

Ontogeny of intersexual head shape and prey selection in the pitviper *Agkistrodon piscivorus*

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Different animal intraspecific classes commonly differ in their prey selection. Such differences in feeding ecology are thought to reduce resource competition between classes, but other factors (i.e. behavioural, morphological, and physiological differences) also contribute to this widespread phenomenon. Although several studies have correlated the size of the feeding apparatus with prey selection in many animals, few studies have examined how the shape of the feeding apparatus is related to prey selection. Furthermore, even though the dietary regimen of many animals changes during ontogeny, few studies have examined how shape changes in the feeding apparatus may be related to these ontogenetic dietary shifts. Here we address these issues by examining how head shape, head size and prey selection change over ontogeny in adult males, adult females and juveniles of the cottonmouth snake *Agkistrodon piscivorus*. Our scaling data for head characteristics showed that all head measurements in adult male and female *A. piscivorus* scaled with significant negative allometry, whereas juvenile head measurements typically scaled isometrically, except for head volume (positive) and head length (negative). Thus, juveniles have relatively broad and high, but short, heads. Large adult male and female *A. piscivorus* have relatively small head dimensions overall. Thus, juveniles appear to undergo a rapid change in head volume, which subsequently slows considerably as sexual maturity is achieved. However, our multivariate analysis of size-adjusted head dimensions showed that juveniles differed only slightly in their head shape compared with adult male and female *A. piscivorus*. In general, prey size increased with snake size across all age and sex groups, but an ontogenetic shift in prey type was not detected in either males or females. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, 81, 151–159.

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INTRODUCTION

A general biological issue concerns how intrasexual or ontogenetic classes differ in morphology, ecology, and behaviour. For example, several authors have shown that prey selection often differs between males and females, as well as between adults and juveniles (i.e. intraspecific classes, Schoener, 1971; Slatkin, 1984; Werner & Gilliam, 1984; Shine, 1991; Pearson, Shine & How, 2002). Differences in prey selection among intraspecific classes are commonly thought to reduce resource competition, but other factors, including

behavioural, morphological, and physiological differences, are also important. Differences in the shape of the feeding apparatus (e.g. beaks in birds, head shape in frogs and snakes) among or within species may be particularly important for prey selection (Emerson, 1985; Lauder, 1985; Houston & Shine, 1993; Forsman, 1996). However, the relationship between prey selection and the shape of the feeding apparatus among intraspecific classes has only been examined comprehensively within a few species (see Werner & Gilliam, 1984).

Within and among species that do not extensively masticate their prey prior to swallowing (i.e. gape-limited predators), the size and shape of the feeding apparatus is often strongly correlated with the size

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and shape of the prey (Grant, 1985; Shine, 1991; Arnold, 1993). For example, bluegill sunfish (*Lepomis macrochirus*) select small invertebrate prey as juveniles but later switch to larger prey as adults (Werner & Hall, 1974). In addition, Emerson (1985) showed that both the length and width of the jaw are important in determining the size of prey consumed by frogs. Unfortunately, Emerson's (1985) study is one of the few that has examined head shape, not simply size, in relation to diet in a gape-limited predator. Thus, in gape-limited predators the functional relationships between the size of the feeding apparatus and prey selection are much better understood than are those between head shape and prey selection. Moreover, even fewer studies have examined how head shape changes over ontogeny, and how such changes influence prey selection.

The size and shape of the feeding apparatus may be especially important for capturing prey within aquatic environments. This is because water is much denser and more viscous than air, which imposes severe constraints on how animals can effectively capture prey. Specifically, aquatic tetrapods that cannot create suction (see Bramble & Wake, 1985), such as aquatic snakes, may be under especially severe hydrodynamic constraints for capturing prey because of the resistance that the aquatic medium presents to movement. For a large animal such as a snake, pressure drag, which is roughly proportional to the surface area exposed to the aquatic medium, is the dominant force impeding movement in that medium (for a review see Vogel, 1981). As a result, the pressure drag on a snake's head will increase as the square of the head length. This relationship between head size and pressure drag thus suggests that the ability to move in the aquatic medium will be more difficult for a large compared with a small snake.

Given these constraints on aquatic prey capture, various authors have suggested that aquatic snakes should have relatively small heads that taper towards the back (streamlining) in order to minimize drag (Drummond, 1983; Taylor, 1987; Young, 1991). However, since snakes are generally gape-limited predators (but see Jayne, Voris & Ng, 2002), the maximum prey size a snake can consume increases as a function of gape, which increases isometrically with head length (Pough & Groves, 1983; Shine, 1991; Arnold, 1993; Forsman & Lindell, 1993). Thus, a small tapering head should narrow the range of possible prey sizes taken by either terrestrial or aquatic snakes. As a result, the functional demands of aquatic prey capture and swallowing may conflict within aquatically feeding snakes. However, no studies to our knowledge have ever explicitly examined this issue within such snakes.

Here we address these issues by examining the relationships among head size, head shape and prey selection in adult males, adult females and juveniles of the semiaquatic cottonmouth *Agkistrodon piscivorus*. This pitviper is particularly appropriate for studying these issues because its bulky, triangular head appears to be poorly suited to reduce turbulent flow during aquatic strikes. Furthermore, previous studies have shown that this species consumes large amounts of fish (Savitzky, 1989; pers. observ.), suggesting that this species commonly forages aquatically. In a previous study (S.E. Vincent, A. Herrel, D.J. Irschick, unpubl. data), we obtained data on the head size, head shape and prey selection of adult male and female *A. piscivorus* in an effort to determine whether snakes with different head shapes consume prey with different shapes. Here, we combine these data with new data on juveniles to address the broader issue of scaling of head morphology and prey, and how head shape differences relate to prey selection when considering all age and sex classes. Thus, we asked the following questions. (1) How do different head characteristics scale with size within *A. piscivorus*? (2) Do adult male, adult female and juvenile *A. piscivorus* differ in head size and shape? (3) Can we relate any observed differences in head size and shape among intraspecific classes to differences in prey selection? To answer these questions, we examined the head morphology and diet of 318 *A. piscivorus*. We then discuss these findings in the context of prey capture and swallowing in *A. piscivorus*.

MATERIAL AND METHODS

SPECIMENS

This study examined 318 *A. piscivorus* specimens from the Tulane University Museum of Natural History. The sex of the specimens could be determined unambiguously by gonadal examination beginning at a snout-vent length (SVL) of 330 mm. Specimens below 330 mm in length were classified as juveniles. Diet data was collected for each specimen by dissection of the stomach. The stomach contents were identified to the lowest possible taxonomic order. For the intact prey items, we measured the length, width and height (in mm) using Mitutoyo digital calipers (± 0.01 mm). For partially digested prey, the dimensions were estimated using regression equations of prey dimensions against body size (based on specimens from the Tulane University Museum of Natural History) where possible. Mass (in g) was recorded for all individual stomach contents using a Denver Instruments M-220 electronic balance (± 0.01 mg).

MORPHOLOGICAL MEASUREMENTS

The following morphological measurements were taken for each *A. piscivorus* specimen: SVL (in mm), body mass (in g), head volume (in mL), head width (at the widest part of the head), head height (at the highest part of the head), head length (from the back of the parietal to the tip of the snout), jaw length (from the retroarticular process to the tip of the lower jaw), and the out-lever of the lower jaw (from the articulation of the lower jaw with quadrate to the tip of the lower jaw) (all in mm). SVL was determined by laying dental floss along the mid-ventral surface of the snake and then measuring the floss using a meter stick; body mass was determined using an Ohaus weighted balance (± 1 g). All head measurements were determined using Mitutoyo digital calipers (± 0.01 mm). Head volume (mL) was estimated as the amount of water displaced in a graduated cylinder by a snake's submerged head. To make this measurement homologous among individuals, the posterior most portion of the back of the jaw was used as a stopping point for submersion.

HEAD SHAPE

Head shape was quantified for a subsample of 25 adult male, 25 adult female and 10 juvenile *A. piscivorus*. For this subsample, digital images were taken of the heads in dorsal, lateral, ventral and frontal views using a Nikon COOLPIX S995 digital camera. An object of known size (wire mesh grid, 35×35 mm) was placed in the field of view for scaling purposes. Images were then imported into tpsdig32 (version 1.31, Rohlf, 2002) and digitized. Homologous landmarks were digitized such that surface areas and several linear measurements could be recorded. In dorsal view, the following four measurements were taken: (1) width at the front of the head; (2) widest part of the head in dorsal view; (3) width of the back of the head; (4) surface area of the head in dorsal view. In lateral view, three measurements were taken: (1) distance from the postocular scale to the tip of the lateral-most supralabial scale; (2) distance from the back of the mouth to the dorsal aspect of the quadrate; (3) surface area of the head in lateral view. In ventral view, five measurements were taken: (1) width of the front of the head; (2) widest part of the head in ventral view; (3) width of the neck; (4) distance between the neck and the snout tip; (5) surface area of the head in ventral view. In frontal view, four measurements were taken: (1) width of the head at its dorsal aspect (above the eyes); (2) distance between the nasal openings; (3) widest part of the head in frontal view; (4) surface area of the head in frontal view.

STATISTICAL ANALYSIS

Scaling relationships of head measurements, body mass and prey dimensions were determined by regressing these variables against SVL using reduced major-axis linear regression (Sokal & Rohlf, 1981). The relationship between prey dimensions and snake body size was analysed across all snakes since there were too few males, females and juveniles with prey in their stomachs to analyse these groups separately. All variables were \log_{10} transformed before analysis in order to meet the assumption of homoscedasticity. Head shape was quantified by performing a principal component analysis (PCA) on the residuals of the head shape measurements. The Broken Stick method (Jackson, 1993) was used to determine which principal components were significant. A multivariate analysis of variance (MANOVA), coupled to univariate *F*-tests, was performed on the factor scores for the first five axes to test for significant differences in head shape between males, females and juveniles. To examine if head shape changed during ontogeny the first principal component (PC 1) was regressed against SVL. PC 1 was used because it was the only principal component that was significant in the univariate *F*-tests (see Results). All statistical tests were performed on SYSTAT 10.0 (SPSS 2000 statistical package).

RESULTS

SCALING AND PREY RELATIONSHIPS

Adult male and female *A. piscivorus* consume very different prey types and sizes (S.E. Vincent A. Herrel, D.J. Irschick, unpubl. data). Males are mostly piscivorous whereas females primarily consume other squamates, especially snakes. The diet of juveniles has not been explored previously. Juveniles in this study consumed a diverse range of taxa (Table 1). Juveniles consumed prey with an average (\pm SD) mass of 1.05 ± 1.6 g, length of 37.5 ± 42 mm, width of 7.86 ± 4.7 mm and height of 10.9 ± 3.6 mm. From frequency count data, juveniles primarily consumed fish (47%), followed by arthropods (31%), reptiles (11%) and amphibians (11%). Analysis of the per cent mass (mass of each prey type divided by total mass of all prey items $\times 100$) of prey items showed that arthropods were the most important prey for juveniles (56%), followed by amphibians (21%), fish (15%) and reptiles (8%). However, there was no apparent shift in diet over ontogeny in either sex (juveniles were added to both males and females for analysis) (Fig. 1). To further examine the relationship between snake body size and diet, the average number of prey items consumed between 100-mm SVL intervals was examined (Fig. 2). The average number of prey for both males and females did not significantly change

throughout ontogeny, with the exception of the 600–700-SVL interval for females (Fig. 2).

The slopes of all morphological variables against SVL deviated strongly from isometry for both male and female *A. piscivorus* (Table 2). Furthermore, all slopes for male measurements were significantly larger than those for females ($P = 0.0001$). Most of the y-intercepts for the male measurements were also significantly larger than those for the females

Table 1. Numbers of the various prey taxa taken by juvenile *Agkistrodon piscivorus*

Prey taxa	<i>N</i>
Vertebrata	
Pisces	
<i>Fundulus</i> sp.	2
Unidentified fish	7
Amphibia	
Caudata	
<i>Ambystoma talpoideum</i>	1
Larval <i>Pseudotriton</i> sp.	1
Unidentified amphibians	1
Reptilia	
Sauria	
<i>Anolis carolinensis</i>	1
<i>Scincella lateralis</i>	1
<i>Eumeces inexpectatus</i>	1
Invertebrata	
Arthropoda	
Coleoptera	1
Hymenoptera	1
Blattodea	6
Total	23

($P = 0.0001$), except for head volume and jaw length (not significant). The scaling of head volume in juveniles significantly exceeded the predicted slope of 3. Thus, head volume scaled with positive allometry in juveniles, but with negative allometry in adult males and females. In addition, head length for all three groups was the measurement that displayed the greatest negative allometry.

Prey mass was significantly correlated with snake SVL when analysed across all snakes (Pearson's $r = 0.31$, d.f. = 108, $P < 0.05$) (Fig. 3). Similar relationships were also revealed for prey length ($r = 0.36$, d.f. = 49, $P < 0.05$) and width ($r = 0.28$, d.f. = 47, $P < 0.05$). Prey height was the measurement that most significantly correlated with snake size ($r = 0.68$, d.f. = 32, $P = 0.001$). Moreover, all four prey measurements consistently increased with snake size when analysed across all sex and age classes. Inspection of the graphs also showed that large *A. piscivorus* rarely consumed small prey.

HEAD SHAPE AND ONTOGENY

The PCA performed on head shape variables yielded five significant new axes, together explaining 78.8% of the total variation. The first five axes combined were significantly different for males, females and juveniles (Wilks' lambda = 0.55, $F_{4,44} = 9.07$, $P < 0.001$). Upon inspection of the univariate F -tests, however, only the first axis remained significant ($F_{2,56} = 9.274$, $P = 0.000$). PC 1 correlated positively with frontal surface area, frontal length 1, frontal length 3, ventral surface area and ventral length 3 (Table 3). From comparisons of the means of the residuals, males were larger than juveniles and females in frontal length 1,

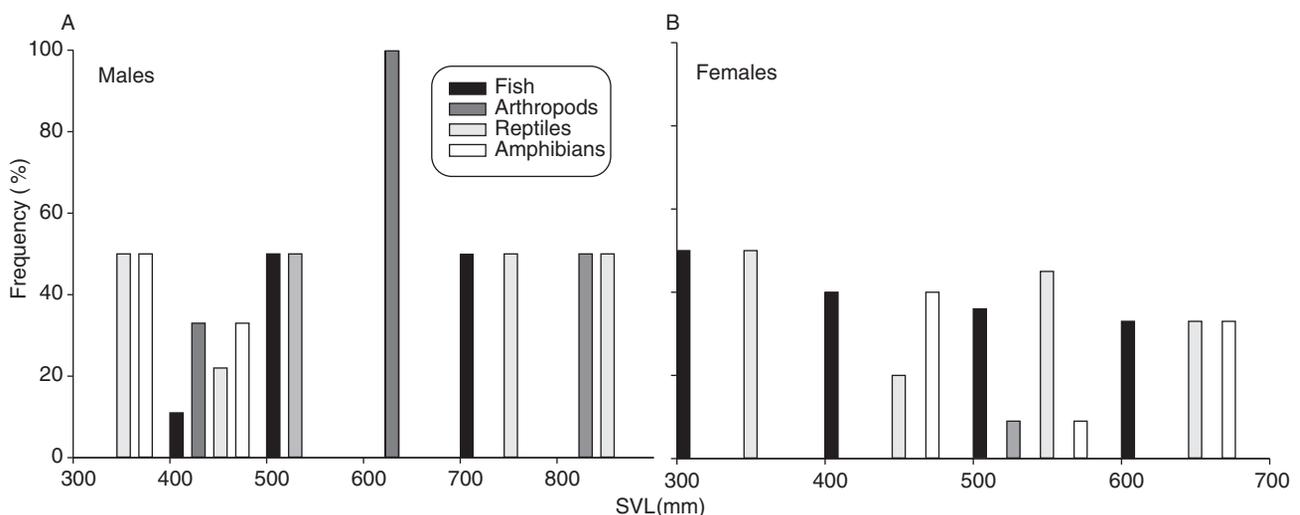


Figure 1. Bar graphs of the percentage of particular prey items taken at 100-mm snake snout-vent-length (SVL) intervals for both male (A) and female (B) *Agkistrodon piscivorus*.

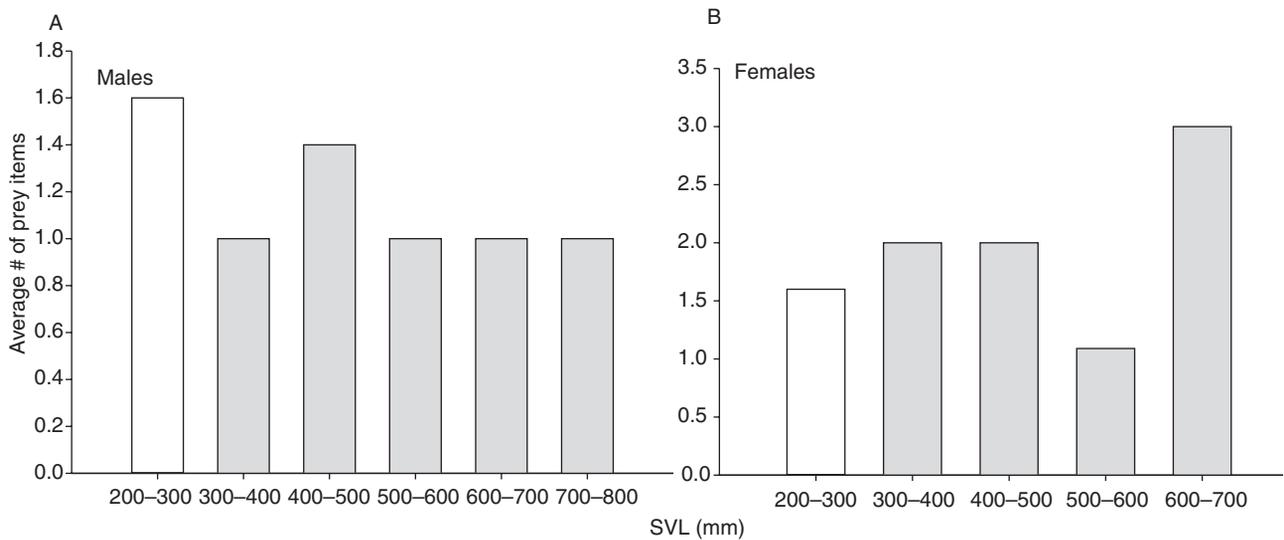


Figure 2. Bar graphs of the average number of prey items taken at 100-mm snake snout-vent-length (SVL) intervals by male (A), female (B) and juvenile (white bars, A and B) *Aghistrodon piscivorus*.

Table 2. Reduced major-axis regressions of \log_{10} morphology (dependent variables) vs. \log_{10} snout-vent length (SVL, independent variable)

Variable	Slope	y-intercept	95% CI (slope)	R
Juveniles ($N = 59$)	2.64	-4.90	2.25-3.03	0.83
Mass (g)	2.64	-4.90	2.25-3.03	0.83
Head volume (mL)	3.90	-9.18	3.04-4.77	0.52
Head width (mm)	1.09	-1.48	0.86-1.32	0.59
Head length (mm)	0.75	-0.56	0.58-0.93	0.43
Head height (mm)	1.31	-2.20	1.00-1.63	0.39
Jaw length (mm)	0.89	-0.79	0.72-1.07	0.65
Out-lever (mm)	0.84	-0.80	0.67-1.01	0.63
Males ($N = 108$)	2.74	-5.10	2.58-2.91	0.95
Mass (g)	2.74	-5.10	2.58-2.91	0.95
Head volume (mL)	2.06	-4.60	1.90-2.22	0.91
Head width (mm)	0.87	-0.97	0.79-0.95	0.88
Head length (mm)	0.62	-0.24	0.57-0.68	0.89
Head height (mm)	0.78	-0.94	0.69-0.89	0.75
Jaw length (mm)	0.67	-0.21	0.62-0.71	0.92
Out-lever (mm)	0.75	-0.58	0.69-0.88	0.90
Females ($N = 110$)	2.38	-4.14	2.22-2.53	0.94
Mass (g)	2.38	-4.14	2.22-2.53	0.94
Head volume (mL)	1.83	-4.60	1.65-2.00	0.87
Head width (mm)	0.83	-0.87	0.73-0.90	0.85
Head length (mm)	0.61	-0.21	0.55-0.68	0.85
Head height (mm)	0.75	-0.85	0.64-0.86	0.62
Jaw length (mm)	0.64	-0.19	0.59-0.70	0.90
Out-lever (mm)	0.68	-0.42	0.62-0.76	0.84

All variables deviate significantly from isometry in males and females but only head volume and head length deviate significantly from isometry in juveniles. The expected slope for mass and volume vs. SVL is 3 and the expected slope of all other variables vs. SVL is 1.

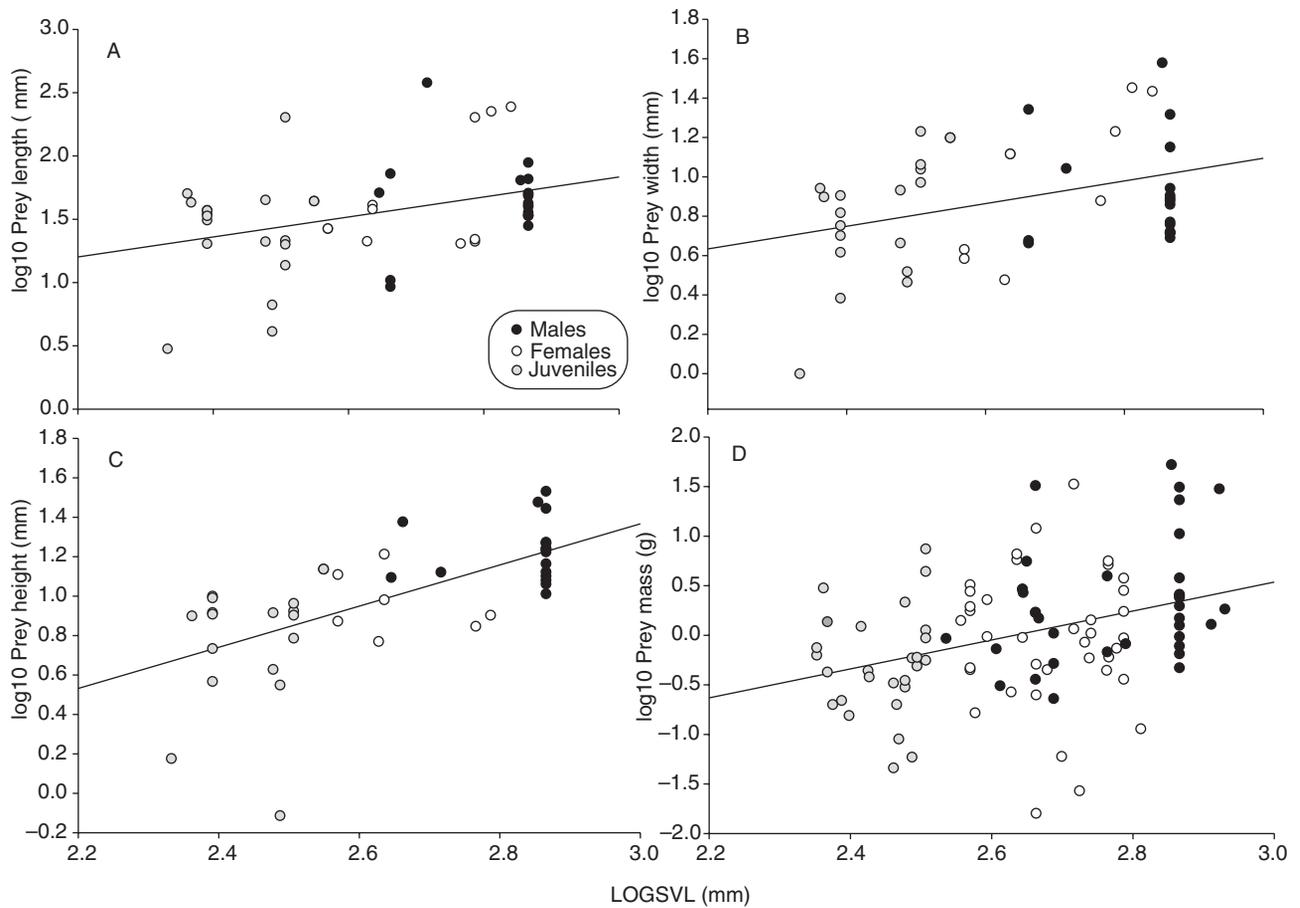


Figure 3. Reduced major-axis regressions of \log_{10} prey measures vs. \log_{10} snake snout-vent length (SVL).

Table 3. Loadings from a principal component analysis of size-adjusted \log_{10} head shape variables of male, female and juvenile *Agkistrodon piscivorus*

Variable	PC1	PC2	PC3	PC4	PC5
Dorsal surface area	0.688*	0.255	-0.293	0.093	-0.183
Lateral surface area	0.509	0.703*	0.281	-0.089	0.167
Ventral surface area	0.763*	0.187	-0.492	0.177	0.052
Frontal surface area	0.742*	-0.306	0.306	-0.314	0.266
Dorsal length 1	0.348	0.010	0.572*	0.489	-0.080
Dorsal length 2	0.152	-0.186	0.296	0.585*	0.550
Dorsal length 3	0.532	-0.251	0.292	0.440	-0.486
Lateral length 1	0.373	0.713*	0.153	-0.260	-0.146
Lateral length 2	0.324	0.626*	0.523*	-0.057	0.122
Ventral length1	0.317	0.507*	0.271	0.115	0.264
Ventral length 2	0.610*	-0.041	-0.309	0.348	0.036
Ventral length 3	0.704*	0.087	-0.177	0.034	-0.421
Ventral length 4	0.438	0.268	-0.65*	0.092	0.397
Frontal length 1	0.747*	-0.387	0.063	-0.216	0.239
Frontal length 2	0.647*	-0.360	0.244	-0.424	-0.040
Frontal length 3	0.759*	-0.515*	-0.055	-0.184	-0.038
Eigenvalue	5.14	2.31	1.87	1.38	1.11
% variation explained	34.3	15.4	12.5	9.2	7.4

*Substantial loadings.

frontal surface area and ventral surface area. Juveniles were the largest for frontal length 3 and ventral length 3. Females were the smallest in all comparisons. In other words, in the frontal view, the top portion of the head in males was wider relative to body size compared with that of females and juveniles. Males also had a larger frontal and ventral surface area relative to body size compared with females and juveniles. However, the bottom portion of the head relative to body size in juveniles was wider than that in both males and females. The back of the head relative to body size was also larger in juveniles than in males and females.

DISCUSSION

We report here on the relationships among head size, head shape and prey selection in adult male, adult female and juvenile *A. piscivorus*. Our scaling data for head characteristics showed that all head measurements in adult male and female *A. piscivorus* scaled with significant negative allometry (Table 2), whereas juvenile head measurements typically scaled isometrically, except for head volume (positive) and head length (negative). In other words, large juveniles had relatively broad and high, but short, heads. Large adult male and female *A. piscivorus* had relatively small head dimensions overall (i.e. low ratios of head dimensions to SVL). Thus, juveniles appear to undergo a rapid change in head volume, which subsequently slows considerably as sexual maturity is achieved. However, our multivariate analysis of size-adjusted head dimensions showed that juveniles differed only slightly in their head shape compared with adult male and female *A. piscivorus*. In general, prey size increased with snake size across all age and sex groups. We know that adult males prefer fish, whereas adult females prefer reptiles (particularly snakes) (S.E. Vincent, A. Herrel, D.J. Irschick, unpubl. data). Here we found that juveniles consumed a variety of different prey, and did not differ from either adult males or adult females in prey type.

HEAD SIZE AND SHAPE WITHIN *A. PISCIVORUS*

Several studies have shown that prey size in snakes is strongly correlated with head size (Pough & Groves, 1983; Shine, 1991; Arnold, 1993; Cundall & Greene, 2000), which is generally accepted as a rough approximation of maximum potential gape width. As a result, one might predict that maximum gape could be optimized within enlarged-gaped (*Macrostomatan*) snakes by increasing head growth relative to body size throughout ontogeny. In contrast, head growth slowed in adult male and female *A. piscivorus*, showing that

gape scales negatively with body size within adult *A. piscivorus*.

The potential functional consequences of this negative head growth are unclear. Although adult *A. piscivorus* achieve slower head growth rate later in life, *A. piscivorus* do obtain large body sizes (maximum SVL recorded here was 89 cm) as adults. As a result, adult *A. piscivorus* may have head sizes large enough to swallow most prey items they encounter. In other words, this slowing of head growth might not substantially affect prey selection among adult *A. piscivorus*. In contrast, the problem of gape width and prey selection is particularly relevant for juvenile *A. piscivorus*. Unlike the slowing of head growth in adults, juvenile *A. piscivorus* exhibited a rapid growth in their head volume, suggesting that, while growing, juveniles are maximizing gape width. In addition, our multivariate head-shape analysis revealed juveniles to have a wider neck relative to body size compared with adult males or females. On the other hand, head length scaled with negative allometry in juveniles as well as in adults. Nevertheless, this substantial increase in head volume might allow juveniles to increase their maximum gape, since gape is not simply controlled by one skeletal element in snakes (see Frazzetta, 1966). Because of the relatively small number of prey items found in the juvenile stomachs, we could not determine whether juveniles consume relatively larger or smaller prey compared with adult males or females. A more comprehensive diet dataset for juveniles would be useful in this regard.

ONTOGENY OF HEAD SHAPE AND DIET

Previous studies have shown that several aquatic feeding snake species exhibit an ontogenetic shift in prey type. For example, Mushinsky, Hebrard & Vodopich (1982) showed that two water snakes (*Nerodia erythrogaster* and *N. fasciata*) feed on fish as juveniles, but switch primarily to amphibians as adults. In contrast, De Queiroz, Henke & Smith, 2001) showed that a garter snake (*Thamnophis validus*) primarily feeds on amphibians as juveniles but later switches to fish as adults. Some garter snakes, such as *T. couchii* and *T. atratus*, have relatively small bullet-shaped heads (Alfaro, 2002; S.E. Vincent, pers. observ.), which may act to minimize drag. Thus, adults of these garter snakes may not be greatly hindered by pressure drag during aquatic strikes. On the other hand, the majority of water snake species are substantially larger bodied (head size and trunk diameter) compared with these highly specialized fish-eating garter snakes. Thus, the relatively larger head size of water snakes compared with that of garter snakes may be a significant factor in explaining why some water snakes switch to more terrestrial

prey as adults. Although it should be increasingly difficult for adult *A. piscivorus* to forage aquatically due to the increased surface area of their head and body, we did not detect a switch from aquatic to terrestrial prey within *A. piscivorus* as size increased. Therefore, a relevant question is whether *A. piscivorus* actively forage on fish as adults. Previous data suggests that *A. piscivorus* consume fish in several ways. For instance, they are known for consuming fish in drying ephemeral pools that contain dead or dying fish (Savitzky, 1992). However, juvenile and adult *A. piscivorus* have been observed foraging on fish in open water both in the laboratory and in the field (S. Vincent, pers. observ.; Savitzky, 1992). Thus, the hydrodynamic problem of capturing active fish in open water is an important issue for these snakes. Based on this concept, one might predict that juvenile *A. piscivorus* should consume more fish than do larger snakes based on the reduced drag they face when foraging in open water. Interestingly in this study, about 47% of the prey of juveniles is composed of fish, but as a proportion of mass, arthropods (mostly cockroaches) made up the majority of their diet (56%). Overall, however, there is no indication that juveniles consume much larger numbers of fish compared with either adult males or adult females.

One means for a snake to make its head more aerodynamic over time is to exhibit negative isometric growth, such as when the snake becomes larger, the head decreases proportionally compared with size. We observed this trend in adult male and female *A. piscivorus*, but can present no functional data to show that negative head growth affects feeding, although such studies are underway (S. Vincent, unpubl. data). One potential negative consequence of negative allometric head growth is a constraint on the ability to swallow prey because of the effect of gape width on prey selection. We are currently undertaking studies to investigate the effects of head shape and size on swallowing in a variety of water snakes, which might shed light on this issue. Experiments with methods such as digital particle image velocimetry might provide insights into the effect of head shape and size on drag.

In summary, our study is among the first to quantitatively explore changes in head shape throughout ontogeny in an aquatically feeding snake. However, we suggest that our scaling results should be interpreted with caution since scaling in snakes is largely unstudied (but see Rossman, 1980). In other words, our scaling exponents may bear little relationship to feeding. However, since swallowing and prey capture are difficult to study directly in most animals, our data show how an analysis of head size and shape coupled to a quantitative analysis of diet can indirectly examine these functional relationships.

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