; thus, prey size did not exert an influence on growth of the head skeleton. In contrast, significant sex effects on SVL and BL (females > males) and TL (males > females) were detected, and sex effects on BM (females > males) approached significance. Because SSDs emerged during early ontogeny under conditions where prey mass consumed was held constant, a genetic role is implicated.

Key words: *Boa constrictor*, snake, reptile, vertebrate, growth, phenotypic plasticity, sexual dimorphism, life-history traits

INTRODUCTION

Adult phenotypes in animals are influenced during early ontogeny by complex interactions of genes and environment (Falconer, 1989; Futuyma, 1998). In many cases these phenotypes respond plastically to a variety of environmental factors, such as temperature, water flow, and diet (DeWitt & Scheiner, 2004; Sakata & Crews, 2004). Studies examining the role of diet on morphological phenotypic plasticity, for example, demonstrate that trophic characters in a wide range of vertebrates show significant effects resulting from the type and size of food consumed (Meyer, 1987; Wimberger, 1991; Robinson & Wilson, 1995; Myers *et al*., 1996; Aubret, Shine & Bonnet, 2004; Stauffer & Gray, 2004). Phenotypic plasticity and trophic polymorphisms have been discussed in the context of adaptive responses (Forsman & Shine, 1997; Shine, 1989, 1993; Krause, Burghardt & Gillingham, 2003; Aubret *et al*., 2004) and causal mechanisms for incipient speciation (Bouton, Witte & Van Alphen, 2002; Adams, Woltering & Alexander, 2004; Stauffer & van Snik, Gray, 2004).

Our primary goal in this study was to determine whether prey size induces skull and jaw (head skeleton) phenotypic plasticity during early ontogeny in juveniles of the snake boa constrictor *Boa constrictor* (Serpentes: Boidae). Specifically, our investigation focused on whether relatively large prey exerts a positive (accelerative) influence on the growth and development of the head skeleton. Additionally, we investigated whether sexual size dimorphisms (SSDs) are expressed before sexual maturity under a

*All correspondence to: G. W. Schuett, Department of Integrated Natural Sciences, Arizona State University West, P.O. Box 37100, Phoenix, AZ 85069-7100, U.S.A. E-mail: biogws@langate.gsu.edu and gwschuett@yahoo.com

feeding schedule where total prey mass consumed by the snakes was held constant. Our two research questions are derived and inspired from recent studies on trophic polymorphisms (Forsman, 1996; Scudder-Davis & Burghardt, 1996; Queral-Regil & King, 1998; Bonnet *et al*., 2001; Aubret *et al*., 2004) and SSDs (Shine, 1989, 1993) in snakes. Snakes are gape-limited predators (Arnold 1993; Greene, 1997) and possess a unique gnathic transport system in which prey is advanced by way of a unilateral jaw-ratcheting mechanism (Cundall & Greene, 2000; Kley, 2001). In contrast to other terrestrial vertebrates, certain snakes are unequalled in their capacity to subjugate and consume large, whole prey in a single meal. Members of the lineage Viperidae, for example, are capable of consuming prey that exceed their own mass by > 50% (Cundall & Greene, 2000). Laboratory studies on snakes suggest that size of prey can induce phenotypic plasticity of the cranium and jaws (e.g. Forsman, 1996; Queral-Regil & King, 1998; Bonnet *et al*., 2001; Aubret *et al*., 2004). Based on studies of invertebrates and other species of vertebrates, the principal idea is that relatively large prey exerts increased mechanical stimuli to elements of the trophic apparatus (e.g. skeleto-muscular system of the head; Cundall, 1983, 1987), which thereby positively influence head skeleton growth through remodelling of bone (e.g. Wimberger, 1991).

Ontogeny of SSDs remains largely unstudied in *B. constrictor*. Although it is established that adult females in most populations are significantly larger (head size, body length, and mass) than adult males (e.g. Pope, 1974; Chiaraviglio *et al*., 2003), no data exist concerning the specific timing of the expression of SSDs. In this study, the feeding schedules were adjusted so that the total mass of prey consumed by individuals was equivalent; thus, potential confounding effects of nutrition on SSDs were controlled.

Boa constrictor was selected for this study for three primary reasons. First, because large *B. constrictor* frequently have large litters (> 20 offspring), experimental designs (e.g. split-plot) that reduce trait variation attributable to maternal effects can be used (Falconer, 1989). Second, the litter studied had known paternity (i.e. it was single-sired), thereby further reducing genetic variation of traits that can result from having multiple sires (Brodie & Garland, 1993). Last, *B. contrictor* exhibits SSDs (F > M in body size) which could be tracked during early ontogeny under a feeding schedule where nutrition was controlled (i.e. total mass of prey consumed held constant).

MATERIALS AND METHODS

Subjects and husbandry

Twenty-three neonatal boa constrictors were used in this study, and were derived from a single litter of 29 born in captivity on 30 April 2000. The dam was a first-generation offspring of a female captured by DLH as a neonate in Gamboa, Panama Canal Zone, in 1983. The sire was purchased as a juvenile in the United States from a commercial dealer in 1985. The present litter was produced by back-crossing the dam to her father, and was the sixth litter produced from this crossing. The present dam was never exposed to other males; therefore, paternity assignment of her progeny was unequivocal.

The snakes were maintained under identical environmental conditions at a common location (Tucson, Arizona). All individuals were housed in commercial plastic storage boxes (15 × 23 × 36 cm) with multiple holes for ventilation, newspaper as substrate, and a hide box. Water was available in bowls *ad libitum*. The holding room was 20.3 m^2 with a 4.3 m high ceiling. A skylight (0.61 m^2) allowed natural light to enter the room and provide a seasonal photoperiod. Room temperature range was 29–31 °C during autumn and winter, and 29–33 °C during spring and summer. Shortly after birth, each subject was implanted with a PIT-tag (AVID, Inc.) subcutaneously for permanent individual identity.

Experimental design

Using a split-plot design (Quinn & Keough, 2002), 23 sexed neonates were randomly selected and partitioned into 2 treatment groups: G1 (small-prey treatment; control) and G2 (large-prey treatment). G1 was composed of 7 males and 5 females, and G2 had 5 males and 6 females. Rodent prey was pre-killed, frozen, thawed, and dried of any excess water using paper towelling. Before feeding, all prey offered to the snakes was individually measured to the nearest 0.1 g using an electronic balance. At the outset of the study, all subjects of both groups were fed small laboratory mice (8–21 g, mean = 13.8 g), but snakes in G2 were fed significantly larger prey (rats; 32–260 g, mean = 87.7 g) as their own size increased. Consequently, to maintain equivalent prey mass in both treatments, subjects of G1 were fed an increasing number of mice to match the increase of prey mass consumed by snakes of G2. Food was offered to each snake from long forceps. In all cases the snakes struck the prey and used constriction, lasting 1–5 min. Subjects of both groups were fed as frequently as possible with the interval determined by: (1) the time required for digestion and colonic dehydration of the scat; (2) the timing of ecdysis. The feeding schedule (interval) for G1 was determined by the feeding schedule (interval) of G2 (10–30 days, mean = 18 days).

Morphological measurements

Subjects were measured twice, at 5 weeks and 58 weeks. All measurements were obtained while the snakes were under general anaesthesia (sevoflurane). General anaesthesia was used to optimize measurements by keeping the body of snakes static. Body measurements (dependent variables) were snout–vent length (SVL, to nearest 1.0 mm), tail length (TL, to nearest 1.0 mm), premaxilla–basioccipital (rostrum–occipital) length (ROL, to nearest 0.1 mm), right mandible length (ML, to nearest 0.1 mm), and body mass (BM, to nearest 0.1 g). Head skeleton measurements (i.e. ROL and ML) were obtained from

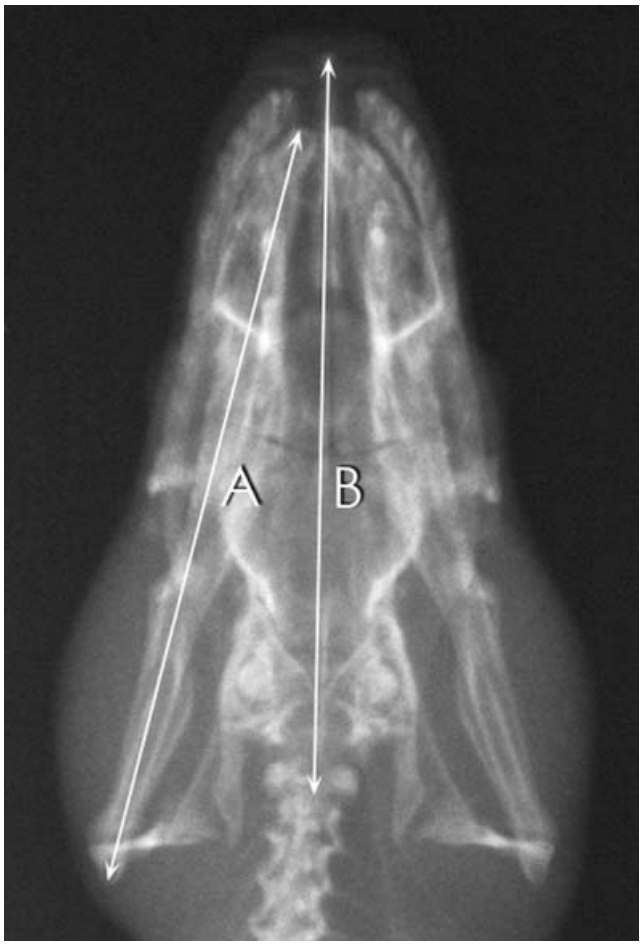

Fig. 1. Radiograph of a *Boa constrictor* (1-year-old) depicting the two head skeleton measurements that were obtained in this study. A, ML (mandible length); B, ROL (premaxilla–basioccipital (rostrum–occipital) length).

radiographs (Fig. 1). Body length (BL) was determined by SVL minus ROL. In both measurement sessions, snakes were sexed by probing (Table 1).

Statistical analysis

Statistical methods follow Quinn & Keough (2002) and tests were performed using SAS Version 8.2 (SAS Institute). The effects of sex, group, and time on morphological data were determined using mixed, within-subjects repeated-measures analyses of variance or covariance (PROC MIXED in SAS; code details follow Wolfinger & Chang, 1995). Sex and group were treated as between-subjects fixed factors, time as a fixed within-subjects repeated-measure, and subjects as a random factor. Assumptions of the analysis of covariance were not met for mass or tail length because all biologically relevant covariates exhibited heterogeneous slopes with the levels of at least 1 between-subjects factor. Accordingly, a covariate was not used for analyses of body mass and tail length. The covariates for all other analyses are given in Table 2. The morphological data were natural-log transformed ($\log_e$) to achieve normality, except for body mass and rostrum–occipital length, which were square-root transformed and untransformed, respectively. Covariance models were fitted using Akaike (AIC) and Schwarz (BIC) information criteria (Wolfinger & Chang, 1995). All independent variables and covariates showed homogeneity of variance across levels of the between-subjects factors (Levene's test; $P \geq 0.05$). Measurements from the same animal are not independent; thus, each morphological parameter was analysed separately and sequential Dunn–Sidak adjustments were applied to prevent compounding of type I error: $\alpha_{adj} = 1 - (1 - \alpha)^{1/k} = 0.008$ for most significant model with $k = 6$ morphological parameters and the original α-level of significance set at $P < 0.05$. Least squares means estimates with sequential Dunn–Sidak adjustments were used to interpret differences among levels of the main and interaction effects and to prevent compounding of type I error. Non-significant interaction terms were dropped consecutively from the analysis of covariance models to yield a reduced model with only main effects and significant interactions for hypothesis testing (Table 2).

RESULTS

Morphological measurements

Non-transformed body measurement data (SVL, BL, TL, ROL, ML, and BM) of the 23 subjects placed in two treatment groups are summarized in Table 1. Total mean mass of rodents (mice only) consumed by subjects of G1 was 1803.6 ± 2.8 g (min–max: 1799–1808 g), based on a mean of 132 mice per snake (min–max: 130–135 mice per snake). Total mean mass of rodents (mice and rats) consumed by subjects of G2 was 1805.5 ± 2.4 g (min–max: 1798–1838 g), based on a mean of 3.09 mice per snake (min–max: 1–5 mice per snake) and a mean of 20.09 rats per snake (min–max: 20–21 rats per snake). The mean difference (1.9 g) of total prey mass consumed in the two groups was not significant (t-test, d.f. $= 22$, $P = 0.554$).

Statistical analyses

Statistical details of the morphological data are presented in Table 2. The covariate used in each of the four analyses was highly significant. There were highly significant differences in all parameters over time, with the values at time 2 always being larger than the values at time 1. Significant differences between the two treatment groups were evident only for BM and TL, with subjects of G1 having greater mass or longer tails than subjects of G2. Sex had a significant effect on BL and SVL; in both cases, females were longer than males. In contrast, TL was significantly greater in males than in females. With the exception of BM, all other interactions between main effects were not significant (sex × group, sex × time, and time × group). Individuals of G1 had significantly greater mass than those of G2 at time 2, but not at time 1.

Table 1. Unadjusted morphological measurements for *Boa constrictor* in two groups measured shortly after birth (April 2000) and 13.5 months after birth (June 2001). All subjects consumed an equivalent mass of food but subjects of group 1 (control) were fed small laboratory mice throughout testing, and subjects of group 2 were fed both mice and rats of increasing size. *n*, number of subjects; SVL, snout–vent length; BL, body length (SVL minus ROL); TL, tail length; BM, body mass; ROL, premaxilla–basioccipital (rostrum–occipital) length; ML, mandible length. Values for ROL and ML were derived from radiographs. Measurements are arithmetic means (± 1 SE) in mm, and parenthetical values denote minimum–maximum

Subjects	*n*	SVL	BL	TL	BM	ROL	ML
Group 1							
Time 1							
Males	7	488 ± 8.5 (453–520)	465 ± 8.4 (431–497)	70 ± 1.7 (63–78)	59.6 ± 2.6 (47–66)	23.1 ± 0.2 (22.5–23.8)	22.1 ± 0.2 (21.2–22.7)
Females	5	507 ± 4.5 (497–524)	483 ± 4.4 (474–500)	67 ± 1.5 (63–72)	64.0 ± 3.0 (54–69)	23.1 ± 0.2 (22.6–23.6)	22.3 ± 0.3 (21.3–23.1)
Time 2							
Males	7	1063 ± 11.9 (1015–1100)	1019 ± 11.7 (973–1056)	140 ± 1.6 (135–147)	854.6 ± 26.9 (736–924)	37.4 ± 0.3 (36.6–38.5)	39.3 ± 0.4 (38.4–41.0)
Females	5	1120 ± 20.7 (1045–1170)	1074 ± 19.7 (1003–1122)	133 ± 2.3 (129–142)	907.8 ± 30.3 (794–971)	38.4 ± 0.7 (35.6–39.8)	40.4 ± 0.9 (36.8–41.9)
Group 2							
Time 1							
Males	5	490 ± 5.6 (475–504)	467 ± 5.6 (452–481)	66 ± 0.9 (63–68)	58.8 ± 1.7 (55–65)	23.2 ± 0.1 (23.0–23.3)	21.9 ± 0.1 (21.5–22.2)
Females	6	492 ± 6.0 (471–514)	469 ± 5.9 (448–491)	66 ± 0.7 (64–69)	59.7 ± 1.8 (55–65)	23.2 ± 0.2 (22.6–23.7)	21.8 ± 0.5 (21.4–22.0)
Time 2							
Males	5	1063 ± 9.3 (1030–1080)	1017 ± 9.3 (984–1034)	134 ± 1.9 (130–140)	762.2 ± 27.8 (697–862)	37.6 ± 0.2 (37.1–38.1)	39.5 ± 0.3 (38.9–40.5)
Females	6	1087 ± 9.4 (1050–1112)	1042 ± 9.5 (1005–1069)	130 ± 5.0 (121–135)	798.2 ± 14.6 (37.1–38.7)	37.7 ± 0.3 (38.2–40.9)	39.4 ± 0.5 (38.2–40.9)

Table 2. Statistical details of the effects of group, sex, time, and analysis-specific covariates on morphological parameters in juvenile *Boa constrictor*. BL, body length; ROL, premaxilla–basioccipital (rostrum–occipital) length; BM, body mass; SVL, snout–vent length; TL, tail length; ML, mandibular length. Due to violation of homogeneous slopes, covariates were not used for the parameters BM and TL (see text)

Parameter	Covariate	Effect	*F*	*P*	Interpretation
BL	ROL	Group	$F_{1,20} = 2.50$	0.1300	
		Sex	$F_{1,20} = 7.80$	0.0110	Females > males
		Time	$F_{1,21} = 30.00$	< 0.0001	Time 2 > time 1
		ROL	$F_{1,21} = 14.40$	0.0010	
BM	–	Group	$F_{1,20} = 16.47$	0.0010	Group 1 > group 2
		Sex	$F_{1,20} = 4.21$	0.0540	Females > males trend
		Time	$F_{1,21} = 82.61$	< 0.0001	Time 2 > time 1
		Time × group	$F_{1,21} = 10.65$	0.0040	T2G1 > T2G2
SVL	ROL	Group	$F_{1,20} = 2.34$	0.1420	
		Sex	$F_{1,20} = 7.82$	0.0110[a]	Females > males
		Time	$F_{1,21} = 31.41$	< 0.0001	Time 2 > time 1
		ROL	$F_{1,21} = 15.53$	0.0010	
TL	–	Group	$F_{1,21} = 8.88$	0.0070	Group 1 > group 2
		Sex	$F_{1,21} = 6.71$	0.0170	Males > females
		Time	$F_{1,19} = 25.59$	< 0.0001	Time 2 > time 1
ROL	BL	Group	$F_{1,20} = 0.68$	0.4190	
		Sex	$F_{1,20} = 0.61$	0.4430	
		Time	$F_{1,21} = 4.88$	0.0380	Time 2 > time 1
		BL	$F_{1,21} = 24.30$	< 0.0001	
ML	BL	Group	$F_{1,20} = 0.98$	0.3350	
		Sex	$F_{1,20} = 0.47$	0.5020	
		Time	$F_{1,21} = 12.50$	0.0020	Time 2 > time 1
		BL	$F_{1,21} = 12.10$	0.0020	

[a] Indicates that the effect was marginally significant after sequential Dunn–Sidak adjustments of the *P*-values for $k = 6$ comparisons.

DISCUSSION

This study shows that large prey size did not induce phenotypic plasticity of head skeleton elements during early ontogeny in the snake *Boa constrictor*. Specifically, within the limits of our experimental design, consumption of large prey did not differentially accelerate growth trajectories of ROL and ML. Thus, our working hypothesis was rejected.

Experimental studies in the laboratory have demonstrated that food availability and increased temperature positively influence growth trajectories in snakes (Arnold & Peterson, 1989; Madsen & Shine, 1993; Forsman, 1996; Scudder-Davis & Burghardt, 1996; Queral-Regil & King, 1998; Bonnet *et al*., 2001), but none demonstrate unequivocally that elements of the trophic apparatus (e.g. jaw and skull) respond plastically to increased mechanical stimuli imposed by large prey. In several of these studies (e.g. Queral-Regil & King, 1998; Bonnet *et al*., 2001) total mass of prey consumed was not controlled and thus was a potential confounding variable in the analysis of head skeleton growth. Recently, Aubret *et al*. (2004) conducted a study similar to the present one but using the Australian elapid *Notechis scutatus*. By controlling both prey size and total mass of prey consumed, they detected a significant effect of the treatment on skull size and jaw length. Their findings, furthermore, were discussed within an adaptive context based on diets in nature (see Barnett & Schwaner, 1985). The study by Aubret *et al*. (2004) thus provides an exception to the general trend that the trophic apparatus of snakes does not respond plastically to large prey.

In contrast to other studies on head growth in snakes, all body measurements were obtained from anaesthetized snakes, which thereby reduced biases resulting from movement. Additionally, radiographs were used for measuring two head skeleton elements (i.e. ROL and ML). Importantly, the radiographs permitted us to differentiate muscle and other connective tissue, a source of bias, from bones of the head skeleton. Not only did radiography provide a clear view of the skull and jaws, but it also permitted us to re-check and re-evaluate measurements.

At 1-year of age, several SSDs were detected in both sexes of *B. constrictor*; and these SSDs emerged at least 15 months before the attainment of sexual maturity. Specifically, significant sex effects were detected for SVL (F > M), BL (F > M), and TL (M > F), whereas results for BM (F > M) approached significance ($P = 0.054$). Our results reflect the values obtained in wild adult *B. constrictor* (e.g. Chiaraviglio *et al*., 2003). Based on the criteria of sexual behaviour and production of offspring, *B. constrictor* maintained in captivity typically attain sexual maturity at *c*. 2.5 years old (Ross & Marzec, 1990; R. Ihle, pers. comm.). Because the design of our study permits us, to some degree, to disentangle genetic and environmental influences regarding growth, the emergence of SSDs early in ontogeny suggests that genes encode for these traits (Aubret *et al*., 2004).

Using three species of congeneric New World water snakes *Nerodia* spp., Scudder-Davis & Burghardt (1996) showed that, under conditions where growth per unit of food consumed (production–ingestion ratio) were considered, juvenile females grew faster in SVL and BM than males, but slower than males in TL. In all species adult females are larger than males. Scudder-Davis & Burghardt (1996) concluded that females seemed to allocate more energy and nutrients to growth than males. Queral-Regil & King (1998) reported similar findings in their laboratory study of the water snake *N. sipedon*. In contrast to these findings, Gregory & Prelypchan (1994) did not detect significant differences in juvenile growth patterns between sexes of the wandering garter snake *Thamnophis elegans*. Our results on sexually dimorphic growth in juvenile *B. constrictor* support the energy allocation hypothesis of Scudder-Davis & Burghardt (1996).

Overall, the two treatment groups in this study responded equivalently to the prey treatment, but significant ($P < 0.01$) group effects were found on BM (G1 > G2) and TL (G1 > G2) (Table 2). Several possible non-mutually exclusive explanations are offered for these disparities. First, the strict diet of laboratory mice consumed by G1 potentially had higher levels of body fat than the rats consumed by G2, and this might explain why G2 had greater mass (fat accumulation) but not greater length (SVL or BL). In general, however, crude protein, fat, and gross energy are similar in these rodents, even at varying ages (Allen & Oftedal, 1994). Bone mass, however, is greater in older and larger individuals of rodents and thus delivers increased quantities of minerals to snakes (K. Nagy, pers. comm.). Examination of fat bodies, as well as muscle and bone mass, of the snakes in this study was not carried out. Second, the feeding schedule itself might have contributed to between-group differences. The subjects of G1 were fed significantly more rodents than those of G2 (G1: mean = 132 meals per subject *vs* G2: mean = 23 meals per subject; *Z*-test, $Z = -9.867$, $P = 0.0001$), and this might have exerted an effect on metabolic processes such as fat deposition (storage). Last, it is possible that the greater body mass of G1 is owing to accumulated and retained waste in the lower gastrointestinal tract based on feeding frequency or prey type (see Lillywhite, De Delva & Noonan, 2002).

The significant difference in TL between the two groups of snakes was puzzling; none the less, we offer one causal interpretation. Because mean TL (sexes pooled) in G1 was slightly greater (but not significant) than in G2 (sexes pooled) at the first measurement shortly after birth, it is suggested that this inherent difference continued to the termination of the study (Table 1). Although it is difficult to implicate diet (mice *vs* rats) as a cause for differences in TL, it is possible that tail growth was accelerated by such a difference.

In conclusion, our study provides important findings and insights to proximate causation related to ontogenetic growth (head skeleton and post cranial elements) and expression of SSDs in the snake *B. constrictor*. We suggest five main directions for future research. First, the use of contrasting diets in this study resulted in interesting between-group differences, but it also placed constraints on the types of analyses that could be performed. Restricting diet to a single type of prey, such as different-sized rats,

would thus be preferred over use of mixed prey species. Second, sample size could be increased by studying multiple litters simultaneously. Third, owing to various limitations, it was not possible to extend observations and measurements beyond 1 year. It would be profitable if future studies conducted similar experiments in *B. constrictor* up to sexual maturity and, if possible, beyond that time. Such studies might be coordinated with zoological parks. Fourth, our subjects originated from parents of different geographical sources. Ideally, subjects should originate from a single geographical location. Fifth, additional and more detailed measurements of body size should be obtained, including terminal analysis of wet- and dry mass of fat bodies, muscle, and bone, as well as muscle size of the head skeleton. This last point is especially important if large prey size positively influences the size of the muscles and other connective tissues of the head skeleton. Finally, other directions should include studies of other species and experimental investigation of additional causative factors. For example, based on studies of the garter snake *Thamnophis sirtalis* (Crews *et al*., 1985; Shine & Crews, 1988; Lerner & Mason, 2001), understanding the role of hormones (e.g. testosterone, oestradiol-17β) might be important in understanding sexually dimorphic growth in *B. constrictor*.

Acknowledgements

We thank Ken Nagy for discussing information on the nutritional value of rodents, Abraham L. Hayward for advice and care of the study animals, and James Jarchow for assistance in taking radiographs of the snakes. Kris Lappin generously discussed feeding dynamics in vertebrates. Rich Ihle provided expert information on the reproductive biology of boa constrictors. Two anonymous referees provide insightful comments that improved our clarity of presentation. Zoo Atlanta generously provided funding for the preparation of this manuscript.

REFERENCES

Adams, C. E., Woltering, C. & Alexander, G. (2004). Epigenetic regulation of trophic morphology through feeding behaviour in Artic charr, *Salvelinus alpinus*. *Biol. J. Linn. Soc*. **78**: 43–49.

Allen, M. E. & Oftedal, O. T. (1994). The nutrition of carnivorous reptiles. In *Captive management and conservation of amphibians and reptiles*: 71–82. Murphy, J. B., Adler, K. & Collins, J. T. (Eds). Ithaca, NY: Society for the Study of Amphibians and Reptiles.

Arnold, S. J. (1993). Foraging theory and prey size–predator size relations in snakes. In *Snake: ecology and behavior*: 87–115. Seigel, R. A. & Collins, J. T. (Eds). New York: McGraw-Hill.

Arnold, S. J. & Peterson, C. R. (1989). A test for temperature effects on the ontogeny of shape in the garter snake *Thamnophis sirtalis*. *Physiol. Zool*. **62**: 1316–1333.

Aubret, F., Shine, R. & Bonnet, X. (2004). Adaptive developmental plasticity in snakes. *Nature (Lond.)* **431**: 261–262.

Barnett, B. & Schwaner, T. D. (1985). Growth in captive born tiger snakes (*Notechis alter serventyi*) from Chappell Island: implications for field and laboratory studies. *Trans. R. Soc. S. Aust*. **109**: 31–36.

Bonnet, X., Shine, R., Naulleau, G. & Thiburce, C. (2001). Plastic vipers: influence of food intake on the size and shape of Gaboon vipers (*Bitis gabonica*). *J. Zool. (Lond.)* **255**: 341–351.

Bouton, N., Witte, F. & Van Alphen, J. J. M. (2002). Experimental evidence for adaptive phenotypic plasticity in a rock-dwelling cichlid fish from Lake Victoria. *Biol. J. Linn. Soc*. **77**: 185–192.

Brodie, E. D. III & Garland, T. (1993). Quantitative genetics of snake populations. In *Snakes: ecology and behavior*: 315–362. Seigel, R. A. & Collins, J. T. (Eds). New York: McGraw-Hill.

Chiaraviglio, M., Bertona, M., Sironi, M. & Lucino, S. (2003). Intrapopulation variation in life history traits of *Boa constrictor occidentalis* in Argentina. *Amphib.-Reptilia* **24**: 65–74.

Crews, D., Diamond, M. A., Whittier, J. & Mason, R. (1985). Small male body size in garter snake depends on testes. *Am. J. Physiol*. **249**: R62–R65.

Cundall, D. (1983). Activity of head muscles during feeding by snakes: a comparative study. *Am. Zool*. **23**: 383–396.

Cundall, D. (1987). Functional morphology. In *Snakes: ecology and evolutionary biology*: 106–140. Seigel, R. A., Collins, J. T. & Novak, S. S. (Eds). New York: Macmillan.

Cundall, D. & Greene, H. W. (2000). Feeding in snakes. In *Feeding: form, function and evolution in tetrapod vertebrates*: 293–333. Schwenk, K. (Ed.). San Diego, CA: Academic Press.

DeWitt, T. J. & Scheiner, S. M. (Eds). (2004). *Phenotypic plasticity: functional and conceptual approaches*. Oxford: Oxford University Press.

Falconer, D. S. (1989). *Introduction to quantitative genetics*. 3rd edn. New York: Wiley.

Forsman, A. (1996). An experimental test for food effects on head size allometry in juvenile snakes. *Evolution* **50**: 2536–2542.

Forsman, A. & Shine, R. (1997). Rejection of non-adaptive hypotheses for intraspecific variation in trophic morphology in gape-limited predators. *Biol. J. Linn. Soc.* **62**: 209–223.

Futuyma, D. J. (1998). *Evolutionary biology*. 3rd edn. Sunderland, MA: Sinauer.

Greene, H. W. (1997). *Snakes: the evolution of mystery in nature*. Berkeley, CA: University of California Press.

Gregory, P. T. & Prelypchan, C. J. (1994). Analysis of variance of first-year growth in captive garter snakes (*Thamnophis elegans*) by family and sex. *J. Zool. (Lond.)* **232**: 313–322.

Kley, N. J. (2001). Prey transport mechanisms in blindsnakes and the evolution of unilateral feeding system in snakes. *Am. Zool*. **41**: 1321–1337.

Krause, M. A., Burghardt, G. M. & Gillingham, J. C. (2003). Body size plasticity and local variation of relative head and body size sexual dimorphism in garter snakes (*Thamnophis sirtalis*). *J. Zool. (Lond.)* **261**: 399–407.

Lerner, D. T. & Mason, R. T. (2001). The influence of sex steroids on the sexual size dimorphism in the red-spotted garter snake, *Thamnophis sirtalis concinnus*. *Gen. comp. Endocrinol*. **124**: 218–225.

Lillywhite, H., de Delva, P. & Noonan, B. P. (2002). Patterns of gut passage time and the chronic retention of fecal mass in viperid snakes. In *Biology of the vipers*: 497–506. Schuett, G. W., Höggren, M., Douglas, M. E. & Greene, H. W. (Eds). Eagle Mountain, UT: Eagle Mountain Publishing.

Madsen, T. & Shine, R. (1993). Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution* **47**: 321–325.

Meyer, A. (1987). Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. *Evolution* **41**: 1357–1369.

Myers, P., Lundrigan, B. L., Gillespie, B. W. & Zelditch, M. L. (1996). Phenotypic plasticity in skull and dental morphology in the prairie deer mouse (*Peromyscus maniculatus bairdii*). *J. Morphol*. **229**: 229–237.

Pope, C. H. (1974). *The giant snakes*. New York: Alfred A. Knopf.

Queral-Regil, A. & King, R. B. (1998). Evidence for phenotypic plasticity in snake body size and relative head dimensions in response to amount and size of prey. *Copeia* **1998**: 423–429.

Quinn, G. P. & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

Robinson, B. W. & Wilson, D. S. (1995). Experimentally induced morphological diversity in Trinidadian guppies (*Poecilia reticulata*). *Copeia* **1995**: 294–305.

Ross, R. A. & Marzec, G. (1990). *The reproductive husbandry of pythons and boas*. Stanford: Institute for Herpetological Research.

Sakata, J. T. & Crews, D. (2004). Developmental sculpting of social phenotype and plasticity. *Neurosci*. *Biobehav. Rev*. **28**: 95–112.

Scudder-Davis, R. M. & Burghardt, G. M. (1996). Ontogenetic changes in growth efficiency in laboratory-reared water snakes of the genus *Nerodia*. *The Snake* **27**: 75–84.

Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q*. *Rev. Biol*. **64**: 419–461.

Shine, R. (1993). Sexual dimorphism in snakes. In *Snakes: ecology and behavior*: 49–86. Seigel, R. A. & Collins, J. T. (Eds). New York: McGraw-Hill.

Shine, R. & Crews, D. (1988). Why male garter snakes have small heads: the evolution and endocrine control of sexual dimorphism. *Evolution* **42**: 1105–1110.

Stauffer, J. R. & van Snik Gray, E. (2004). Phenotypic plasticity: its role in trophic radiation and explosive speciation in cichlids (Teleostei: Cichlidae). *Anim*. *Biol*. **54**: 137–158.

Wimberger, P. H. (1991). Plasticity of jaw and skull morphology in the Neotropical cichlids *Geophagus brasiliensis* and *G. steindachneri*. *Evolution* **45**: 1545–1563.

Wolfinger, R. & Chang, M. (1995). Comparing the SAS® GLM and MIXED procedures for repeated measures. In *Proceedings of the Twentieth Annual SAS Users Group Conference,* 1–11. Cary, NC: SAS Institute Inc.