ECOPHYSIOLOGY

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The functional meaning of "prey size" in water snakes (*Nerodia fasciata, Colubridae*)

Abstract The evolutionary success of macrostomatan (enlarged-gape) snakes has been attributed to their ability to consume large prey, in turn made possible by their highly kinetic skulls. However, prey can be "large" in several ways, and we have little insight into which aspects of prey size and shape affect skull function during feeding. We used X-ray videos of broad-banded water snakes (*Nerodia fasciata*) feeding on both frogs and fish to quantify movements of the jaw elements during prey transport, and of the anterior vertebral column during post-cranial swallowing. In a sample of additional individuals feeding on both frogs and fish, we measured the time and the number of jaw protractions needed to transport prey through the buccal cavity. Prey type (fish vs. frog) did not influence transport kinematics, but did influence transport performance. Furthermore, wider and taller prey induced greater movements of most cranial elements, but wider prey were transported with significantly less anterior vertebral bending. In the performance trials, heavier, shorter, and wider prey took significantly more time and a greater number of jaw protractions to ingest. Thus, the functional challenges involved in prey transport depend not only upon prey mass, but also prey type (fish vs. frog) and prey shape (relative height, width and length), suggesting that from the perspective of a gape-limited predator, the difficulty of prey ingestion depends upon multiple aspects of prey size.

Keywords Diet · Feeding performance · Foraging ecology

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Introduction

Most snakes can consume prey that is larger than their own heads. This phenomenal ability enables them to feed on prey items that encompass a broad range in terms of type, size, and shape (e.g., Gans 1952, 1961; Cundall and Greene 2000). The dietary diversity among snakes is paralleled by an equal diversity in morphology and function of the cranial and post-cranial systems in snakes (see Cundall and Greene 2000 for an overview). For example, feeding on large prey requires extensive mobility of the cranial elements, which is made possible by the liberation of multiple jaw elements from one another and from the braincase, as well as the elongation of various skull and jaw elements (e.g., Dullemeijer 1956; Gans 1952, 1961; Frazzetta 1966; Kardong 1977; Cundall and Gans 1979; Cundall 1987, 1995; Cundall and Shardo 1995; Kardong and Berkhoudt 1998). Anterior bending of the vertebral column aids in ingestion and swallowing once the leading edge of the prey animal moves into the esophagus, and especially after the prey animal passes the jaws completely (e.g., Dullemeijer and Povel 1972; Kardong 1986; Janoo and Gasc 1992; Cundall 1995; Moon 2000; Kley and Brainerd 2002).

Much of the extensive research on the feeding mechanics of snakes has been stimulated by the hypothesis that adaptations to ingest large prey have played a central role in the spectacular evolutionary and ecological success of snakes (Gans 1961; Greene 1997;

Cundall and Greene 2000). Certainly, the most speciose and abundant snakes belong to a single clade, the macrostomatans, named so for their ability to ingest relatively large prey (Rieppel 1988; Cundall and Greene 2000). In contrast to most lizards and to basal snakes, many macrostomatan species ingest prey that are very large relative to the size of the predator (e.g., Forsman and Lindell 1993; Rodriguez-Robles et al. 1999). However, Greene (1983) has argued that prey can be "large" in more than one dimension such that (for example), the physical challenges associated with ingesting a short rounded prey item (e.g., a rat) may be greater than, and/or different from, the challenges imposed by ingesting an elongate prey item of the same mass (e.g., an eel). We need to understand the nature and magnitude of those challenges if we are to comprehend the functional and ecological significance of gape-limitation in snakes. However, although many studies have addressed the anatomy and mobility of the cranial elements, few have examined how prey size, shape, or type influence feeding performance in snakes (reviewed in Cundall 1987; Cundall and Greene 2000). As with the transport of prey by the jaws, the movements of post-cranial swallowing probably also depend upon the size and shape of prey, but to our knowledge no study has examined this question.

As snakes cannot reduce the size of a prey item by mastication, they must swallow prey items as a whole (except in unusual circumstances: Shine and Schwaner 1985). Hence, tall or wide prey may be difficult to ingest (Cundall and Greene 2000), and thus, prey shape relative to mass may play a key role in the foraging ecology of snakes. The nutritional benefit obtainable from a given prey item likely will be broadly proportional to its mass, whereas the feasibility of ingesting it (or the time and energy required to do so) will depend not only on prey mass, but also on features such as prey type (some kinds of animals may be easier to ingest than others) and shape (relatively tall or wide prey may pose particular problems). In an influential conceptual model, Arnold (1993) predicted that the major functional challenges associated with ingestion of relatively tall or wide prey by gape-limited predators may increase handling times

and thus render snakes vulnerable to predation, increase their energy costs relative to nutritional benefit, and reduce the amount of time available for other biologically important activities such as reproduction and thermoregulation. Nonetheless, the influence of prey shape on feeding performance and foraging ecology has received little study (but see Pough and Groves 1983; Shine 1991). As a result, it remains unclear which aspects (if any) of prey shape affect feeding performance and thus, at least potentially, the foraging ecology of snakes.

Within a species, larger snakes often consume absolutely wider, taller, longer, and heavier prey than do smaller conspecifics; prey type often changes also (reviewed in Arnold 1993; Cundall and Greene 2000). Gape-limitation often has been invoked as the primary cause for these ontogenetic shifts in prey type (reviewed in Arnold 1993; Cundall and Greene 2000). As required by this hypothesis, absolute prey dimensions influence the amount of distention undergone by the macrostomatan skull during prey transport (Kardong 1977; Cundall 1987; Cundall and Greene 2000). However, we do not know how a prey animal's overall shape (i.e., the effect of its height, width and length) will determine which cranial elements are involved in the transport process, the extent to which they are used, or which prey dimensions present the most difficultly to the transport process. As a result, we have little understanding of *how* gape may become limited when snakes feed on differently shaped prey, or of the proximate factors potentially influencing foraging ecology in snakes.

In order to understand relationships among morphology, performance, ecology, and fitness in the snake feeding system, we must first understand the mechanistic interactions among these elements. The banded water snake, *Nerodia fasciata*, is well suited for research on these issues because it is a dietary generalist that undergoes an ontogenetic change from eating mainly fishes as juveniles to eating mainly frogs as adults (Mushinsky et al. 1982; Gibbons and Dorcas 2004). In this study, we examined the influence of prey attributes (size, shape, and type) on cranial and post-cranial transport in this species, as well as on feeding performance (transport time, number of jaw protractions).

Table 1 Relevant morphological measurements and numbers of trials analyzed for each *Nerodia fasciata* used in the kinematics portion of this study

Variable	*N. fasciata* 1	*N. fasciata* 2	*N. fasciata* 3	*N. fasciata* 4	*N. fasciata* 5
SVL (cm)	58.5	58	59	42	52.5
# Trials	13	3	2	13	1
Head length (cm)	2.24	2.41	2.14	1.75	2.05
Head width (cm)	1.71	1.91	1.53	1.15	1.57
F-P quadrate right (cm)	2.20	1.96	1.91	1.66	1.84
F-P quadrate left (cm)	2.23	2.01	1.91	1.68	1.75
F-P maxilla right (cm)	6.37	6.77	6.68	4.98	6.53
F-P maxilla left (cm)	6.37	6.77	6.68	4.98	6.53

Head length was measured as the distance from the snout-tip to the posterior most portion of the parietal bone, head width was taken at the widest point along the head, and all F-P measures are the distances from the most distal portions of these bones to the frontoparietal joint

Materials and methods

Subjects and experiments

Our experimental procedures were approved by ethics committees at the University of Antwerp and Tulane University. To study movements of the cranial and post-cranial elements, we used X-ray videography to record feeding in five adult (42–58 cm snout to vent length, =SVL) broad-banded water snakes (*N. fasciata*) obtained from a commercial supplier in Antwerp, Belgium (Table 1). We maintained each snake separately in a 37.8-l terrarium at a temperature of 25°C and 12-h light cycle, with access to water at all times.

To increase each snake's motivation to feed, snakes were fasted for up to 2 weeks prior to the recordings. To test the effects of *prey shape*, we used prey of different sizes and shapes: pre-killed fish (*Carassius auratus* and *Poecilia latipinna*) and frogs (*Rana esculenta* and *Xenopus laevis*) from 0.7 to 62 g in mass, from 0.92 to 2.30 cm in height, and from 0.68 to 3.23 cm in width. To test the effects of *prey type*, we used fish and frogs that overlapped in size and shape, from 3 to 6 cm (SVL for frogs, total length for fish), 2–3 cm maximum width, and 1.42–2.10 cm maximum height. Overall, we recorded X-ray videos, in dorsal view, of 40 feeding trials from the five individuals.

To measure feeding performance, we used a standard video system (60 Hz) to record feeding in eight snakes ranging in size from 38 to 62 cm SVL (Table 2) that were collected near Lafayette, Louisiana and housed as above.

Kinematics

For X-ray videography, we used a Philips Optimus X-ray generator at 60 kV. Images were captured with a Redlake MotionPro digital video camera set at 60 fps and mounted on a 42 cm diameter image intensifier. An object of known length visible in each video sequence enabled scaling of all measurements to real units. We analyzed the X-ray videos by importing them into PEAK Motus 6.1 (PEAK Inc., Englewood, CO USA) and digitizing homologous landmarks on the heads of snakes for each frame of the feeding sequence. The landmarks used (see Fig. 1) were the center of the midline of the frontoparietal joint (1); the posterior most edge of the right and left retroarticular processes (2,3); the posterior most portions of the right and left maxillary bones (4,5); the anterior most portion of the right and left mandibular tips (6,7); the tip of the snout (8); and three analogous landmarks placed at the center of the anterior vertebral column just anterior to, at the point of greatest curvature, and just posterior to the "bend" in the anterior vertebral column (9,10,11; see Fig. 1). We used analogous landmarks in the anterior vertebral column instead of morphologically homologous landmarks because bending was not confined to specific vertebrae.

From the landmarks, we calculated the following kinematic variables: maximum displacements of right and left maxillae from the frontoparietal joint; maximum displacements of right and left quadrates from the frontoparietal joint; maximum and minimum angles between the individual retroarticular processes, the frontoparietal joint and the snout tip; maximum lateral displacements of the mandibular tips from one another; and the maximum anterior vertebral bending angle among the three vertebral landmarks. We defined a bent vertebral column as having a bending angle $>0°$. We calculated bone displacements by subtracting the maximum distance of each bone from its resting position relative to the frontoparietal joint (Table 2). For analysis, we retained the greatest bone displacements observed during each feeding sequence.

Performance

To examine how prey types, sizes and shapes affect prey transport, we fed eight snakes live frogs of 6.2–7.0 g (*Hyla cinerea, Rana clamitans, R. esculenta*, and *Xenopus laevis*) and fish of 0.5–15 g (*Fundulus grandis*). To con-

Table 2 Relevant morphological measurements, numbers of trials, and mean ± 1 SEM performance values for each *Nerodia fasciata* used in the performance portion of this study

Individual	SVL (cm)	# Trials	Transport time (s)		Jaw protractions (#)	
			Fish	Frogs	Fish	Frogs
N. fasciata 6	62	10	43.1 ± 1.52	**568 ± 1.65**	14.1 ± 1.32	**96.4 ± 1.23**
N. fasciata 7	38	6	**143.2 ± 1.29**	158 ± 1.63	15.1 ± 1.12	57.0 ± 1.01
N. fasciata 8	45	2	33 ± NA	416 ± NA	26 ± NA	61.9 ± NA
N. fasciata 9	52	6	19.4 ± 1.27	140 ± 1.24	16.9 ± 1.16	46.7 ± 1.61
N. fasciata 10	65	4	20.6 ± 1.12	488 ± 1.72	16.8 ± 1.07	72.4 ± 1.67
N. fasciata 11	60	32	12.2 ± 1.07	194 ± 1.66	12.8 ± 1.06	63.4 ± 1.43
N. fasciata 12	44	2	**141 ± NA**	254 ± NA	30 ± NA	48 ± NA
N. fasciata 13	38	4	**117.7 ± 1.29**	188 ± 1.23	27.6 ± 1.15	42.2 ± 1.07
Total		66				

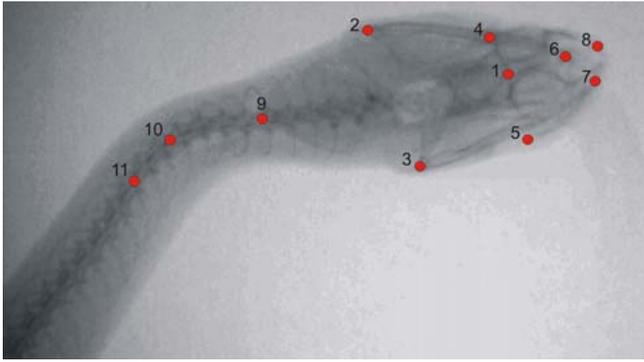Performance variables that had a significant individual effect are indicated in bold

Fig. 1 Frame taken from an X-ray video sequence showing the landmarks used to quantify prey transport and swallowing

trol for the snake's motivation to feed, snakes were fed one prey item per trial every 2 weeks. We used live prey to approximate the true handling requirements for different prey types. For these trials, we measured two aspects of prey transport performance. First, we recorded the time required to pass an entire prey item from the most anterior portion of the buccal cavity through to the anterior most part of the esophagus, which was determined by observing the external "bulge" of the prey item as it passed into the anterior trunk. Timing was initiated once the snake aligned the prey with the long axis of its braincase and began the jaw movements of ingestion, and ceased once the most posterior portion of the prey passed the anterior most portion of the esophagus. Timing measurements were recorded to the nearest tenth of a second. Second, we recorded the number of jaw protractions used to transport each prey item.

Statistical analyses

We used SPSS (version 11.5; SPSS Inc.) for all statistical analyses. Prior to the analyses, we $\log_{10}$ transformed all variables to meet the assumption of homoscedascity for regression analyses (Sokal and Rohlf 1981; Kachigan 1991), and used Lillifores tests to test for the normality of the $\log_{10}$ transformed data.

Kinematics

To test for the effects of *prey type*, independently of size or shape, on prey transport kinematics, we used a MANCOVA with all prey dimensions and snake SVL as the covariates, bone displacements and kinematic variables as the dependent variables, and prey type as the factor. Individual was introduced into this analysis as a random factor in the subsequent one-way ANCOVAs. All fish and frog species were pooled in this analysis because two one-way MANCOVAs showed that all kinematic variables did not significantly differ between fish or frog species once prey dimensions and snake SVL

were taken into account ($P > 0.50$ for both MANCOVAs), and all subsequent one-way ANCOVAs (with individual effects introduced as a random factor) were also non-significant ($P > 0.50$ for all kinematic variables for both fish and frog species).

To test the effects of *prey size* on feeding kinematics, we used multiple regression (backward model). In these regressions, maximum mandibular displacement, maximum maxillary displacement, maximum quadratic displacement, right and left quadratic rotations, and maximum anterior vertebral angle were each used as the dependent variables, with prey dimensions as the independent variables. To account for individual variation among kinematic trials, we used dummy variables to represent individuals (following Sokal and Rolf 1981). The results from the multiple regression analyses show the bivariate relationship between the dependent variable and each independent variable when all other independent variables (including individual variability represented by the dummy variables) were held constant at their means.

To examine the effects of *prey shape* on transport kinematics, we first generated several "size-free" variables for prey dimensions by regressing prey width, length, and height against prey mass using typical linear least-squares regressions. Residual scores from these regressions provided size-free dependent variables in multiple regression models in the same manner as was done for the absolute prey dimensions described above.

Performance

To examine whether *prey type* significantly influenced transport performance, independently of prey size or shape, we used a MANCOVA with prey dimensions and snake SVL as the covariates, transport time and number of jaw protractions as dependent variables, and prey type as the factor. Individual was introduced into this analysis as a random factor in the subsequent one-way ANCOVAs. All frog species were pooled in this analysis because two one-way ANCOVAs (with individual effects introduced as a random factor) showed that feeding performance did not significantly differ among frog species once prey dimensions and snake SVL were taken into account ($P > 0.50$ for both transport time and number of jaw cycles used to transport different frog species).

To examine the effects of *prey size* on transport performance, we computed two multiple regressions using backwards models, with transport time and number of jaw protractions as the dependent variables, and absolute prey dimensions as the independent variables. To account for individual variation among performance trials, we used dummy variables to represent individuals in the regression analysis.

To examine the effects of *prey shape* on transport performance, we used "size-free" variables (residual scores) as described above.

Results

Kinematics

Thirty-one out of the 40 feeding trials recorded here yielded a full kinematic data set. One additional trial yielded data for post-cranial transport only. Overall, the MANCOVA testing for differences in ingestion kinematics between prey types—independent of size or shape—was non-significant (Wilk's Lambda = 0.58, $F_{5, 17}$ = 2.28, $P > 0.05$), as well as all subsequent one-way ANCOVAs (all $P > 0.50$ for both kinematic variables and the interaction term prey type * individual). Therefore, prey type—independent of size or shape—did not significantly influence ingestion kinematics.

In the multiple regression analyses, prey height significantly influenced maxillary ($\beta = 0.37$, $r^2 = 0.67$, $P < 0.05$), and quadratic displacement ($\beta = 0.45$, $r^2 = 0.46$, $P < 0.05$; Fig. 2) even after controlling for significant variation among individuals ($P < 0.05$). However, wider prey were significantly associated with increased mandibular displacement ($\beta = 0.53$, $r^2 = 0.65$, $P < 0.05$), and this relationship did not vary significantly among individuals ($P > 0.05$). No significant model was produced for quadratic rotation ($P > 0.05$). Size-adjusted prey height significantly influenced both maxillary ($\beta = 0.39$, $r^2 = 0.67$, $P < 0.05$), and quadratic displacement ($\beta = 0.21$, $r^2 = 0.66$, $P < 0.05$) even after controlling for significant variation among individuals ($P < 0.05$), and was the only size-adjusted prey dimension to significantly influence ingestion kinematics.

As with ingestion kinematics, post-cranial transport kinematics were not affected by prey type (Wilk's Lambda = 0.58, $F_{5,17}$ = 2.28, $P > 0.05$), individual ($F_{4, 2.31}$ = 1.67, $P > 0.50$), or the interaction term between these two variables ($P > 0.50$). However, in addition to affecting jaw kinematics, prey width influenced anterior vertebral bending ($\beta = -0.40$, $r^2 = 0.60$, $P < 0.05$), even after controlling for significant variation among individuals ($P < 0.05$). Specifically, wide prey were transported with less anterior vertebral bending during the period of concertina (i.e., accordion-like) bending as the prey moved completely into the esophagus (Fig. 2). Size-adjusted prey measures did not significantly influence anterior vertebral bending ($P > 0.05$). Overall, both absolute prey dimensions (mainly height and width), and prey shape (relative height), affected transport kinematics.

Performance

The MANCOVA testing for differences in feeding performance between prey types, independent of size or shape, was significant (Wilk's Lambda = 0.685, $F_{2, 53}$ = 13.7, $P < 0.05$). Upon inspection of the subsequent one-way ANCOVAs, both the number of jaw protractions used during ingestion (univariate $F_{1, 2.79}$ = 25.5, $P < 0.001$; individual: $F_{7, 1.87}$ = 6.70, $P < 0.05$) and ingestion time (univariate $F_{1, 2.78}$ = 6.71, $P < 0.05$; individual: $F_{7, 1.46}$ = 4.76, $P < 0.05$) differed between prey types and individuals, independently of prey size and shape (Fig. 3a, b), even after Bonferonni correction for multiple comparisons (following Rice 1989). Additionally, the interaction term between individual and prey type also significantly influenced ingestion time ($F = 19.0$, $P < 0.05$) and the number of jaw protractions used during ingestion ($F = 10.5$, $P < 0.05$). Therefore, transport performance differed significantly between prey types and individuals. Specifically, when snakes fed on live frogs, the frogs often wedged their hind legs into the corners of the snakes' mouths, thereby slowing down
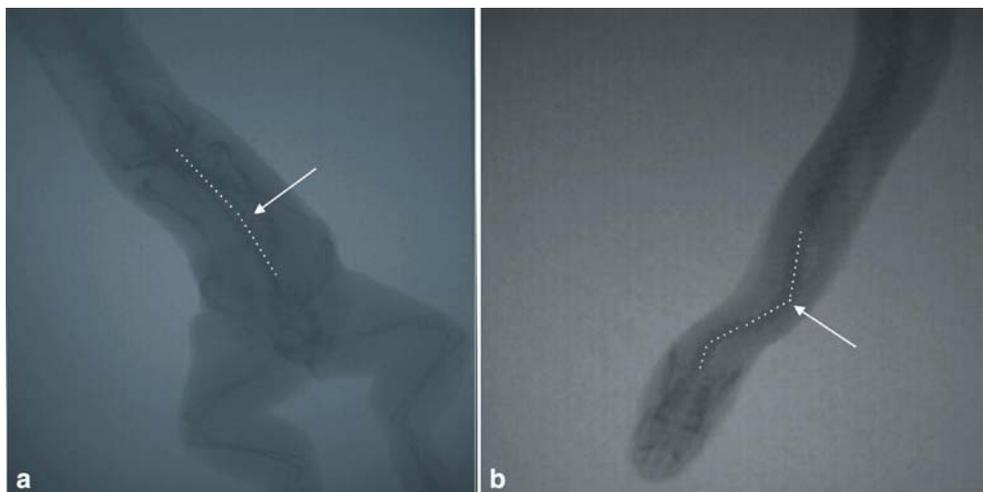

Fig. 2 Representative videographic images of the ingestion and post-cranial swallowing of **a** a frog and **b** a fish. Note the extensive displacement of all cranial elements for both frog and fish, and that anterior vertebral bending (measured at the *arrow* as the angle among the adjacent *white dotted lines*) has not yet become pronounced for the frog, which has not yet fully passed the jaws

the transport process and causing the snakes to continually ratchet their pterygoid bones and teeth over the frog in order to maintain their hold. Additionally, all frog species in this study exhibited this anti-predatory behavior in at least one feeding trial. Fish presented no such defense, and hence were transported faster and with fewer jaw protractions.

Prey size and dimensions also influenced ingestion time ($r^2 = 0.88$, $P < 0.05$) as indicated by the multiple regression. Ingestion time was affected by prey mass ($\beta = 0.54$, $P < 0.05$), prey length ($\beta = -0.35$, $P < 0.05$), prey width ($\beta = 0.40$, $P < 0.05$), and individual ($P < 0.05$). Similarly, the overall effects of prey size and dimensions on the number of jaw protractions used to ingest prey were significant ($r^2 = 0.76$, $P < 0.05$) in the multiple regression. The number of jaw protractions used to ingest prey was influenced by prey length ($\beta = -0.50$, $P < 0.05$), prey mass ($\beta = 0.53$, $P < 0.05$), prey width ($\beta = 0.48$, $P < 0.05$), and individual ($P < 0.05$). Therefore, absolutely heavy, short, and wide prey took more time and jaw protractions to swallow than did the other kinds of prey tested.

Size-free residuals representing prey shape significantly affected ingestion time ($r^2 = 0.77$, $P < 0.05$) in the stepwise regression. Ingestion time was solely affected by residual prey width ($\beta = 0.29$, $P < 0.05$). Similarly, the overall regression of residual prey dimensions on the number of jaw protractions used to ingest prey was significant ($r^2 = 0.58$, $P < 0.05$). The number of jaw protractions used to ingest prey was influenced by residual prey length ($\beta = -0.33$, $P < 0.05$) and residual prey width ($\beta = 0.34$, $P < 0.05$). Furthermore, transport time was highly correlated with the number of jaw protractions used to ingest prey ($R = 0.86$, d.f. = 65, $P < 0.05$). Therefore, relatively short and wide prey took more jaw protractions to transport than did other prey shapes in this sample, and relatively wide prey took more time to ingest.

Discussion

The prey items consumed by snakes vary in many respects that may influence the ease with which they can be ingested. Although a high proportion of previous papers on this topic simply refer to "prey size" constraining ingestion, the reality is more complex. Absolute prey mass relative to snake mass certainly is one such trait, but even at identical relative prey mass, some prey may pose greater functional challenges than others. Our analysis provides the first detailed examination of such parameters. At least for banded water snakes, the difficulty of transporting a prey item is influenced by prey type (frogs are more difficult than fishes) and prey shape (relatively short, wide, tall prey items pose greater difficulties) as well as prey size. Although some of these results are not surprising, they provide empirical support for critical but rarely examined assumptions about prey transport and especially, about the functional meaning of commonly used terms such as "gape-limitation" and "prey size".

In particular, our data clarify the specific functional challenges imposed on snakes by prey items that vary in behavior, relative mass and/or relative circumference. The exact relationships are likely to be complex, and to vary among species. For example, the height of prey items consumed by cottonmouth moccasins (Agkistrodon piscivorus) was significantly correlated with relative quadrate length (corrected for body size) of the predator (Vincent et al. 2004). Therefore, snakes with relatively longer quadrate bones may be able to consume a wider range of the prey sizes and shapes available in their habitat. This scenario is plausible because a longer jaw suspension would enable the jaws to better conform to a prey's overall shape through increased gape (Cundall 1987). Nevertheless, the functional data we present here clearly show that multiple aspects of predator morphology and function, and prey size, shape, and anti-predator
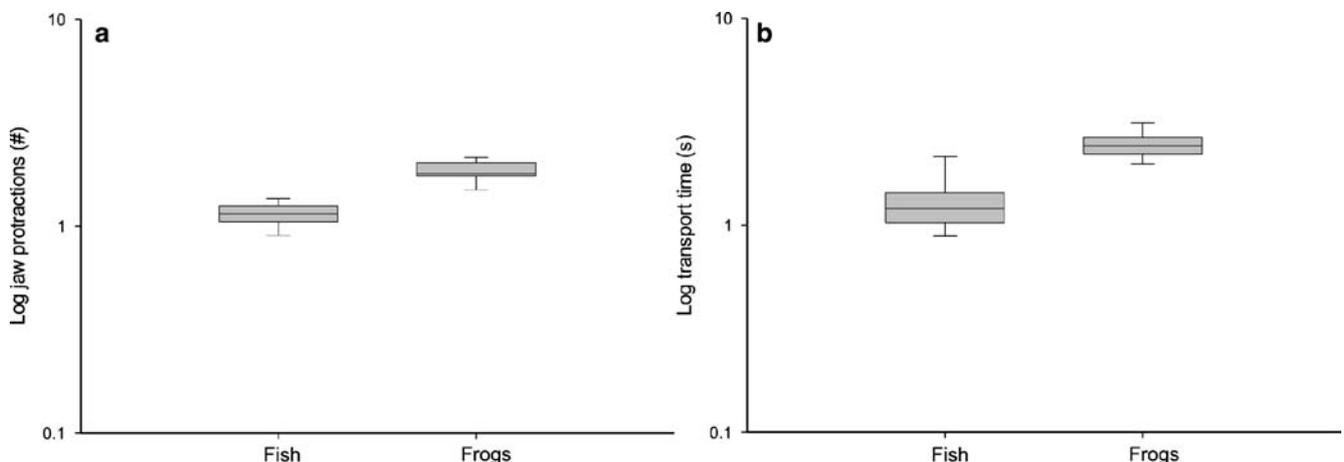

Fig. 3 Box plots of the $\log_{10}$ value of **a** jaw protractions for fish versus frogs and **b** transport time for fish versus frogs. The *solid line* indicates the mean for each plot, bottom of the box indicates the 25th percentile, the top of the box indicates the 75th percentile, *error bars* indicate ± 1 SEM. Note that frogs require significantly more jaw protractions and time to transport than fish

behavior must be taken into account simultaneously in order to understand the feeding dynamics of snakes.

Although a few previous studies have reported statistically significant correlations between skull shape (not only size) and consumed prey dimensions (Shine 1991; Forsman and Lindell 1993; Vincent et al. 2004) in snakes, this study is the first to quantitatively demonstrate that prey shape significantly influences skull function in any snake. Specifically, we found that prey height (in both absolute and relative terms) significantly influenced both maxillary and quadratic displacement in the banded water snake, whereas prey width was significantly associated with greater intermandibular separation (see Results). These data thus provide the first functional link between consumed prey dimensions and skull form in a macrostomatan snake (i.e., different prey dimensions have different effects on feeding kinematics/performance). Yet, no study to our knowledge has tested whether skull form and diet are significantly related after correction for phylogenetic history. Nevertheless, a robust comparative study—that accounts for phylogenetic history—is the necessary next step before one can invoke adaptive explanations for these observed relationships among feeding morphology, function, and diet in macrostomatan snakes.

In most snakes, once the leading edge of the prey animal moves past the jaws and into the esophagus, concertina (i.e., accordion-like) bending by the anterior most vertebrae begins to aid in ingestion, probably by enhancing upper-jaw protraction (e.g., Dullemeijer and Povel 1972; Kardong 1986; Cundall 1995; Kley and Brainerd 2002). After the prey animal completely passes the jaws, concertina bending of the vertebral column draws prey further into the esophagus and then undulatory bending pushes it to the stomach (Janoo and Gasc 1992; Moon 2000; Kley and Brainerd 2002). In contrast to most snakes, banded water snakes typically use little anterior vertebral bending during post-cranial swallowing (Kley and Brainerd 2002; present study). Although we observed considerable anterior vertebral bending ($>90°$ of bending) during a few feeding sequences on small fish prey, the snakes typically used only modest amounts of bending during post-cranial swallowing (28° mean bending angle).

We expected that wider prey would require more anterior vertebral bending to ingest and swallow, but the reverse was true: wider prey induced less anterior vertebral bending during ingestion and post-cranial swallowing. Why did our snakes use so little vertebral bending during the initial phases of post-cranial transport? During the first two phases of swallowing in snakes, concertina bending of the axial skeleton mainly helps to protract the upper jaws (Kley and Brainerd 2002). Elongate and firm prey may not require substantial movements by the anterior most vertebrae to aid in ingestion because such prey do not bulge outward at the mouth, and thus do not hinder jaw protraction via lateral rotation of the head (Kley and Brainerd 2002). Thus, the shape and stiffness of the prey we used simply may not require anterior vertebral bending to aid in feeding, particularly for relatively small prey animals. However, prey width did affect transport kinematics and performance. Very wide prey animals may stretch the neck and abduct the anterior ribs so far that vertebral bending becomes difficult. This would explain why the snakes in our study used only jaw movements to ingest relatively tall fish and wide frogs.

Once the prey item has moved completely past the jaws, the last two phases of swallowing involve first a brief period of concertina bending of the anterior vertebral column that pulls prey further into the esophagus, and then undulatory bending that pushes it toward the stomach (Janoo and Gasc 1992; Moon 2000; Kley and Brainerd 2002). In our study, snakes feeding on relatively large fishes or frogs used vertebral (undulatory) bending to push the prey item toward the stomach. Wide prey items were associated with increased anterior vertebral bending during this phase. Overall, the type and degree of vertebral bending used during post-cranial transport depend upon the size, shape, and stiffness of the prey consumed. Therefore, diet in snakes depends not only on prey availability but also on the size and shape of the prey relative to both the snake's head and trunk (i.e., the ability of snakes to consume available prey types).

The effect of prey type on transport performance, due in part to the anti-predator behavior of frogs, is particularly interesting because our study taxon undergoes an ontogenetic shift in diet. Juvenile banded water snakes primarily consume small fish (mosquito fish and killifish) whereas adults primarily take large ranid and bufonid frogs (Kofron 1978; Mushinsky et al. 1982). Why do juvenile water snakes not consume large quantities of frogs that are common in their marshland habitat? Possible explanations include:

1) Large frogs are mechanically too difficult for juveniles to consume. In keeping with this idea, wider prey required greater displacement of all cranial elements (implying an increased mechanical difficulty). Therefore, juveniles simply may be unable to open their jaws wide enough to ingest large frogs.
2) Large frogs are energetically too costly for juveniles to consume. In keeping with this idea, increased prey size was associated with increased transport time and number of jaw protractions, suggesting an increased energetic cost.
3) Juvenile snakes are at risk if prey swallowing requires a long time. Juvenile water snakes are vulnerable to avian, anuran, and mammalian predators (Werler and Dixon 2000; S.E. Vincent, personal observation), whereas adult water snakes are too large for most of these predators to consume. Thus, the additional time required to ingest a large anuran prey item might expose a juvenile water snake to greater risk of predation (see Fig. 3a, b). The almost tenfold difference in maximum transport time for fish compared to frogs (188 vs. 1,680 s) might thus enhance survival

rates in juvenile snakes that select small fish rather than large frogs.

As few previous studies have examined the effects of prey shape on the kinematics of intraoral transport in snakes (but see Cundall 1995; Kley and Brainerd 2002), the generality of our results is difficult to assess. Further studies are needed to investigate how prey shape and behavior, rather than simply prey size, influence effective gape size across a phylogenetically diverse group of snakes. Such an approach likely would shed significant light on the evolution of dietary breadth in snakes, as well as currently unknown functional details of the unique macrostomatan feeding mechanism. Finally, we suggest that more laboratory and field-based studies examining feeding performance within macrostomata are needed, especially studies examining snakes feeding upon prey types other than standard laboratory prey such as mice. Such studies are key to elucidating how gape is related to feeding ecology, and ultimately to fitness, in snakes, and consequently how the enlarged gape of macrostomatan snakes evolved.

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