

Are ontogenetic shifts in diet linked to shifts in feeding mechanics? Scaling of the feeding apparatus in the banded watersnake *Nerodia fasciata*

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Summary

The effects of size on animal behaviour, ecology, and physiology are widespread. Theoretical models have been developed to predict how animal form, function, and performance should change with increasing size. Yet, numerous animals undergo dramatic shifts in ecology (e.g. habitat use, diet) that may directly influence the functioning and presumably the scaling of the musculoskeletal system. For example, previous studies have shown that banded watersnakes (*Nerodia fasciata*) switch from fish prey as juveniles to frog prey as adults, and that fish and frogs represent functionally distinct prey types to watersnakes. We therefore tested whether this ontogenetic shift in diet was coupled to changes in the scaling patterns of the cranial musculoskeletal system in an ontogenetic size series (70–600 mm snout–vent length) of banded watersnakes. We found that all cranial bones and gape size exhibited significant negative allometry,

whereas the muscle physiological cross-sectional area (pCSAs) scaled either isometrically or with positive allometry against snout–vent length. By contrast, we found that gape size, most cranial bones, and muscle pCSAs exhibited highly significant positive allometry against head length. Furthermore, the mechanical advantage of the jaw-closing lever system remained constant over ontogeny. Overall, these cranial allometries should enable watersnakes to meet the functional requirements of switching from fusiform fish to bulky frog prey. However, recent studies have reported highly similar allometries in a wide diversity of vertebrate taxa, suggesting that positive allometry within the cranial musculoskeletal system may actually be a general characteristic of vertebrates.

Key words: biomechanics, functional morphology, jaws, morphology, muscle, ontogeny, reptile, snake.

Introduction

The fact that an organism's size has profound effects on its ecology, behaviour, and physiology is now axiomatic within biology (e.g. Calder, 1984; McMahon, 1984; Schmidt-Nielsen, 1984; Peters, 1986; LaBarbera, 1989; Brown and West, 2000). Accordingly, previous authors have developed several theoretical models to both understand and predict the functional challenges imposed on organisms by the physical laws of increasing size (e.g. Hill, 1950; McMahon, 1984; Richard and Wainwright, 1995; West et al., 2003). Because ectotherms often exhibit indeterminate patterns of growth, they are predicted to scale according to geometric similarity models [i.e. larger individuals are simply scaled-up versions of smaller individuals (Hill, 1950; McMahon, 1984)]. Yet, empirical data have revealed that few ectotherms actually display isometric growth for all of their morphological traits [e.g. frogs (Birch, 1999); fish (Richard and Wainwright, 1995); snakes (Vincent et al., 2006a; Herrel and Gibb, 2006)]. For example, Birch

(Birch, 1999) showed that the skull of marine toads (*Bufo marinus*) exhibits subtle, yet functionally important, changes over the course of post-metamorphic ontogeny in these animals (i.e. adductor foramen area scales allometrically whereas all other cranial elements scale geometrically). Although the proximate cause(s) of these allometric changes in form are often unclear, one plausible scenario is that ontogenetic shifts in ecology may drive adaptive changes in the scaling and hence functioning of the musculoskeletal system in animals (reviewed in McMahon, 1984; Carrier, 1996; Herrel and O'Reilly, 2006). Indeed, a wide diversity of animals exhibit marked ontogenetic shifts in habitat use and/or diet (e.g. Werner and Hall, 1974; Mushinsky et al., 1982; Werner and Gilliam, 1984; Shine and Wall, 2004), and these ecological shifts are commonly associated with modifications in whole-organismal behaviour and/or performance (e.g. Reilly and Lauder, 1988; Shaffer and Lauder, 1988; Carrier, 1996; Cook, 1996; Irschick, 2000; Herrel and O'Reilly, 2006).

Previous authors have argued cogently that alterations in feeding mechanics, and presumably feeding performance, are likely to be tightly linked to ontogenetic dietary shifts in animals [i.e. one of the 'ecological sieves' that contribute to realized diet in animals (Ferry-Graham et al., 2002)]. For instance, slider turtles (*Trachemys scripta*) switch from soft invertebrate prey as juveniles to tougher plant material as sub-adults, and increase notably in head size and bite force throughout this transition (Herrel and O'Reilly, 2006). Therefore, we suggest that it is crucial to understand the quantitative links amongst ontogenetic shifts in form, function, and ecology in order to understand why some taxa largely conform to the scaling predictions of geometric similarity models (e.g. Meyers et al., 2002) and others clearly do not (e.g. Richard and Wainwright, 1995; Vincent et al., 2006a).

In many ways snakes represent ideal candidates for studies of this nature, because numerous species are known to exhibit ontogenetic shifts in diet, especially semi-aquatic natricines such as watersnakes (Mushinsky et al., 1982; Cundall and Greene, 2000; Gibbons and Dorcas, 2004). The banded watersnake (*Nerodia fasciata*), for example, switches from relatively light (compared to the snake's body size), fusiform fish prey as juveniles and sub-adults to massive frog prey as adults (Mushinsky et al., 1982). Specifically, Mushinsky et al. (Mushinsky et al., 1982) showed that individuals less than 500 mm snout-vent length (SVL) primarily consume relatively light mosquito fish (e.g. *Gambusia affinis*) and topminnows (*Fundulus* sp.), whereas individuals exceeding 500 mm SVL begin taking massive bufonid (toad) and ranid (frog) prey. Interestingly, previous functional work has shown that fish and frog prey pose conflicting functional challenges to gape-limited animals such as snakes (i.e. predators that do not mechanically reduce the size of their prey prior to ingestion). For this reason, the banded watersnake is an excellent study species to test whether ontogenetic shifts in diet are coupled with changes in cranial form and function.

Previous research on the banded watersnake demonstrated that the greater width (independent of mass), but not length, of the frogs consumed by these snakes requires substantially more displacement of both the upper and lower jaw elements (relative to the braincase) compared to the transport of fusiform fish prey (Vincent et al., 2006b). The consumption of wide frog prey by gape-limited snakes thus appears to require relatively large feeding structures and hence maximum gapes (also see Mutoh, 1981; Phillips and Shine, 2006). In addition, if the frogs consumed are more massive than the fish (which we test in this study), then feeding on larger prey should require an increase in the maximum force outputs of the cranial musculature to presumably subdue larger prey. Therefore, snakes that feed on wide and massive frog prey are predicted to have long suspensorial elements (e.g. quadrate, supratemporal) in order to spread their jaws laterally over the frog's wide body and strong cranial musculature to transport heavy prey.

By contrast, feeding on fast, elusive fish prey poses radically different functional challenges to snake predators. Namely, when animals move through water they will experience

considerable drag forces and bow waves due to the high density and viscosity of the aquatic medium (Vogel, 1994). To overcome these hydrodynamic constraints when feeding, most aquatically feeding tetrapods have evolved a robust hyoid apparatus to enable inertial suction feeding mechanisms (Lauder, 1985; Bramble and Wake, 1985; Van Damme and Aerts, 1997; Herrel and Aerts, 2003). Yet, the hyoid has become largely reduced in snakes as a consequence of its specialization for chemoreception (Langebartel, 1968; McDowell, 1972; Schwenk, 1994), and hence snakes presumably cannot generate the substantial negative pressure within the oral cavity required to suction feed effectively. Instead, aquatically feeding snakes must strike at aquatic prey in a manner similar to that observed in terrestrial environments (e.g. Alfaro, 2002; Vincent et al., 2005); therefore, drag and bow waves are believed to have had a strong influence over the evolution of form-function relationships in aquatically feeding snakes (Young, 1991; Vincent et al., 2004; Hibbits and Fitzgerald, 2005). For these reasons, previous authors have predicted that aquatically feeding snakes should have relatively small heads for their body size, given that these hydrodynamic constraints scale as a function of the surface area exposed to the direction of flow (Young, 1991; Alfaro, 2002; Vincent et al., 2004; Hibbits and Fitzgerald, 2005).

Furthermore, feeding on fast, elusive fish prey has been hypothesized to require high jaw-closing velocities in snakes (Alfaro, 2002; Vincent et al., 2005). One possible way for aquatically feeding snakes to accomplish this task is by increasing the speed advantage of their jaw-closing lever system [i.e. a longer out-lever for a given in-lever resulting in a low mechanical advantage (MA) of the jaws (Herrel and Aerts, 2003; Westneat, 2003)]. However, vertebrate jaw lever systems optimized for speed have decreased force production, due to the fact that greater force transmission is achieved *via* a longer in-lever for a given out-lever [i.e. high MA of the jaws (Herrel and Aerts, 2003)]. Hence, one would predict that snakes that feed on fast prey should have low jaw-closing MAs for increased speed, whereas snakes that feed on slower and more massive prey should have high jaw-closing MAs for increased force transmission.

The average mass of frogs consumed by adult banded watersnakes is nearly four-times greater than the average mass of the fish prey consumed primarily by juveniles and sub-adult snakes (present study) (Mushinsky et al., 1982). However, little data exists on differences in the shape of these two types of prey. We therefore measured a large number of individuals of the most commonly consumed prey species of banded watersnakes to test for differences in both the size and shape of prey taken by juvenile *versus* adult banded watersnakes. If the assumption that these two prey types are morphologically distinct is correct, we expect that the cranial musculoskeletal system of banded watersnakes will exhibit specific patterns of allometric growth to accommodate this ontogenetic dietary shift. Specifically, we make three predictions about how the cranial musculoskeletal system should scale if frogs and fishes represent morphologically and functionally distinct prey items

to banded watersnakes: (1) the cranial bones should scale with positive allometry *versus* body size, so that fish-eating juveniles and sub-adults will have relatively smaller heads to minimize hydrodynamic constraints, and frog-eating adults will have relatively larger heads for consuming wider and more massive frog prey; (2) the maximum force outputs of the cranial muscles should exhibit positive allometry *versus* body size to enable larger frog-eating snakes to feed effectively on heavier prey; and (3) the mechanical advantage of the jaw-closing lever system should exhibit a positive slope against body size. In this way, fish-eating snakes will have low jaw-closing MAs for increased speed, and larger frog-eating snakes will have higher MAs for increased force transmission. We also tested these scaling predictions within the head alone to take into account differences in the growth rate of the head and body that may be due to factors unrelated to foraging ecology (i.e. sexual dimorphism, reproduction, etc.). We tested these scaling predictions by dissecting and measuring the cranial bones and muscles from an ontogenetic series of 18 preserved specimens of *Nerodia fasciata*.

Materials and methods

Prey morphometrics

To test for differences in size and shape between the frog prey consumed by snakes exceeding 500 mm SVL, and the fish prey consumed primarily by snakes less than 500 mm SVL (Mushinsky et al., 1982), we measured 432 preserved museum specimens of the most commonly consumed prey species of banded watersnakes throughout their geographic range (Table 1). Specimens were provided by the Tulane Museum of Natural History and from one private collection (S.E.V.). For each prey item, we recorded the mass (g), length (mm; i.e. standard length for fish and SVL for frogs), maximum head width (mm), and maximum body height (mm). We also recorded the lowest possible taxonomic order of each prey item (Table 1). We recorded the mass of the prey using a Denver instruments M-220 electronic balance (± 0.01 mg), and all linear prey dimensions to within 0.01 mm using Mitutoyo (Aurora, IL, USA) CD-15 DC digital callipers.

Snake specimens and morphometrics

To examine the ontogenetic scaling of the feeding system, we examined 18 preserved specimens of the banded watersnake, *Nerodia fasciata* (Linnaeus), from south-central Louisiana. The sample included five adult females [461.2 \pm 97.5 mm (mean SVL \pm 1 s.d.)], six adult males (436.6 \pm 146.3 mm) and seven juveniles (197.4 \pm 99.2 mm). This sample thus consisted of a large range of body sizes (70–600 mm SVL).

We first recorded the SVL for each specimen by measuring the length of dental floss required to reach along the mid-ventral surface of the specimen from the tip of the snout to the cloaca. Prior to dissection, we measured the maximum head width [widest part of the head when applying pressure on the posterior portion of the head to spread the quadrates and

Table 1. Prey species and number measured in this study

Prey type	No. sampled
Anura	
Bufonidae	
<i>Bufo terrestris</i>	1
Hylidae	
<i>Acris crepitans</i>	1
<i>Hyla cinerea</i>	18
<i>H. gratiosa</i>	3
Ranidae	
<i>Rana catesbiana</i>	3
<i>R. clamitans</i>	6
<i>R. sphenoccephala</i>	6
Pisces	
Centrarchidae	
<i>Lepomis macrochirus</i>	3
<i>L. punctatus</i>	9
<i>Micropterus salmoides</i>	2
Cyprinidae	
<i>Notemigonus crysoleucas</i>	52
Fundulidae	
<i>Fundulus grandis</i>	156
Ictaluridae	
<i>Ameiurus catus</i>	5
Poeciliidae	
<i>Gambusia affinis</i>	147
<i>Heterandria formosa</i>	20
Total	432

This sample represents the fish and frog species most commonly consumed by banded watersnakes (*Nerodia fasciata*) throughout their geographic range [see Gibbons and Dorcas (Gibbons and Dorcas, 2004) and references therein for an overview.

mandibles laterally (Miller and Mushinsky, 1990; King, 2002)] and jaw length (from the posterior end of the retroarticular process to the tip of the dentary). We used these two head measurements to compute a gape index that represents the cross-sectional area as the area of an ellipse with major and minor axes equal to jaw length and head width, respectively (see King, 2002):

$$\text{Gape index} = (\pi \times \text{jaw length} \times \text{head width}) / 4. \quad (1)$$

This index is based on the expected contributions of head width and jaw length to overall gape (Arnold, 1983; Miller and Mushinsky, 1990; King, 2002).

Second, we dissected the right side of the head of each specimen to measure the length (straight-line distance in mm) of the following cranial bones: ectopterygoid, maxilla, palatopterygoid (measured as one functionally integrated unit), quadrate and the supratemporal (Fig. 1A).

Third, we measured two lever-arm lengths (Fig. 1B): (1) the in-lever for mandibular rotation (jaw closing) was the straight-

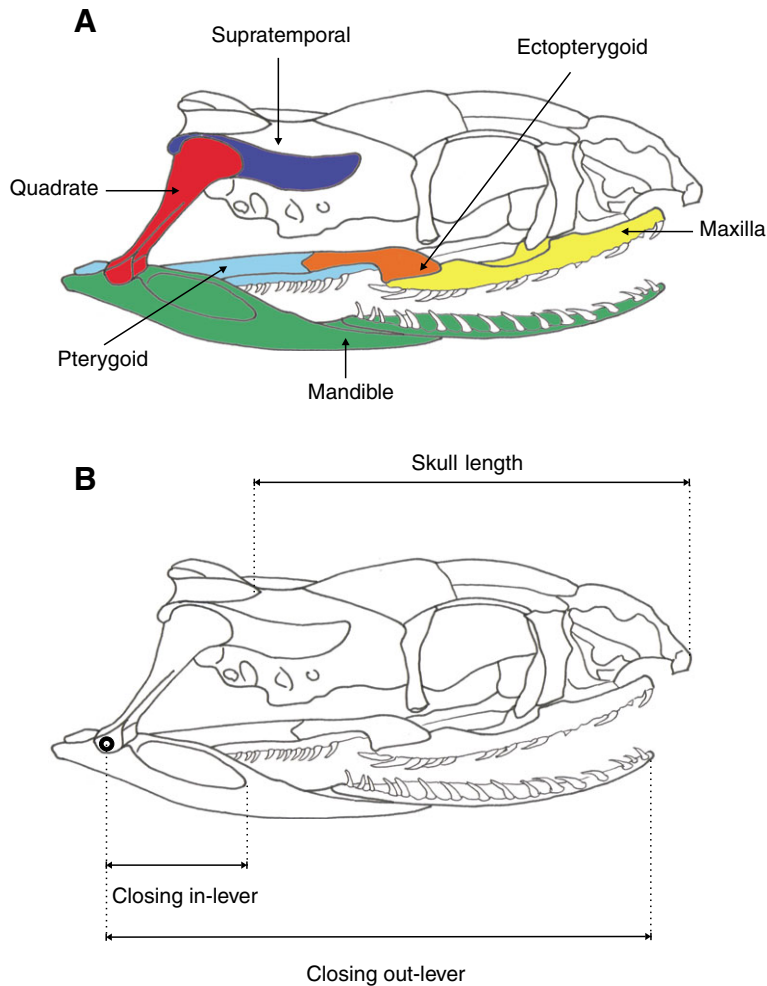


Fig. 1. Anatomical illustrations of (A) the cranial bones and (B) jaw-closing levers that were examined in banded watersnakes (*Nerodia fasciata*).

line distance from the anterior edge of the insertion of the three jaw adductor muscles onto the dorsal surface of the compound bone to the quadrato-mandibular articulation; and (2) the out-lever for mandibular rotation (jaw closing) was the straight-line distance from the quadrato-mandibular joint to the tip of the dentary.

Fourth, we measured head length (in mm) by recording the straight-line distance from the posterior edge of the parietal bone to the tip of the premaxillary bone. We used head length as the measure of 'head size' to analyze how the cranial musculoskeletal elements scale within the feeding apparatus (see below).

Finally, we measured the masses and lengths (from origin to insertion, in mm) of the following parallel-fibered (based on dissection) cranial muscles (Fig. 2A–C): *m. depressor mandibulae*, *m. adductor externus profundus*, *m. adductor externus medialis*, *m. adductor externus superficialis*, *m. retractor quadratri*, *m. protractor pterygoidei*, and the *m. retractor pterygoidei*. To do this, we detached the muscles from their origins and insertions with the aid of a binocular microscope and then measured the muscle masses using a

Denver instruments (Denver, CO, USA) M-220 electronic balance (± 0.01 mg), and all lengths to within 0.01 mm using Mitutoyo CD-15 DC digital callipers. In order to minimize measurement error, we took all morphological measurements three times and used the average of these measurements in the analysis.

This muscle architecture allowed us to estimate the average physiological cross-sectional area (pCSA) of each muscle. The pCSA of a muscle is its cross-sectional area perpendicular to the fibers, and is a key indicator of its maximum force output (McMahon, 1984; Biewener, 2003). We measured it using the relation:

$$\text{PCSA} = m / \rho_m l_f, \quad (2)$$

where m is the muscle mass, ρ_m is the muscle density (1060 kg m^{-3} for typical skeletal muscles) (Biewener, 2003) and l_f is the muscle fibre length (McMahon, 1984; Biewener, 2003). Because the fibres appeared to extend throughout the entire length of the short muscles, we measured fibre length as the total muscle length from origin to insertion.

Statistical analyses

We used SPSS (version 11.5; SPSS Inc., Chicago, IL, USA) for all statistical analyses. All variables were \log_{10} -transformed to meet the assumption of homoscedasticity for regression analyses (Sokal and Rohlf, 1981; Kachigan, 1991), and tested the transformed data for normality using Lillifores tests.

To test for morphological differences between the frog and fish prey consumed by banded watersnakes, we first performed a varimax-rotated principal components (PC) analysis using the \log_{10} -transformed prey measurements as the model variables. We then determined which axes explained a significant amount of variation in the data using the broken stick method (Frontier, 1971; Jackson, 1993) and a varimax rotation to maximize the differences between prey types in multivariate space (Kachigan, 1991). To test for morphological differences between prey types, we used the significant PC axes as dependent variables in a one-way MANOVA with prey type (fish or frog) as the factor.

For the scaling analyses, we followed the recommendation of Rayner (Rayner, 1985) and used reduced major axis (RMA) regression of the log-transformed cranial osteometric variables (y -axis) against the log-transformed SVL (x -axis). We first examined the allometry of the slopes by testing (using two sample t -tests) whether the observed slopes deviated significantly from those predicted values under a model of geometric similarity (Hill, 1950; McMahon, 1984). Moreover, we analyzed the allometry of the mechanical advantage of the jaw-closing lever system by first computing the residuals of a least-squares regression of log-transformed in-lever arm length (y -axis) against the log-transformed out-lever arm length (x -axis), and then computing a RMA regression of the residual in-

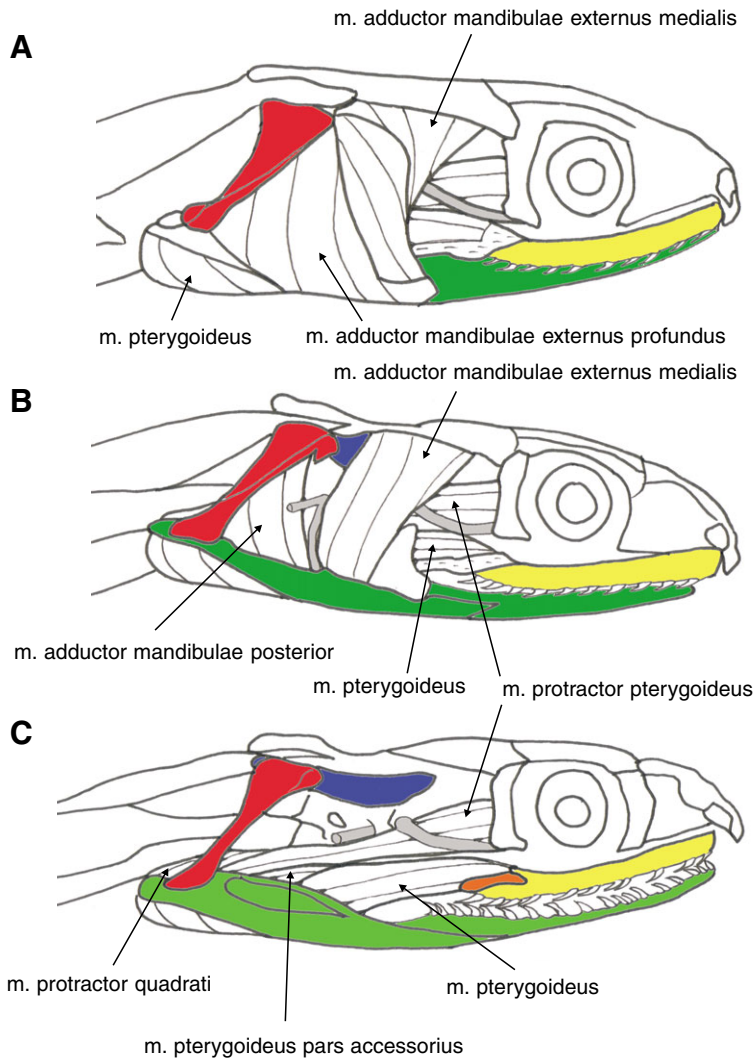


Fig. 2. The cranial muscles that were examined in banded watersnakes (*Nerodia fasciata*). Note that some additional cranial muscles not examined here have been included in this illustration. The illustration was drawn using a Wild Heerbrug (M3Z) binocular microscope with camera lucida. (A) Lateral view of the superficial adductor mandibulae muscle group. (B) Lateral view of cranium with the m. adductor externus profundus (AEP) removed to expose the m. adductor posterior (not measured here). (C) Lateral deep view of the cranium showing the deeper muscles of the adductor mandibulae group.

lever value against \log_{10} -transformed head length. Our use of residuals in this case is mathematically equivalent to calculating the ratio of the in-lever divided by the out-lever (L_i/L_o); but this approach is statistically more robust because it prevents spurious correlations from arising from the use of ratios in regression analysis (e.g. Atchley et al., 1976; Packard and Boardman, 1999). With these RMA regression results, we tested whether the slope of jaw mechanical advantage remained the same or changed with increasing body and head size.

Because most snakes grow very rapidly during the first year of life (Gibbons and Dorcas, 2004; Vincent et al., 2006a), we also analyzed the scaling of these cranial musculoskeletal elements relative to \log -transformed head length (x -axis). In

this way, we were able to examine how the cranial musculoskeletal elements scale *within* the feeding apparatus, without being confounded by differences in overall body size.

Results

Prey size and shape

The principal components analysis (PCA) performed on the prey morphological variables yielded two significant axes, together explaining 81.9% of the total variation in the data (Table 2). Prey mass and width both loaded highly and positively on PC 1, whereas only prey height loaded highly and positively on PC 2 (Fig. 3). Thus, PC 1 is an indicator of prey mass and width, and PC 2 is an indicator of prey height. The MANOVA testing for differences between fish and frog prey on these two axes was highly significant (Wilks' Lambda=0.299, $F_{2,428}=501.3$, $P<0.0001$). Fisher's protected least-significant difference *post-hoc* tests revealed that frogs have significantly higher loadings on PC 1 than fish ($P<0.0001$), but fish have significantly higher loadings on PC 2 than frogs ($P<0.0001$). Therefore, the frog species consumed by adult banded watersnakes are significantly more massive and wider than the fish species consumed primarily by sub-adult and juvenile snakes. However, the fish prey of sub-adult and juvenile snakes are significantly taller than the frogs consumed by adult banded watersnakes. Even so, the largest frogs consumed by adult banded watersnakes do have similar heights to the largest fishes consumed by juvenile and sub-adult snakes (Fig. 3).

Myology

Here we give a brief overview of the cranial muscles in *Nerodia fasciata* based on their mechanical function during feeding, and largely follow the detailed anatomical descriptions of Varkey (Varkey, 1979) for North American watersnakes.

The lower jaw is closed primarily by three robust adductor muscles that are all innervated by branches of the mandibular division of the trigeminal nerve (V_3): the m. adductor externus superficialis (AES), m. adductor externus medialis (AEM), and m. adductor externus profundus (AEP). Of these three adductor muscles, the AES is the most anterior and superficial. It originates from the lateral wall of the parietal bone and the uppermost part of the postorbital and inserts primarily onto the lateral edge of the anterior portion of the compound bone (a small anterior slip of this muscle inserts onto the rictal plate at the corner of the mouth). The AEM originates primarily from the sagittal crest of the parietal bone and the supraoccipital ligament; it has a broad insertion along the dorsomedial and dorsolateral surfaces of the compound bone, extending from the anterior portion of the adductor fossa to a point just posterior to the intramandibular joint. The AEM

Table 2. Loadings from a varimax rotated principal components analysis of \log_{10} -transformed morphometric measurements on prey animals

Variable	PC 1	PC 2
Mass (g)	0.805	0.445
Length (mm)	0.536	0.581
Width (mm)	0.843	0.442
Height (mm)	0.457	0.833
Eigenvalue	1.85	1.42
% Variation explained	46.3	35.6

Variables loading strongly on each principal component are indicated in bold.

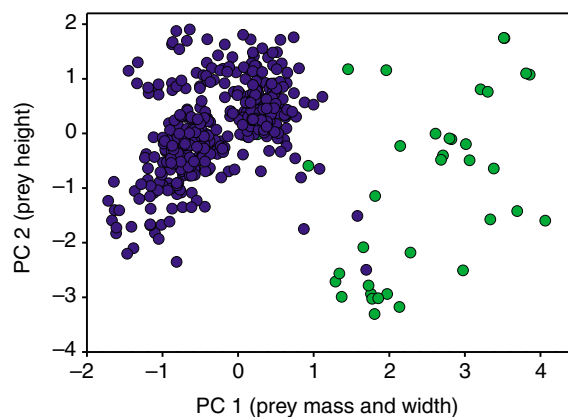


Fig. 3. Plot of principal component 1 (*x*-axis) versus principal component 2 (*y*-axis) showing the size and shape differences between the most commonly consumed fish and frog prey of banded watersnakes (*Nerodia fasciata*). Overall, the frogs (green circles) consumed by these snakes are significantly more massive and wider than most fish (blue circles; see Results). See Table 2 for variable loadings.

is largely covered by the AES and AEP. The AEP is a triangular muscle that originates on the anterolateral edge of the quadrate bone and inserts broadly along the lateral surface of the compound bone between the quadratomandibular and intramandibular joints (Fig. 2A).

Opposing these three adductors is the sole jaw abductor muscle, the *m. depressor mandibulae* (DM), which is innervated by branches of the facial nerve (VII). The DM originates from the proximal end of the quadrate, with fibers arising from both the lateral and medial sides of the bone. It inserts onto the dorsomedial aspect of the retroarticular process.

The *m. retractor quadratri* (RQ) is the muscle chiefly responsible for quadrate retraction. It has a relatively broad origin, arising aponeurotically from the fascia overlying the epaxialis muscles in the 'cervical' region. It then tapers gradually as it passes anteroventrally, ultimately inserting onto a small spot on the lateral surface of the quadrate bone,

immediately dorsal to the mandibular condyle. The RQ is innervated by branches of the facial nerve.

The *m. protractor pterygoidei* (PP) is responsible for palatopterygoid protraction (in concert with the *m. levator pterygoidei*; not measured here). It originates from the ventrolateral surface of the parabasisphenoid bone and inserts dorsomedially along the posterior half of the pterygoid bone. The PP is innervated by a branch of the mandibular division of the trigeminal nerve (V_3) (Fig. 2B,C).

Finally, the *m. retractor pterygoidei* (RP), despite its name, plays little to no role in palatopterygoid retraction (Cundall and Gans, 1979; Cundall, 1983). Rather, it protracts the braincase relative to the fixed ipsilateral jaw during advance of the contralateral jaw (Cundall, 1983). The RP originates from the parabasisphenoid bone, anterolateral to the origin of the PP, and inserts onto the dorsomedial edge of the palatine bone. It is innervated by a twig from the CID branch of the mandibular division of the trigeminal nerve (V_4).

Scaling patterns

Scaling of skeletal elements vs SVL

All cranial bone lengths, the length of the head, and the gape index exhibited significant negative allometry compared to the slopes predicted by a model of geometric similarity (Table 3). Therefore, smaller snakes have relatively longer cranial bones, heads and larger gapes for their body size compared with larger snakes. Further, the jaw-closing in- and out-levers both scaled with significant negative allometry (Table 3). Even so, the jaw-closing MA did not change with increasing SVL in banded watersnakes.

Scaling of muscles vs SVL

The masses of four out of seven cranial muscles (i.e. DM, AEP, RQ and RP) scaled according to the predictions of geometric similarity, whereas the masses of the other three muscles (AES, AEM and PP) exhibited significant negative allometry compared to the predicted slope of 3 (Table 3). The total adductor mass also scaled with significant negative allometry. Therefore, smaller snakes have relatively more massive jaw adductors (except AEP) and palatopterygoid protractors than larger snakes.

The lengths of five out of seven cranial muscles (AEP, AES, AEM, RQ and PP) scaled with significant negative allometry compared to the predicted slope of 1 (Table 3), whereas the other two muscle lengths scaled isometrically (DM and RP). Therefore, for the majority of muscles measured here, smaller snakes have relatively longer cranial muscles.

The pCSAs of five out of seven muscles (DM, AES, AEM, PP and RP) scaled according to the predictions of the geometric similarity model (Table 3). However, for two muscles (AEP and RQ), pCSA scaled with significant positive allometry. The positive allometry for the pCSA of the AEP and RQ is the result of an ontogenetic decrease in muscle length compared to mass of these muscles over ontogeny (i.e. muscle mass scales isometrically whereas muscle length scales with negative allometry in these two muscles; Table 3). Hence, small and

Table 3. Results from reduced major axis regression of \log_{10} -transformed gape index, cranial bones and muscle variables against \log_{10} -transformed snout–vent length

Variable	Predicted slope	Observed slope	Y intercept	R	P
Gape index (mm ²)	2	1.50	-1.83	0.97	<0.01
Cranial bones					
Head length (mm)	1	0.551	-0.207	0.97	<0.0001
Maxilla length (mm)	1	0.617	-0.548	0.96	<0.0001
Palatopterygoid length (mm)	1	0.703	-0.600	0.98	<0.0001
Supratemporal length (mm)	1	0.806	-1.24	0.96	<0.0001
Ectopterygoid length (mm)	1	0.750	-1.08	0.92	<0.0001
Jaw lever-arm lengths					
Jaw-closing in-lever (mm)	1	0.810	-2.29	0.94	<0.01
Jaw-closing out-lever (mm)	1	0.676	-0.438	0.96	<0.0001
Jaw-closing MA	0	0	0	0	0
Muscle masses					
Depressor mandibulae mass (g)	3	2.85	-8.85	0.93	>0.05
Add. ext. profundus mass (g)	3	2.72	-8.06	0.92	>0.05
Add. ext. medialis mass (g)	3	2.27	-7.23	0.92	<0.01
Add. ext. superficialis mass (g)	3	2.32	-7.69	0.94	<0.01
Total adductor mass (g)	3	2.45	-7.33	0.95	<0.01
Retractor quadratri mass (g)	3	2.91	-8.74	0.97	>0.05
Protractor pterygoidei mass (g)	3	2.20	-6.94	0.89	<0.0001
Retractor pterygoidei mass (g)	3	2.90	-9.42	0.93	>0.05
Muscle length					
Depressor mandibulae length (mm)	1	0.900	-1.39	0.97	>0.05
Add. ext. profundus length (mm)	1	0.501	-0.305	0.90	<0.0001
Add. ext. medialis length (mm)	1	0.630	-0.552	0.90	<0.0001
Add. ext. superficialis length (mm)	1	0.803	-0.951	0.86	<0.01
Retractor quadratri length (mm)	1	0.722	-0.580	0.89	<0.01
Protractor pterygoidei length (mm)	1	0.710	-0.712	0.91	<0.001
Retractor pterygoidei length (mm)	1	1.17	-2.44	0.92	>0.05
Muscle pCSAs					
Depressor mandibulae (mm²)	2	1.88	-10.3	0.94	>0.05
Add. ext. profundus (mm ²)	2	2.36	-10.7	0.88	<0.0001
Add. ext. medialis (mm²)	2	1.71	-9.56	0.89	>0.05
Add. ext. superficialis (mm²)	2	1.60	-9.31	0.87	>0.05
Retractor quadratri (mm ²)	2	2.21	-10.9	0.95	<0.0001
Protractor pterygoidei (mm²)	2	1.57	-9.15	0.82	>0.05
Retractor pterygoidei (mm²)	2	1.75	-9.93	0.86	>0.05

Add., adductor; Ext., externus; pCSAs, physiological cross-sectional areas; MA, mechanical advantage.

See text for description of how these variables were measured. All head variables scaled with significant negative allometry *versus* snout–vent length (SVL) *versus* the slopes predicted under a model of geometric similarity (Hill, 1950; McMahon, 1984). By contrast, the majority of muscle pCSAs scaled isometrically *versus* SVL. The slope for jaw-closing MA did not significantly differ from 0. All variables that scaled isometrically *versus* SVL are indicated in bold.

large snakes have similar muscle force outputs for most of the cranial muscles measured here, with the notable exceptions of the AEP and RQ, which increase in thickness and hence strength over ontogeny in banded watersnakes.

Scaling of skeletal elements vs head length

The slopes of most cranial bone lengths relative to head length significantly exceeded the predicted slope of 1 (Table 4; Fig. 4), except for the length of the maxilla, which scaled

isometrically with head length. Therefore, larger snakes generally have relatively longer cranial bones than smaller snakes. The slope of gape index against head length also significantly exceeded the predicted slope of 2 (Table 4; Fig. 4); thus, larger snakes have significantly larger gapes than smaller snakes relative to head length.

The jaw-closing out-lever scaled with significant positive allometry relative to head length, whereas the jaw-closing in-lever scaled isometrically, although the change was close to

Table 4. Results from reduced major axis regression of \log_{10} -transformed gape index, cranial bones and muscle variables against \log_{10} -transformed head length

Variable	Predicted slope	Observed slope	Y intercept	R	P
Gape index (mm ²)	2	2.56	-1.83	0.97	<0.001
Cranial bones					
Maxilla length (mm)	1	1.10	-0.258	0.97	>0.05
Palatopterygoid length (mm)	1	1.28	-0.308	0.97	<0.05
Supratemporal length (mm)	1	1.47	-0.910	0.97	<0.001
Ectopterygoid length (mm)	1	1.33	-0.640	0.92	<0.05
Jaw lever-arm lengths					
Jaw-closing in-lever (mm)	1	1.15	-0.220	0.84	>0.05
Jaw-closing out-lever (mm)	1	1.21	-0.217	0.99	<0.05
Jaw-closing MA	0	0	0	0	0
Muscle masses					
Depressor mandibulae mass (g)	3	4.93	-7.79	0.97	<0.0001
Add. ext. profundus mass (g)	3	4.55	-6.87	0.96	<0.0001
Add. ext. medialis mass (g)	3	4.29	-6.64	0.93	<0.0001
Add. ext. superficialis mass (g)	3	4.43	-7.19	0.95	<0.0001
Total adductor mass (g)	3	4.32	-6.40	0.98	<0.0001
Retractor quadratri mass (g)	3	4.88	-7.17	0.96	<0.0001
Protractor pterygoidei mass (g)	3	4.04	-6.36	0.92	<0.0001
Retractor pterygoidei mass (g)	3	5.47	-8.68	0.94	<0.0001
Muscle length					
Depressor mandibulae length (mm)	1	1.62	-1.12	0.99	<0.0001
Add. ext. profundus length (mm)	1	0.89	-0.084	0.86	>0.05
Add. ext. medialis length (mm)	1	1.11	-0.351	0.91	>0.05
Add. ext. superficialis length (mm)	1	1.44	-0.811	0.94	<0.0001
Retractor quadratri length (mm)	1	1.31	-0.393	0.92	<0.0001
Protractor pterygoidei length (mm)	1	1.29	-0.490	0.91	<0.0001
Retractor pterygoidei length (mm)	1	2.32	-1.59	0.89	<0.0001
Muscle pCSA					
Depressor mandibulae (mm ²)	2	3.33	-6.67	0.95	<0.0001
Add. ext. profundus (mm ²)	2	3.77	-6.83	0.96	<0.0001
Add. ext. medialis (mm ²)	2	3.31	-6.30	0.89	<0.0001
Add. ext. superficialis (mm ²)	2	3.34	-6.40	0.89	<0.0001
Retractor quadratri (mm ²)	2	3.67	-6.78	0.94	<0.0001
Protractor pterygoidei (mm ²)	2	2.79	-5.86	0.90	<0.0001
Retractor pterygoidei (mm ²)	2	3.23	-6.71	0.95	<0.0001

Add., adductor; Ext., externus; pCSAs, physiological cross-sectional areas; MA, mechanical advantage.

See text for description of how these variables were measured. Most head variables scaled with significant positive allometry *versus* the slopes predicted under a model of geometric similarity, except the jaw-closing in-lever, maxilla length, and the lengths of the Add. ext. profundus and medialis (indicated in bold) which all scaled isometrically. The slope for the jaw-closing MA did not significantly differ from 0.

statistical significance ($P=0.056$) (Table 4). Because the jaw-closing levers scaled with similar slopes, the jaw-closing mechanical advantages did not change significantly with head length in banded watersnakes (Table 4; Fig. 5).

Scaling of muscles vs head length

The slopes of all cranial muscle masses against head length significantly exceeded the predicted slope of 3 (Table 4), with most slopes being close to 4 or 5. Hence, larger snakes have larger cranial muscles than smaller snakes relative to head length.

The slopes of most cranial muscle lengths against head length significantly exceeded the predicted slope of 1 (Table 4), except the lengths of the AEP and AEM, which scaled isometrically with head length. Therefore, larger snakes generally have longer cranial muscles than smaller snakes relative to head length.

The slopes of all muscle pCSAs against head length significantly exceeded the predicted slope of 2 (Table 4; Fig. 6), with most slopes being close to 3. Therefore, larger snakes had relatively thicker and hence stronger, cranial muscles than smaller snakes relative to head length.

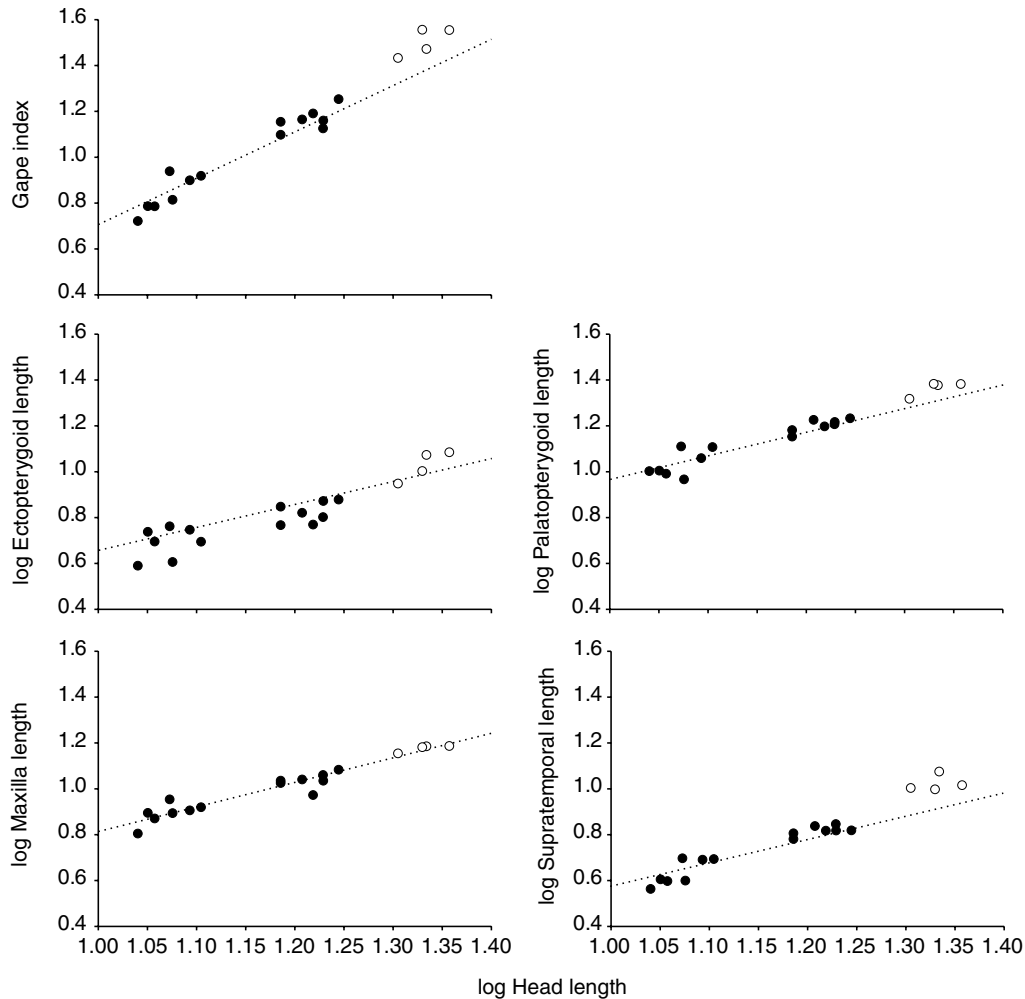


Fig. 4. The relationships between gape, cranial bone lengths and head length in banded watersnakes (*Nerodia fasciata*). The dotted lines indicate the slope predicted under a model of geometric similarity (length=1, area=2). Closed circles indicated individuals <500 mm snout-vent length (SVL) that almost exclusively consume fish, and open circles indicate individuals >500 mm SVL that almost exclusively consume frogs.

Discussion

The cranial bones of banded watersnakes scaled with significant negative allometry relative to body size, in contrast to our predictions, whereas the muscle pCSAs scaled either isometrically or with positive allometry *versus* body size as predicted (Table 3). Hence, even though larger frog-eating snakes have relatively smaller heads for their body size compared to smaller snakes, their cranial muscles are either equally as strong or even stronger relative to body size. An examination of the slopes of these cranial elements against head length, however, revealed that all cranial elements and their associated muscle pCSAs exhibited very strong positive allometry in banded watersnakes (Table 4; Figs 4 and 6). Therefore, when head length is used as a measure of 'head size', it becomes clear that frog-eating adults have relatively larger gapes and stronger cranial muscles than fish-eating juveniles, as predicted, which should aid in the intraoral transport of the wide and massive frog prey consumed by these snakes as adults (Fig. 3) (Vincent et al., 2006b).

Moreover, the smaller head dimensions, relative to head length, of fish-eating juveniles and sub-adults should minimize hydrodynamic constraints when feeding underwater (Young, 1991; Alfaro, 2002; Vincent et al., 2004; Vincent et al., 2005).

By contrast, jaw-closing MA did not change with either increasing body or head size in banded watersnakes, as predicted (Fig. 5; Tables 3 and 4); therefore small and large snakes have similar jaw-closing MAs. This finding is somewhat counterintuitive given that aquatic snakes are expected to have jaw-closing lever systems designed for fast closure to capture elusive fish prey underwater (note that jaw opening in aquatic snake strikes occurs very early in the sequence and therefore should not be under selection for increased speed) (Alfaro, 2002; Vincent et al., 2005). Nonetheless, previous studies have shown that the jaw MAs (both opening and closing) of a wide diversity of vertebrate taxa remain constant with increasing body size [e.g. fish (Richard and Wainwright, 1995); frogs (Birch, 1999); lizards

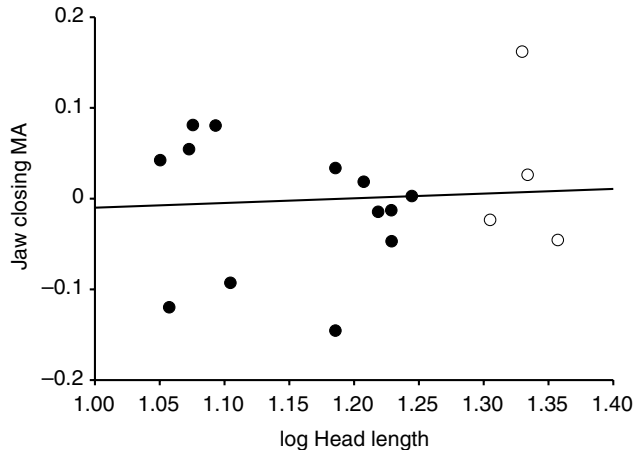


Fig. 5. The relationship between jaw-closing mechanical advantage (MA) (based on the residuals of \log_{10} -transformed data as described in the text) and head length in banded watersnakes (*Nerodia fasciata*). The solid line indicates the empirical slope calculated using reduced major axis regression. This slope did not significantly differ from 0 (Table 4). Closed circles indicated individuals <500 mm snout-vent length (SVL) that almost exclusively consume fish, and open circles indicate individuals >500 mm SVL that almost exclusively consume frogs.

(Meyers et al., 2002)]. Therefore, jaw MA may often be an unreliable estimate of performance capacities *within* species (all else being equal) (but see Huber and Motta, 2004), even though it is widely used as a proxy for performance potential among species (e.g. Adams and Rolhf, 2000; Westneat, 2003; Wainwright et al., 2004; Metzger and Herrel, 2005; Stayton, 2006).

Interestingly, the realized maximum performance capacities (e.g. maximum bite force, suction feeding performance, etc.) of nearly all vertebrate feeding systems studied thus far exhibit marked positive allometry against either body or head size [e.g. alligators (Erickson et al., 2003); birds (van der Meij and Bout, 2004); fishes (Wainwright and Richard, 1995; Hernandez, 2000; Herrel et al., 2005; Van Wassenbergh et al., 2005); lizards and turtles (Herrel and O'Reilly, 2006); mammals (Thompson et al., 2003; Herrel and Gibb, 2006)]. In general, this ontogenetic increase in maximum feeding performance capacity is typically the result of an increase in muscle mass coupled to a subsequent decrease in muscle length over ontogeny, which results in thicker muscles and higher muscle force outputs (e.g. Hernandez and Motta, 1997; van der Meij and Bout, 2004; Herrel et al., 2005; Herrel and Gibb, 2006). In a similar manner, we found that the cranial muscle pCSAs of banded watersnakes generally scale with significant positive allometry, with most slopes far exceeding the predicted slope of 3 under a model of geometric similarity *versus* head length, and this positive allometry was primarily due to an ontogenetic increase in muscle mass relative to length in banded watersnakes (Tables 3 and 4). Coupled with this positive allometric growth in muscle pCSA, a recent study showed that both handling time and the number of jaw protraction-retraction cycles for banded watersnakes feeding on fish prey

decreased with increasing head size (Vincent et al., 2006a). Therefore, this marked positive allometry of the cranial muscle pCSAs of banded watersnakes is linked to a positive ontogenetic increase in feeding performance in a highly similar manner compared to the other vertebrate feeding systems (reviewed in Herrel and Gibb, 2006).

However, this widespread positive allometry of cranial muscle pCSA and feeding performance amongst vertebrates may present serious logical and statistical problems to testing the adaptive nature of these ontogenetic changes in animal form, function and ecology. Specifically, many authors, including us, have often tried to link maximum muscle force output, and thus feeding performance, to specific mechanical properties of the diet in vertebrates (e.g. van der Meij and Bout, 2004; Herrel et al., 2005; Herrel and O'Reilly, 2006). Yet, if most vertebrates exhibit positive allometry for their jaw muscle pCSAs and feeding performance, this scenario would suggest that positive allometric growth of the feeding system is ancestral within vertebrates as a whole, and is not a good indicator of adaptation for feeding on certain kinds of prey. Alternatively, this current trend may simply be an artefact of the particular taxa sampled for these kinds of studies, namely taxa in which an increase in muscle force output is suspected to play a key role in feeding ecology (e.g. present study) (see also Hernandez and Motta, 1997; van der Meij and Bout, 2004; Herrel et al., 2005). Hence, we suggest that comparative evolutionary studies are needed to directly test for adaptive links amongst muscle pCSA, feeding performance, and diet in a group of closely related vertebrates. In this way, one could directly test whether positive allometric growth within the feeding system is adaptively linked to foraging ecology or alternatively, the result of a shared evolutionary history.

Conclusions

These data clearly show that most aspects of the feeding system of banded watersnakes do not scale according to the predictions of geometric similarity models. Rather, most cranial bones and muscle pCSAs scaled with highly significant positive allometry, relative to head length, compared to the slopes predicted under a model of geometric similarity. Moreover, this positive allometric growth of the musculoskeletal system in banded watersnakes appears to be directly linked to both an ontogenetic increase in intraoral transport performance (handling time and number of jaw protraction-retraction cycles needed to transport prey) (Vincent et al., 2006a), and to the specific functional demands imposed by prey throughout ontogeny. Even so, very similar scaling patterns have now been reported for diverse vertebrate feeding systems, suggesting that allometric growth may be ancestral to vertebrates as a whole. Consequently, we suggest that phylogenetically controlled comparative studies are needed to test whether allometric scaling patterns within vertebrate feeding systems are adaptively linked to ontogenetic shifts in diet, or alternatively, are the result of a shared evolutionary history. More generally, however, we suggest that such a study would significantly advance our understanding of

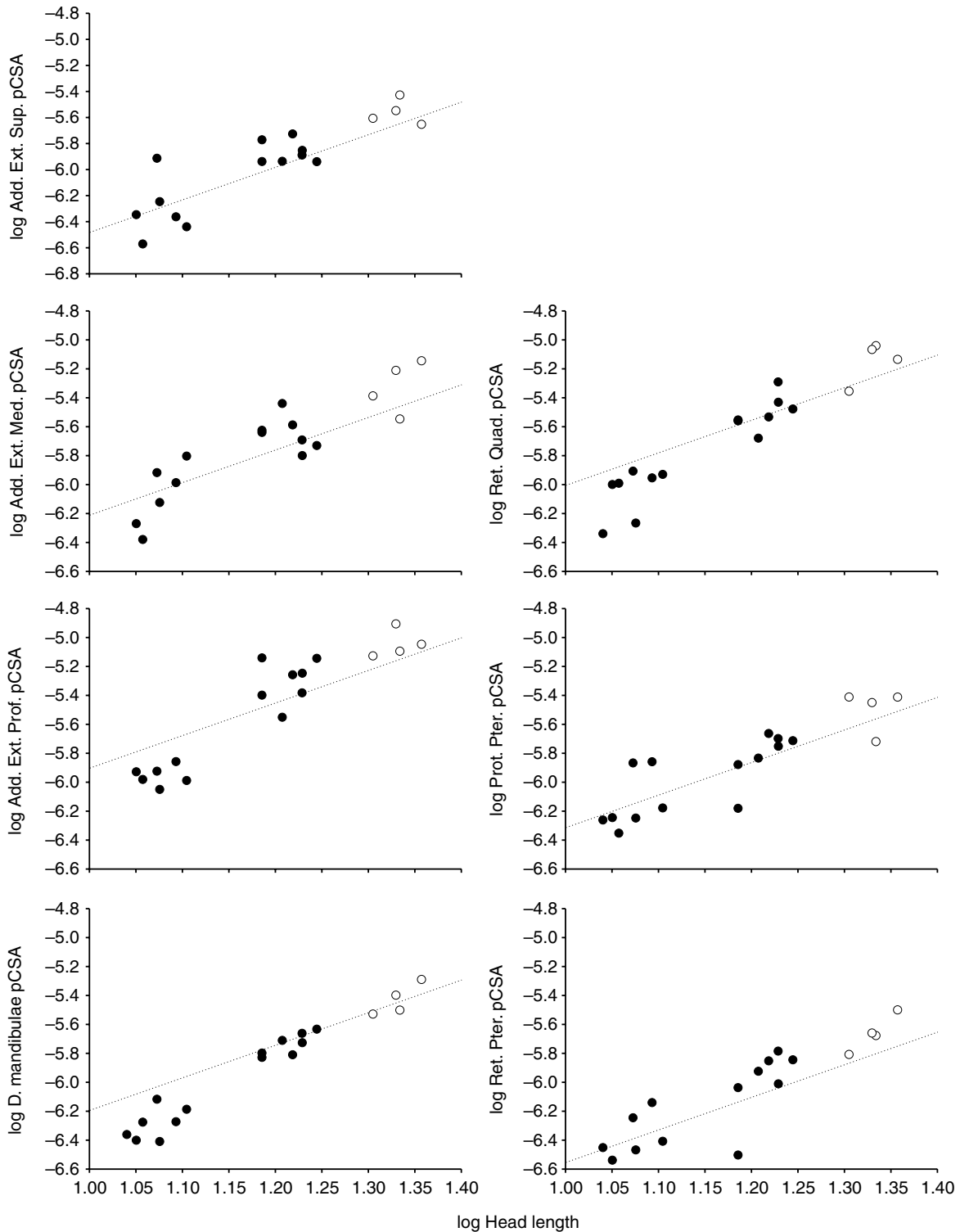


Fig. 6. The relationships between muscle physiological cross-sectional areas (pCSA) and head length in banded watersnakes (*Nerodia fasciata*). Dotted lines indicate the slope predicted under a model of geometric similarity (area=2). All slopes were significantly greater than the predicted value of 2 (Table 4). Closed circles indicated individuals <500 mm snout-vent length (SVL) that consume fish almost exclusively and open circles indicate individuals >500 mm SVL that consume frogs almost exclusively. Add. Ex. Sup., adductor externus superficialis; Add. Ex. Med., adductor externus medialis; Ret. Quad., retractor quadratri; Add. Ext. Prof., adductor externus profundus; Prot. Pter., protractor pterygoidei; D. mandibulae, depressor mandibulae; Ret. Pter., retractor pterygoidei.

why some ectothermic organisms tightly conform to the scaling predictions of geometric scaling models, whereas others clearly do not.

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