

RESEARCH ARTICLE

Allometry of skull morphology, gape size and ingestion performance in the banded watersnake (*Nerodia fasciata*) feeding on two types of prey

Paul M. Hampton^{1,*}**ABSTRACT**

Small body size imposes limitations on the feeding capabilities of juveniles, particularly in species that consume their prey whole. It has been hypothesized that juveniles exhibit exceptional performance measures to compensate for their small size. However, few studies have examined whether juveniles have better feeding performance relative to adults and investigations of snake feeding ontogeny have not shown enhanced performance in smaller snakes. I tested the hypothesis that juvenile snakes have better feeding performance by comparing maximum gape circumference and ingestion performance (time and number of pterygoid protractions) in a series of banded watersnakes (*Nerodia fasciata*) of different sizes fed fish and frogs. I also measured several external and osteological dimensions of the head and used Akaike's information criterion to determine which morphological measurements were the strongest predictors of relative gape. All skull measurements and maximum gape circumference showed negative allometry relative to snout–vent length (SVL). Given the available models, Akaike information criterion (AIC) analysis indicated that both skull length and mandible length were the strongest predictors of gape circumference for both external and osteological measurements. Multiple regression analysis of ingestion performance indicated SVL was negatively correlated with the time and number of pterygoid protractions required to consume fish or frogs, indicating that juveniles do not have a higher ingestion performance than adults. While exaggerated morphology in juvenile snakes does not appear to improve ingestion performance, a larger gape should increase the ability of juvenile snakes to consume a wide range of encountered prey shapes and sizes.

KEY WORDS: Feeding, Ontogeny, Osteology, Scaling, Snake**INTRODUCTION**

The selective pressures favoring allometric patterns are generally uncertain and may simply reflect constraints of physiology or genetics (Hayssen and Lacy, 1985; Johnson et al., 1993; Egset et al., 2012). Vertebrate allometry shows that juveniles typically have exaggerated features, and it has been hypothesized that such characteristics enhance performance and reduce the disadvantages associated with small body size (Carrier, 1996). This compensation hypothesis has been tested using locomotor performance in several species that exhibit scaling of characteristics associated with movement. Studies have resulted in both confirmation and rejection

of the compensation hypothesis, with the outcome seemingly dependent upon the taxa and mode of locomotion (Johnson et al., 1993; Katz and Gosline, 1993; Wilson et al., 2000; McHenry and Jed, 2003; Noren et al., 2006; Maie et al., 2007). The feeding apparatus also shows conspicuous allometric changes in many vertebrates that consume their prey whole (Richard and Wainwright, 1995; Meyers et al., 2002; Robinson and Motta, 2002). The scaling of trophic morphology with body size may exist to improve feeding performance in juveniles of some species (Van Wassenbergh et al., 2005). Nevertheless, performance compensation for small body sizes with regard to feeding has received comparatively less attention (Herrel and Gibb, 2006).

For predators that consume prey whole, prey capture and the costs of feeding are often influenced by gape size (Pough and Groves, 1983; Carroll et al., 2004). In addition, the diet (prey size and type/shape) is constrained by what can physically fit in the mouth (Forsman and Lindell, 1993; Scharf et al., 2000). Gape size is thought to be one of the primary characteristics driving the radiation of snakes (Rodríguez-Robles et al., 1999), and many modifications have occurred to the bones and soft tissues of the snake head to increase maximum gape size (Cundall and Greene, 2000). For snakes, the term gape can be interpreted in various ways and may refer to the maximum distance capable at the anterior end of the mouth, the maximum angle at the corner of the mouth (where the quadrate and mandible articulate) or the maximum circumference of the posterior oral cavity. Each interpretation can have a particular functional significance, though the most important may be the circumference of the posterior oral cavity because this is the final factor limiting prey consumption and because snakes occasionally die attempting to consume very large prey (P.M.H., personal observation).

Several approaches have been taken to compare maximum gape in snakes. Most commonly, gape is estimated from a single linear dimension, such as head length, head width or mandible length (Pough and Groves, 1983; Hampton, 2011a). Although such measurements are effective for making comparisons, they are limited by a single dimension. With regard to the size or shape of prey that can be consumed, maximum gape should be considered a two-dimensional measurement, such as circumference. Miller and Mushinsky (Miller and Mushinsky, 1990) and King (King, 2002) developed separate equations that incorporate linear dimensions to estimate gape; however, they may not accurately estimate gape or the scaling of gape with body size (Hampton and Moon, 2013). Furthermore, morphological diversity among linear dimensions does not necessarily equate to functional diversity among individuals because of the emergent properties of complex structures (Alfaro et al., 2005; Wainwright et al., 2005). Consequently, maximum gape may not be comparable among individuals or species with different morphologies, justifying empirical measures of gape in multiple lineages.

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List of abbreviations	
BW	braincase width
FL	frontal length
FWpf	width of the frontals taken at the prefrontal process
MdL	mandible length
MxL	maxilla length
PalL	palantine length
ParL	parietal length taken at midline
ParW	maximum parietal width
PtL	pterygoid length
QL	quadrate length
SL	skull length from the nasal to the occipital condyles
StL	supratemporal length

While evidence suggests that the negative allometry of trophic morphology improves feeding performance in juveniles in some species (Van Wassenbergh et al., 2005), an explanation for the scaling pattern remains inconclusive for some taxa (Reilly, 1995; Hampton, 2011a). For many snake species, juveniles exhibit relatively large heads compared with larger conspecifics (Vincent et al., 2006; Hampton, 2011a; Hampton and Moon, 2013). At least two studies have tested whether negative allometry of head size lowers feeding effort (time and mechanical effort) in snakes, yet ingestion performance has not been shown to vary with body size within a species (Vincent et al., 2006; Hampton, 2011a), suggesting that alternative phenomena are driving negative allometry of head size. For instance, in many species that consume their prey whole, juveniles consume larger prey relative to body size than the adult conspecifics (Miller and Mushinsky, 1990; Scharf et al., 2000; Ford and Hampton, 2009). Furthermore, a relatively large gape may effectively increase the probability of successful prey encounters as a result of the snake having a greater range of consumable prey sizes and types. Amalgamated, these factors could increase juvenile growth rates

(Galatti, 1992; Madsen and Shine, 2000). The goal of this study was to take an integrated approach to understand the trophic allometry in the banded watersnake, *Nerodia fasciata* (Linnaeus 1766). Specifically, I compared several dimensions of the skull and direct measurements of maximum gape circumference over a series of body sizes. I also measured ingestion effort (time and number of pterygoid protractions) required to consume prey among a series of snake sizes. I predicted that although small snakes would have larger heads and gape sizes relative to body size, the feeding effort (time and number of pterygoid protractions) required to ingest either frogs or fish would not be lower for juveniles. If smaller snakes have relatively large gapes but feeding costs are not reduced, this would suggest an alternative functional explanation for this allometric pattern, specifically the ability to consume larger prey relative to predator size. Further, I evaluate which skull characteristics are the most important contributors to maximum gape circumference in individuals of *N. fasciata*.

RESULTS

Morphology

All 12 skull bones showed significant negative allometry with snout–vent length (Table 1), indicating that smaller individuals have larger skull bones relative to body size than larger conspecifics. Measures of cranial width were also negatively allometric when compared with skull length (Table 2). However, palantine length, pterygoid length and the suspensorium illustrated positive allometry with skull length (Table 2). Gape circumference ranged from 3.5 to 10.1 cm (mean ± s.d. 6.3±2.0 cm) and exhibited negative allometry with respect to body size (slope=0.720; $F_{1,36}=35.86$, $P<0.001$; Fig. 1). Gape and snout–vent length (SVL) illustrated a significant linear relationship ($R^2=0.937$, $P<0.001$). Yet, a *post hoc* polynomial regression also showed a significant relationship ($R^2=0.96$; $P<0.001$), and an *F* probability distribution test confirmed that the

Table 1. Summary statistics from reduced major axis regressions of skull bones against snout–vent length (SVL) in *Nerodia fasciata*

Variable	Slope	Intercept	R ²	F	P
Skull length	0.618	0.267	0.953	282.1	<0.001
Braincase width	0.498	0.031	0.938	561.7	<0.001
Frontal width	0.535	−0.16	0.743	17.6	<0.001
Frontal length	0.570	−0.263	0.755	102.4	<0.001
Parietal length	0.536	−0.051	0.823	165.8	<0.001
Parietal width	0.532	0.017	0.833	178.6	<0.001
Supratemporal length	0.802	−0.438	0.945	44.3	<0.001
Quadrate length	0.941	−0.706	0.969	6.3	0.014
Maxilla length	0.660	−0.018	0.968	279.7	<0.001
Palantine length	0.903	−0.656	0.751	7.5	0.008
Pterygoid length	0.762	−0.056	0.929	54.6	<0.001
Mandible length	0.750	0.143	0.971	133.6	<0.001

F- and P-values are the result of homogeneity of slopes tests in which the slope of each variable against SVL was compared with a slope of 1 (isometry).

Table 2. Summary statistics from reduced major axis regressions of skull bones against skull length in *N. fasciata*

Variable	Slope	Intercept	R ²	F	P
Braincase width	0.816	−0.1966	0.956	44.87	<0.001
Frontal width	0.989	−0.554	0.858	2.24	0.140
Parietal width	0.868	−0.221	0.893	12.81	0.001
Supratemporal length	1.299	−0.785	0.953	28.93	<0.001
Quadrate length	1.514	−1.099	0.955	72.31	<0.001
Maxilla length	1.071	−0.306	0.976	3.87	0.054
Palantine length	1.467	−1.052	0.775	5.59	0.021
Pterygoid length	1.238	−0.389	0.931	11.37	0.001
Mandible length	1.219	−0.186	0.966	25.21	<0.001

F- and P-values are the result of homogeneity of slopes tests in which the slope of each variable against skull length was compared with a slope of 1 (isometry).

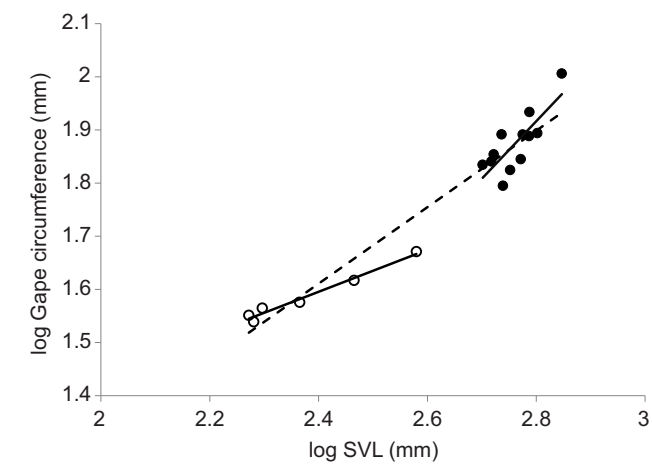


Fig. 1. The relationship between gape circumference and snout–vent length (SVL) in *Nerodia fasciata*. Open circles indicate juveniles (SVL <500 mm); filled circles indicate adults (SVL >500 mm). Solid lines indicate linear relationships for the respective age class. The dashed line indicates the linear relationship for all individuals.

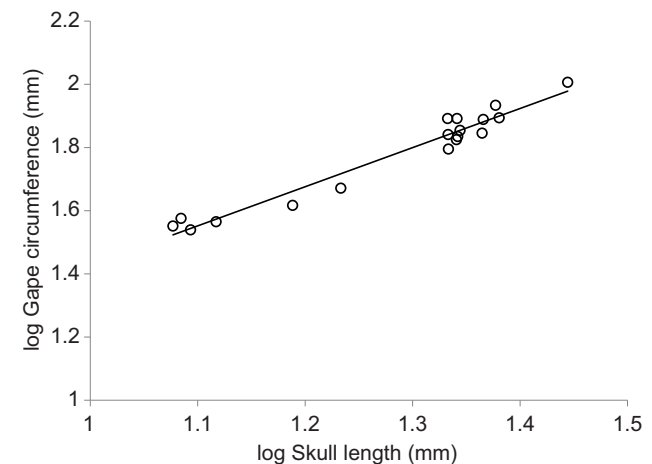


Fig. 2. The relationship between gape circumference and skull length in *N. fasciata*.

R^2 value increased significantly ($P<0.001$), indicating that a quadratic regression is a better fit for the data. Furthermore, the slope of gape circumference against SVL was much smaller for juveniles (slope=0.396, $R^2=0.975$; SVL <560 mm) than for adults (slope=1.08, $R^2=0.633$; SVL >560 mm; Fig. 1). Gape circumference and skull length illustrated a significant linear relationship ($R^2=0.953$, $P<0.001$; Fig. 2).

External measurements of head length and jaw length were equally strong predictors of gape compared with other external head dimensions (Table 3). While head width, intermandibular distance and quadrate length ranked higher than the null model, each had Δ_i values (the change in Akaike information criterion) >2 and very low Akaike weights; both indices indicate weak model support (Burnham and Anderson, 2002). For the osteological model analysis, skull length ranked the highest among the models, suggesting that it is the best predictor of gape circumference (Table 4). Mandible, supratemporal and quadrate lengths also proved to be good indicators of gape, though considerably less than skull length based upon Akaike weight values. The change in Akaike information criterion (Δ_i) values and Akaike weights of all other models suggested that they contribute relatively little to maximum gape despite ranking above the null model (Table 4).

Ingestion performance

Multiple regression using fish as the prey type indicated a significant model using time as the dependent variable ($F_{2,13}=15.35$, $R^2=0.773$,

$P<0.001$; Table 5). As prey mass increased, the time required to consume fish increased, but as SVL increased, ingestion time decreased (Table 5). The regression model with pterygoid protractions as the dependent variable was also significant ($F_{2,13}=4.87$, $R^2=0.520$, $P=0.037$). As before, the number of pterygoid protractions was positively correlated with prey mass and negatively correlated with snake size (Table 5). An analysis of fish ingestion time that excluded positioning indicated a significant model ($F_{2,13}=7.49$, $R^2=0.577$, $P=0.009$). In this model, time was negatively correlated with SVL and prey mass was positively correlated with time. Using pterygoid protractions as the dependent variable did not result in a significant model when positioning was excluded ($F_{2,13}=2.40$, $R^2=0.304$, $P=0.136$; Table 6).

The regression model with frogs as the prey type and ingestion time as the dependent variable was significant ($F_{2,17}=14.29$, $R^2=0.687$, $P=0.001$). Prey mass was positively correlated with ingestion time, but no significant correlation occurred between SVL and time (Table 5). Using the number of pterygoid protractions as the dependent variable, the regression model was significant ($F_{2,17}=15.31$, $R^2=0.702$, $P<0.001$). A positive correlation occurred between the number of protractions and prey mass, but no significant correlation occurred between the number of protractions and SVL (Table 5). A multiple regression using the time required to ingest a frog, excluding positioning time, as the dependent variable resulted in a significant model ($F_{2,17}=20.73$, $R^2=0.734$, $P<0.001$). Using the number of pterygoid protractions required to ingest prey, excluding those required to position the frog, also resulted in a significant model ($F_{2,17}=15.36$, $R^2=0.672$, $P<0.001$). In both models, the number of pterygoid protractions required to ingest the prey after

Table 3. Summary statistics for external skull measurements that contribute to gape circumference in *N. fasciata*

Model	R^2	RSS	K	AICc	Δ_i	w
Head length	0.93	0.02	3	−34.63	0.00	0.45
Jaw length	0.93	0.02	3	−34.63	0.00	0.45
Head width	0.89	0.04	3	−31.30	3.33	0.09
Intermandibular distance	0.70	0.10	3	−24.73	9.90	0.00
Quadrate length	0.58	0.13	3	−22.65	11.98	0.00
Null		0.32	2	−20.17	14.46	0.00
All bone	0.96	0.01	7	−15.45	19.18	0.00

The ‘all bone’ model includes all dimensions except intermandibular distance.
RSS, residual sum of squares; AICc, Akaike information criterion corrected for small sample sizes; Δ_i , change in AIC; w, Akaike weights.

Table 4. Summary statistics for osteological measurements that contribute to gape circumference in *N. fasciata*

Model	R ²	RSS	K	AICc	Δ _i	w
Skull length	0.953	0.018	3	−46.29	0.00	0.40
Mandible length	0.946	0.021	3	−45.08	1.21	0.22
Supratemporal length	0.939	0.023	3	−44.37	1.92	0.15
Quadrate length	0.936	0.024	3	−44.04	2.25	0.13
Parietal Width	0.929	0.027	3	−43.12	3.17	0.08
Suspensorium	0.973	0.020	5	−42.79	8.49	0.01
Full model	0.981	0.014	7	−38.79	18.69	0.00
Null		0.378	2	−25.40	20.88	0.00

Suspensorium includes supratemporal length, quadrate length and mandible length.

positioning decreased with snake size and increased with frog size (Table 6).

DISCUSSION

Morphology

All measured skull bones displayed negative allometry relative to body length, with slopes comparable to those observed in a similar study of ontogeny in *N. fasciata* (Vincent et al., 2007). In agreement with Vincent and colleagues (Vincent et al., 2007), the jaw bones and suspensorium elicited positive allometry with skull length. Interestingly, the braincase and parietal widths displayed negative allometry whereas frontal width was isometric relative to skull length. This is slightly contradictory to previous studies that have shown head width is positively correlated with head length (e.g. Vincent et al., 2006). However, measurements in these studies used external measures of head width, often at its widest point, which would include the lateral projection of the quadrate bones. The data in the current study suggest that the width of the anterior region of the skull increases proportionately with increasing skull length while the posterior region remains relatively narrow. The relatively high slope of the quadrate suggests that it may compensate for the narrow posterior region to maintain a large gape. The cause of this pattern is uncertain but may be related to a dietary shift from fish to frog prey. For instance, a comparison of cranial bones among natricines indicated that anurophagous species tend to have wider cranial components than their piscivorous relatives (Hampton, 2011b). Mori and Vincent also found that a frog specialist snake species had a wider head than a syntopic generalist species (Mori and Vincent, 2008). While anurophagy appears to influence head width, a functional explanation for how this morphology is related to prey capture and ingestion is warranted.

Maximum gape circumference was negatively allometric with respect to body size, indicating that small individuals have relatively larger gapes. Having a relatively large gape may be particularly advantageous to juvenile snakes. A wide gape should allow the consumption of relatively large prey and increase the variety of prey shapes and sizes that can be consumed (Forsman and Lindell, 1993;

Cundall and Greene, 2000), both of which will increase energy acquisition and speed the rate of growth. Dietary data collected from natricines *in situ* provide support for this interpretation in that the juveniles typically consume relatively larger prey than adults (Miller and Mushinsky, 1990; Ford and Hampton, 2009). Furthermore, based upon data reported in Mushinsky et al. (Mushinsky et al., 1982), I estimated the relationship between relative prey size and body size to have a slope of ~0.71 [estimated from fig. 4 of their study (Mushinsky et al., 1982); change in $y=1$, change in $x=1.4$]. This is remarkably similar to the slope of the relationship between gape and body size in this study (0.72).

A noteworthy pattern in this study is that rather than a linear relationship, the association between gape circumference and body length was better described by a quadratic regression in which the slope increases faster in larger individuals. In some populations of *N. fasciata*, individuals experience a shift in diet from primarily fish to primarily frogs (Mushinsky et al., 1982). Based upon the data in Mushinsky et al. (Mushinsky et al., 1982), this shift occurs at the approximate size at which *N. fasciata* reach maturity, 500–600 mm SVL. Incidentally, the slope of gape against body size noticeably increases at a similar size range in this study, suggesting that individuals are experiencing a relatively rapid allometric change in morphology. Specifically, adult *N. fasciata* increase gape size relatively quickly with increasing body size. This is a different relationship from that observed for the rattlesnake *Crotalus atrox*, in which there is no conspicuous change in slope between juveniles and adults (Hampton and Moon, 2013). The relatively steady rate of gape growth may be because *C. atrox* primarily consumes mammals regardless of size. Notable differences in slope between juveniles and adults that coincide with changes in diet have also been observed in a python (*Morelia viridis*) (Natusch and Lyons, 2012) and a pitviper (*Agkistrodon piscivorus*) (Vincent et al., 2004). A shift in prey type near maturity may be a corollary to energy demands for reproduction, in which prey with a higher energy content are selected (Santos et al., 2000), in turn increasing reproductive output (Ford and Seigel, 1989). Comparisons of the gape allometry across a broad range of snake taxa, that do or do not ontogenetically shift prey type, are necessary to

Table 5. Coefficients for multiple regression of total fish and frog ingestion times and the number of upper jaw protractions (including prey positioning) for *N. fasciata*

Prey	Variable	Time				Protractions			
		β	s.e.	t	P	β	s.e.	t	P
Fish	SVL	−3.29	0.59	−1.08	<0.001	−1.46	0.48	−3.03	0.014
	Prey mass	1.98	0.64	0.60	0.013	1.24	0.52	2.37	0.042
Frog	SVL	−2.11	1.02	−2.08	0.06	−0.62	0.52	−1.21	0.249
	Prey mass	1.15	0.24	4.89	<0.001	0.55	0.12	4.58	0.001

SVL and prey mass were the independent variables.

Table 6. Coefficients for multiple regression of fish and frog ingestion times and the number of upper jaw protractions (following positioning) for *N. fasciata*

Prey	Variable	Time				Protractions			
		β	s.e.	<i>t</i>	<i>P</i>	β	s.e.	<i>t</i>	<i>P</i>
Fish	SVL	−2.62	0.75	−3.50	0.005	−0.83	0.49	−1.70	0.117
	Prey mass	0.75	3.19	2.35	0.039	0.36	0.208	1.71	0.116
Frog	SVL	−2.42	0.96	−2.51	0.024	−1.79	0.77	−2.32	0.035
	Prey mass	1.12	0.18	6.35	<0.001	0.78	0.14	5.49	<0.001

SVL and prey mass were the independent variables.

confidently demonstrate and explain the non-linear relationship between gape and body length for *N. fasciata*.

Ingestion performance

The functional demands associated with differences in body size have been explored for many taxa, and trophic allometry has been related to enhanced feeding performance in juveniles for some species (Van Wassenbergh et al., 2005). This pattern does not seem to hold true for snakes when performance is a measure of the effort required to consume a prey item (Vincent et al., 2007; Hampton, 2011a) (this study). While studies have shown that relative prey size affects the time and functional effort required for ingestion (Pough and Groves, 1983; Hampton, 2011a), ingestion performance does not explain the allometry of trophic morphology when corrected for prey size. Large snakes typically consume a disproportionately high number of small prey, which is thought to be a consequence of prey availability (Voris and Moffett, 1981). Thus, as snake size increases, the encounter rate of large relative prey sizes may decrease and the ingestion of relatively large prey is less common. Moreover, the energetic costs of prey handling are quite inconsequential for snakes (Cruz-Neto et al., 2001). As a result, it is not likely that selection strongly favors reducing the costs of prey ingestion, suggesting that ingestion performance is not likely to explain trophic allometry in snakes given typical prey sizes consumed *in situ* (Hampton, 2013).

Conclusions

Previous studies have used a variety of morphological measurements and geometric equations to estimate maximum gape size in snakes (Pough and Groves, 1983; Miller and Mushinsky, 1990; King, 2002). Recently, a study empirically measured gape circumference in rattlesnakes and determined which skull elements were the primary contributors to maximum gape (Hampton and Moon, 2013). Hampton and Moon (Hampton and Moon, 2013) found that mandible length and quadrate length were the strongest contributors to maximum gape when corrected for body size. However, as the authors noted, skull morphology is very diverse among snakes and the primary contributors to gape may vary among species. In comparison, the data for *N. fasciata* suggest skull length and mandible length are the two best contributors to maximum gape. The high model ranking of mandible length in both studies emphasizes its general association with maximum gape size. The disparity among the effectively equal ranking of quadrate length in *Crotalus atrox* and skull length in *N. fasciata* illustrates that there are multiple ways to increase mandible length in snakes. Among the more conspicuous dimensions for increasing mandible length are increasing skull length, supratemporal length and quadrate length (assuming it is caudally oriented).

The heads of snakes play many functional roles, and various ecological pressures may constrain which bones are modified and to

what limit. While the number of jaw protractions required to ingest prey varies among snake species (Pough and Groves, 1983), head size has not been shown to influence ingestion time or jaw protractions within a species (Vincent et al., 2007; Hampton, 2011a). This suggests that other factors are influencing head size and shape. The general shape of a species' primary prey type is one likely factor influencing how the skull bones are modified. For example, increased piscivory in natricines is associated with an increase in quadrate length, which may help maneuver the head around oblong shapes and erect spines (Vincent et al., 2009). In contrast, anurophagous snakes tend to have comparatively wider heads than generalist or piscivorous snakes (Mori and Vincent, 2008; Hampton, 2011b). Prey size can also affect head size and skull dimensions (Aubret et al., 2004). For instance, Aubret and colleagues (Aubret et al., 2004) found a disparity in the relative jaw length of two populations of tiger snakes, in which the population consuming larger prey had longer jaws. Hampton and Moon (Hampton and Moon, 2013) found that the slope of gape against SVL for a rattlesnake (*Crotalus atrox*) was lower (0.57) and the intercept higher (0.43) than that for *N. fasciata* (slope=0.72, intercept=−0.12). This suggests that individuals of *C. atrox* have greater gape sizes for their body sizes, and that relative gape size does not increase as rapidly during growth in individuals of *C. atrox* compared with *N. fasciata*. This disparity is likely due to the fact that rattlesnakes frequently consume relatively larger and more robust prey throughout their lives (Beavers, 1976). Factors influencing drag and prey capture success during aquatic strikes have also been associated with head shape in snakes (Van Wassenbergh et al., 2010).

Body size can have a profound influence on an organism's level of performance, and it has been proposed that juveniles experience exaggerated morphologies to compensate for being smaller than adult conspecifics (Carrier, 1996; Irschick et al., 2005). For many taxa larger individuals exhibit greater performance among a variety of measures associated with trophic morphology, including bite force (Herrel and O'Reilly, 2006; Meyers et al., 2002), jaw opening and closing velocities (Richard and Wainwright, 1995; Meyers et al., 2002), and suction strength (Robinson and Motta, 2002; Van Wassenbergh et al., 2005). When considering the mechanical effort required to consume prey, adult snakes are no better or worse than juveniles (Vincent et al., 2007; Hampton, 2011a), possibly because this measure of performance is rather inconsequential to the feeding success of snakes. In contrast, gape circumference is a measure of trophic performance relevant to foraging success in snakes. For snakes, a large gape circumference can increase dietary breadth and allow the exploitation of large prey (Forsman and Lindell, 1993), which should increase growth rates and thereby improve the probability of juvenile survival. This study demonstrates that, for snakes, increasing gape size is a more probable ecological explanation for negative trophic allometry than prey ingestion performance.

MATERIALS AND METHODS

Morphology

Skull allometry

To determine allometric changes in trophic morphology, I measured 34 individuals of *N. fasciata* from southern Louisiana (187–703 mm SVL, mean \pm s.d. 492 ± 136 mm). For analytical purposes, I estimated the size to maturity to be ~560 mm based upon a previous study of a population of *N. fasciata* (formerly *Natrix sipedon*) in southern Louisiana (Tinkle, 1959). I recorded SVL of previously frozen but not chemically preserved specimens by placing string along the ventral side of the snake then measuring the length of the string. I measured the following external head dimensions: head length (from the posterior tip of the parietal scale to the anterior tip of the snout), maximum head width at rest, jaw length (from the tip of the retroarticular process to the anterior tip of the lower jaw) and quadrate length. I used dermestid beetles (*Dermestes* sp.) to remove the soft tissue from the skeletons. For each skull, I recorded 12 osteological dimensions from each individual using digital calipers (Fig. 3): braincase width; frontal length; width of the frontals, taken at the prefrontal process; mandible length; maxilla length; palantine length; parietal length, taken at the midline; maximum parietal width; pterygoid length; quadrate length; skull length from the nasal to the occipital condyles; and supratemporal length. The specimens used for the morphological data were deceased before this experiment began; they were not the same individuals from the feeding experiment described below.

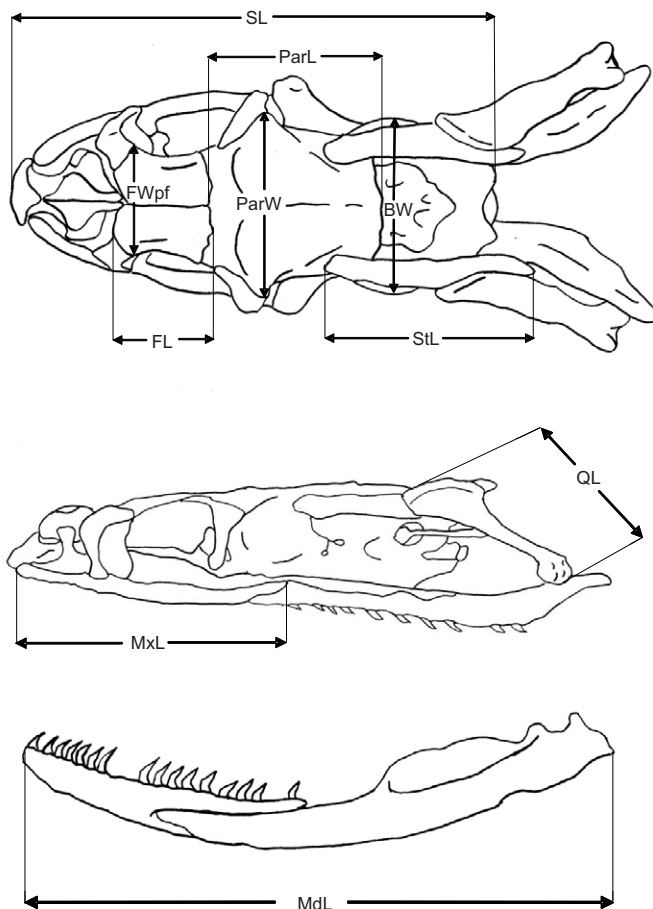


Fig. 3. Dorsal (upper) and lateral (lower) views of a natricine skull to show osteological measurements. Adapted from Dwyer and Kaiser (Dwyer and Kaiser, 1997). BW, braincase width; FL, frontal length; FwPp, width of the frontals taken at the prefrontal process; MdL, mandible length; MxL, maxilla length; ParL, parietal length taken at midline; ParW, maximum parietal width; QL, quadrate length; SL, skull length from the nasal to the occipital condyles; StL, supratemporal length. Pterygoid and palantine length measurements are not shown.

Gape

For this study, I define gape as the circumference of the posterior oral cavity. I empirically measured maximum gape using 18 previously frozen but not chemically preserved individuals (187–703 mm SVL, mean \pm s.d. 469 ± 173 mm). In each case, the head was separated from the body ~3 cm posterior to the cranium. This reduced physical resistance as the mouth of the snake was slid down a tapered metal cone (a ring or bracelet mandrel). To determine maximum gape, I moved each head down the mandrel until it would not continue any farther without substantial force and potential damage to the bones or soft tissue. At this point, I measured the diameter of the cone at the corner of the mouth and the straight-line distance between the distal ends of the left and right mandible (intermandibular distance). The skulls were then cleaned of soft tissue and I measured the osteological dimensions described above.

Ingestion performance

Herein, I define ingestion performance or effort in two ways: (1) total time (defined below) and (2) total number of pterygoid protractions (both anterior and lateral) required to position and ingest prey. I video-recorded 21 individuals of *N. fasciata* (235–551 mm SVL, mean \pm s.d. 439 ± 85 mm) feeding on shiner minnows (*Notemigonus* sp.) and frogs (*Acris* or *Lithobates* spp.). Some individuals were used in both fish and frog feeding trials, but no individual was used more than once for a single prey type. Feeding trials were conducted in a small arena with a mirror placed at a 45 deg angle to allow both a dorsal and a lateral view of the feeding. I used live prey in the feeding trials to ensure that the costs of feeding included overcoming any antipredatory behaviors. Relative fish mass ranged between 3 and 24% of the snake's mass and frog mass was between 3 and 27% of the snake's mass. By using a range of relative prey sizes and types, I was able to evaluate general feeding performance rather than what may be optimal according to predator size (Hampton, 2013). Prey were presented on a flat dry surface in the arena. If the fish were not quickly attacked, they were returned to water to ensure that they displayed vigorous antipredatory behaviors during successful feeding trials. For each feeding trial, I recorded the feeding time defined as the total time between initial prey capture and the time at which the prey had passed from the oral cavity into the esophagus. I also counted the total number of pterygoid protractions (both lateral and anterior), starting from initial capture, including positioning and ingestion until the prey had passed through the buccal cavity and pterygoid protractions ceased. The methods used in this study were approved by the University of Louisiana at Lafayette Institutional Animal Care and Use Committee no. 2008-8717-016.

Analyses

All data were log₁₀-transformed prior to analysis. I used homogeneity of slopes tests to determine how each skull bone and gape scaled with SVL and with skull length. Specifically, I compared the slopes of gape and each osteological dimension against SVL to an isometric line.

To determine which morphological characteristics were most important to gape circumference, I used the residual sums of squares from multiple regressions to compute the goodness of model fit using Akaike information criterion corrected for small sample sizes (AICc). With AIC model selection, the model with the lowest value is considered to be the best fit, given the models available. Using the AICc values, I calculated the change in AIC (Δ_i). Typically, well-supported models have $\Delta_i < 2$, and those with higher values have considerably less support. Finally, I calculated Akaike weight (w_i), which is the ratio of the Δ_i for a given model divided by the sum of all weights. Akaike weights provide a quantification of the likelihood for each model (Burnham and Anderson, 2002; Mazerolle, 2006).

For the external measurements, I compared the following models: head length, head width, quadrate length, jaw length, intermandibular distance, and an all-bone model that included head length, head width, quadrate length and jaw length. I analyzed the osteological dimensions using the following models: skull length, mandible length, supratemporal length, quadrate length, parietal width, a jaw-and-suspensorium model (supratemporal length, quadrate length and mandible length), and a full model that included all five measurements. For both external and osteological model comparisons, I also included a null model for which the variance of the grand mean of gape circumference served

as the sums of squares. I did not include body size in the model comparison because I was interested in the effects of skull bones on absolute gape, regardless of body size.

I used a multiple regression to determine whether gape size influenced ingestion performance using either total feeding time or the number of pterygoid protractions as the dependent variables. A similar analysis was performed using only the time and number of pterygoid protractions required to ingest the prey, after SVL and relative prey mass were included as the independent variables. I ran separate analyses for snakes fed fish and those fed frogs.

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Competing interests

The author declares no competing financial interests.

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