

Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*)

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Abstract

Sexual dimorphism is a common phenomenon among animals. The usual cause cited for sexual dimorphism in animals is sexual selection acting through female choice or male–male combat. Natural selection acting to reduce resource competition between the sexes, however, is an important alternative evolutionary scenario, but this possibility has received little empirical study. Here this issue is addressed by examining the relationships among body size, head shape and the functional aspects of diet in the adult male and female cottonmouth snake *Agkistrodon piscivorus*. In this species, males are larger in overall body and head size. Whereas an analysis of gross head measurements (simple linear head dimensions) shows little dimorphism in head shape, a more detailed analysis of head shape (using digital images of the snakes' heads) revealed some subtle, yet functionally significant, differences in head shape between adult male and female cottonmouths. Specifically, male cottonmouths have longer quadrate bones, and have greater lateral surface areas than females. Male cottonmouths also consumed relatively taller prey (prey size relative to snake body size) than conspecific females, and the sexes consumed significantly different proportions of prey. Because the size of the quadrate bone is a strong determinant of maximum gape in snakes, we suggest that the observed shape differences may reflect functional differences in maximum gape between similarly sized male and female cottonmouths. In turn, such differences in maximum gape width may explain why males consume taller prey than similarly sized females.

Key words: ecological divergence, functional morphology, pit viper, squamates, trophic ecology, *Agkistrodon piscivorus*

INTRODUCTION

Sexual dimorphism in size, shape, colour and behaviour is a widespread phenomenon among animals. Whereas sexual selection acting through female choice or male–male competition is the explanation most often cited for the evolution of sexual dimorphism (Darwin, 1871), natural selection acting to reduce competition between the sexes is an important alternative evolutionary scenario (e.g. Schoener, 1971; Slatkin, 1984; Shine, 1989, 1994; Pearson, Shine & How, 2002; Shetty & Shine, 2002; Shine, Reed *et al.*, 2002). These scenarios are often not mutually exclusive, however, and can act in concert or sequentially. For example, a dimorphic trait may be initially produced by sexual selection, but a secondary effect of this dimorphism may be a shift in resource use between the sexes (e.g. male body size increases owing to male–male combat and larger animals can eat absolutely larger prey).

Furthermore, because this differential resource use between the sexes should reduce intraspecific competition, the dimorphism could be favoured (stabilizing selection) or even amplified by non-sexual selection in certain ecological settings. Although it is difficult to retrace the evolutionary causes of dimorphism, dimorphic traits associated with resource use may shed light on the evolutionary causes of dimorphism, since they are presumably not under selective pressure through sexual selection (Selander, 1972; Ralls, 1976; Slatkin, 1984; Shine, 1989, 1991).

Recent studies on snakes have shown that many snake species are sexually dimorphic in both head size and maximum consumed prey size (Shine, 1989, 1994; Houston & Shine, 1993; Madsen & Shine, 1994; Pearson *et al.*, 2002; Shetty & Shine, 2002; Shine, Reed *et al.*, 2002). Although the initial cause(s) of such dimorphisms cannot be completely known, previous authors have suggested that sexual dimorphism in head shape in snakes is maintained by intersexual resource competition, not sexual selection (e.g. Shine, 1991). This argument is

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probably correct because head size plays little role in either male–male combat or female choice in snakes (for an overview see Shine, 1991). Furthermore, because snakes are generally gape-limited predators (i.e. predators that do not extensively masticate their prey before swallowing; Cundall & Greene, 2000, but see Jayne, Voris & Ng, 2002), one would expect that the sex with the larger head would consume larger prey as well. Indeed, several empirical studies on snakes have upheld this prediction (for an overview see Shine, 1991; Arnold, 1993).

Although sexual dimorphism in head size and consumed prey size has been well documented in snakes, sexual dimorphism in head shape and prey shape have rarely been explored (but see Grudzien *et al.*, 1992; Houston & Shine, 1993; Forsman, 1996). This issue is problematic because both prey subjugation and manipulation for snakes are not simply controlled by a single head dimension, but rather by the interaction of a suite of cranial elements (e.g. Frazzetta, 1966; Houston & Shine, 1993; Forsman, 1996). Exactly which aspects of head shape are important in feeding remains unclear in snakes, but we suggest that aspects of the head that allow for the consumption of wide or high prey will be under especially strong selection (Camilleri & Shine, 1990). This prediction stems from the fact that the width and height of prey is related to its overall bulk, and hence, such items should be more difficult to swallow for gape-limited predators. Prey length is presumably not constrained by snake head size or shape since it is not limited by gape. As a result, if natural selection for niche divergence (i.e. natural selection resulting in sexes eating different prey) occurs in a snake species, then it should be reflected in intersexual differences in not only head size, but also in those aspects of head shape (i.e. the lengths of the quadrate, supratemporal and mandible bones) associated with maximum gape width.

To assess the role of intersexual resource competition driving sexual dimorphism in the cottonmouth snake *Agkistrodon piscivorus*, the relationships among body size, head shape and diet were examined in male and female adult cottonmouth snakes. The cottonmouth is known to be sexually dimorphic in body size (Shine, 1994), but whether sexual dimorphism in either head shape or diet occurs in this species is currently unknown. Here, whether male and female cottonmouths differ in head shape and whether any such differences are associated with differences in prey type or shape were addressed. These goals were accomplished by measuring head dimensions, body size, prey type (e.g. reptiles, mammals) and prey shape in a large sample of adult male and female cottonmouths.

MATERIALS AND METHODS

Specimens

An examination was made of 108 adult male and 106 adult female specimens of *A. piscivorus* from the Tulane

University Museum of Natural History. The sex of specimens could be unambiguously determined by gonadal examination beginning at a snout–vent length (SVL) of 330 mm. Diet data were collected for each specimen by dissection of the stomach. Stomach contents were identified to the lowest possible taxonomic order. The length (mm), width (mm), and height (mm) of the intact prey items were measured using Mitutoyo digital callipers (± 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. Food items were blotted dry, and the mass (g) was recorded for all individual stomach contents using a Denver Instruments M-220 electronic balance (± 0.01 mg).

Morphological measurements

Overall, 2 morphological datasets were gathered:

(1) To test for intersexual differences in gross aspects of size and head shape ('gross' dataset), the following morphological measurements were recorded for each specimen: snout–vent length (SVL, mm), body mass (g), 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 back to the tip of the lower jaw), and the jaw out-lever (from the articulation of the lower jaw with the quadrate to the tip of the lower jaw). SVL was determined by laying dental floss along the mid-ventral surface of the snake and then measuring the length (mm) of the dental floss using a metre stick; body mass was determined using an Ohaus weighted balance (± 0.1 g) and all head measurements were determined using Mitutoyo digital callipers (± 0.01 mm). In addition, head volume (ml) was measured 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.

(2) Because our 'gross' dataset only examined relatively broad aspects of intersexual head shape, a second dataset was generated to test for more subtle differences ('detailed' dataset) in head shape. To test for more subtle differences in head shape, several head measurements were taken from a sub-sample of 20 adult male and 20 adult female cottonmouths (SVL ranging between 600 and 850 mm). These particular specimens were chosen because their heads qualitatively seemed to be in the best condition of the entire sample (i.e. least distorted by preservation). For this sub-sample, digital images of the heads in dorsal, lateral, ventral and frontal views (Fig. 1) were taken 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. Anatomically homologous landmarks were placed on the images such that surface

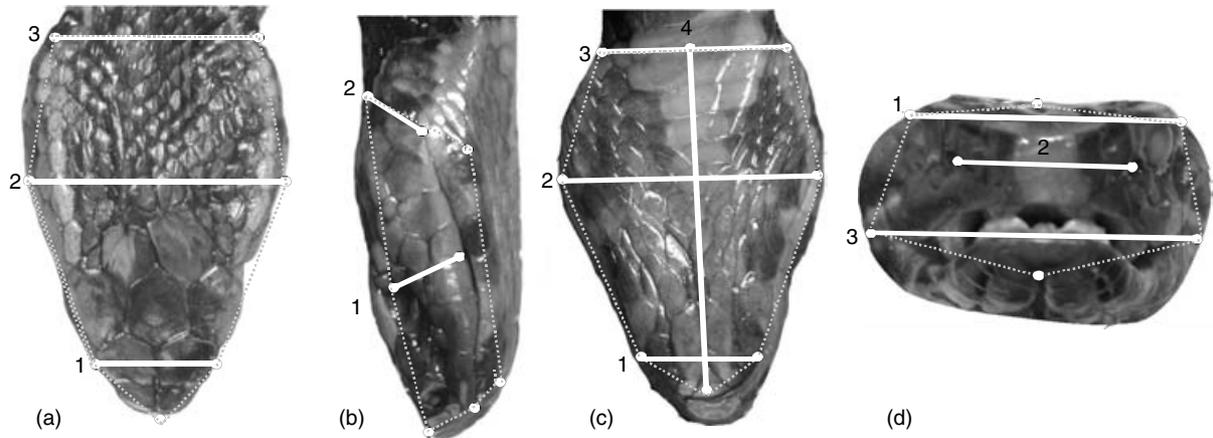


Fig. 1. Landmarks used to determine head shape of *Agkistrodon piscivorus* in (a) dorsal, (b), lateral, (c), ventral and (d) frontal views. Numbers of the lines correspond to the measurements as outlined in the Materials and methods. Dotted lines delineate the area used to calculate the surface area for each view.

areas, as well as several linear measurements could be recorded (Fig. 1).

Additionally, functionally homologous landmarks were placed on the images to record measurements of the heads that may be functionally important during feeding (e.g. widest part of the head in dorsal view):

dorsal view: (1) width at the front of the head (dorsal length 1); (2) widest part of the head in dorsal view (dorsal length 2); (3) width of the back of the head (dorsal length 3); (4) surface area of the head in dorsal view;

lateral view: (1) distance from the postocular scale to the tip of most lateral supralabial scale (lateral length 1); (2) distance between the retro-articular process and the dorsal aspect of the quadrate (lateral length 2); (3) the surface area of the head in lateral view;

ventral view: (1) width of the front of the head (ventral length 1); (2) widest part of the head in ventral view (ventral length 2); (3) the width of the neck (ventral length 3); (4) the distance between neck and the snout tip (ventral length 4); (5) the surface area of the head in ventral view;

frontal view: (1) width of head at its dorsal aspect (above the eyes) (frontal length 1); (2) distance between the nasal openings (frontal length 2); (3) widest part of the head in frontal view (frontal length 3); (4) the surface area of the head in frontal view.

In this way, whether adult male and adult female cottonmouths differ in relatively gross aspects of head shape, more detailed aspects of head shape, or both was tested.

Statistical analysis

To meet the assumption of homoscedasticity, all measurements were \log_{10} transformed before analysis. We

analysed both the 'gross' and 'detailed' datasets using principal components analysis (PCA). The broken stick method (Jackson, 1993) was used as a cut-off criterion to determine which axes explained a significant portion of the variation. Multivariate analyses of variance (MANOVA) were then conducted to compare relevant PC scores between males and females for both the 'gross' and 'detailed' datasets separately. Significance levels of all multiple comparison tests were adjusted using the sequential Bonferroni correction (Rice, 1989).

To determine if a particular prey type was preferred by either sex, the relative importance of different prey categories was expressed as the mass of each category relative to the total mass of all prey for each sex. Potential dimorphism in prey preference (expressed as relative mass) was assessed using a Kolmogorov–Smirnov test (KS). To test for differences in the average dimensions of consumed prey between sexes, a MANCOVA with \log_{10} SVL as the covariate, coupled to univariate F -tests, was performed using data for all prey for which at least 1 dimension could be determined. To test for differences in maximum consumed prey dimensions between the sexes, the maximum consumed prey dimensions were first calculated for each sex and then used as input into separate KS tests. All tests were performed using either SYSTAT (V. 10, SPSS Inc.) or SPSS (V. 10.05 SPSS Inc.).

RESULTS

Snake size and head shape

Gross dataset

The PCA performed on the gross dataset yielded two axes, which together explained 92.2% of the variation in the data (Table 1). The overall MANOVA testing for differences between the sexes was statistically significant (Wilks' $\lambda = 0.95$, $F_{3,238} = 4.06$, $P < 0.01$), yet the univariate

Table 1. Loadings from a principal components analysis of the \log_{10} transformed head measurements of *Agkistrodon piscivorus* from the 'gross' morphological dataset. Variables loading strongly on each principal component are bold

Variable	PC 1	PC 2
Head volume (ml)	0.937	-0.002
Head width (mm)	0.912	0.292
Head length (mm)	0.953	0.07
Head height (mm)	0.797	-0.595
Jaw length (mm)	0.969	0.04
Out-lever (mm)	0.935	0.105
Eigenvalue	5.079	0.457
% variation explained	84.6	7.62

Table 2. The means \pm standard deviations of morphological variables for both sexes of *Agkistrodon piscivorus*

Variable	Males	Females
SVL (mm)	601.1 \pm 149.2	543.4 \pm 121.4
Mass (g)	383.5 \pm 253.7	254.1 \pm 130.2
Head volume (ml)	14.54 \pm 7.58	11.05 \pm 4.20
Head width (mm)	27.93 \pm 6.46	25.51 \pm 4.99
Head length (mm)	31.74 \pm 5.17	29.79 \pm 4.17
Head height (mm)	17.19 \pm 3.53	15.82 \pm 2.94
Jaw length (mm)	40.37 \pm 6.99	37.31 \pm 2.94
Out-lever (mm)	30.89 \pm 6.13	28.60 \pm 4.54
Prey mass (g)	8.03 \pm 14.1	8.07 \pm 12.3
Prey length (mm)	55.6 \pm 73.4	80.8 \pm 92.7
Prey width (mm)	10.3 \pm 7.80	13.0 \pm 9.64
Prey height (mm)	16.4 \pm 7.40	9.59 \pm 3.72

F-tests showed that only PC 1 differed significantly between the sexes, and remained so after correction for multiple comparisons ($F_{1,240} = 10.98$, $P = 0.001$). Inspection of the variable loadings (Table 1) revealed that while PC 1 is an indicator of overall size, PC 2 is an indicator of head shape. Thus, from this initial analysis, adult male and adult female cottonmouths differ in overall head and body size (Table 2), but not in gross aspects of head shape.

Detailed dataset

The PCA performed on the digitized head shape variables yielded two axes, together explaining 73.46% of the total variation (Table 3). Inspection of the loadings indicated that whereas the first axis was a clear indicator of overall head size, the second axis represented head shape and correlated strongly with two measures: (1) the lateral surface area; (2) lateral length 2 (see Table 3), with lateral length 2 being an estimate of quadrate length. The MANOVA performed on the factor scores revealed that males and females differed significantly overall (Wilks' lambda = 0.52, $F_{2,36} = 16.38$, $P < 0.001$). Subsequent univariate *F*-tests showed significant sexual differences on both the first ($F_{1,37} = 16.70$, $P < 0.001$; $P < 0.05$) and second axes ($F_{1,37} = 6.29$, $P = 0.01$; $P < 0.05$). When considering \log_{10} SVL as a covariate (ANCOVA), sexual

Table 3. Loadings from a principal components analysis of the \log_{10} transformed digitized head measurements of *Agkistrodon piscivorus* from the 'detailed' dataset. Variables loading strongly on each principal component are bold

Variable	PC 1	PC 2
Dorsal surface area	0.912	-0.197
Lateral surface area	0.714	-0.577
Ventral surface area	0.934	-0.253
Frontal surface area	0.866	0.068
Dorsal length 1	0.843	0.254
Dorsal length 2	0.918	-0.224
Dorsal length 3	0.880	-0.175
Lateral length 1	0.655	0.424
Lateral length 2	0.353	-0.866
Ventral length 1	0.646	0.373
Ventral length 2	0.809	-0.215
Ventral length 3	0.862	-0.129
Ventral length 4	0.730	-0.300
Frontal length 1	0.770	-0.181
Frontal length 2	0.830	0.017
Frontal length 3	0.876	-0.298
Eigenvalue	10.43	2.06
% variation explained	61.37	12.09

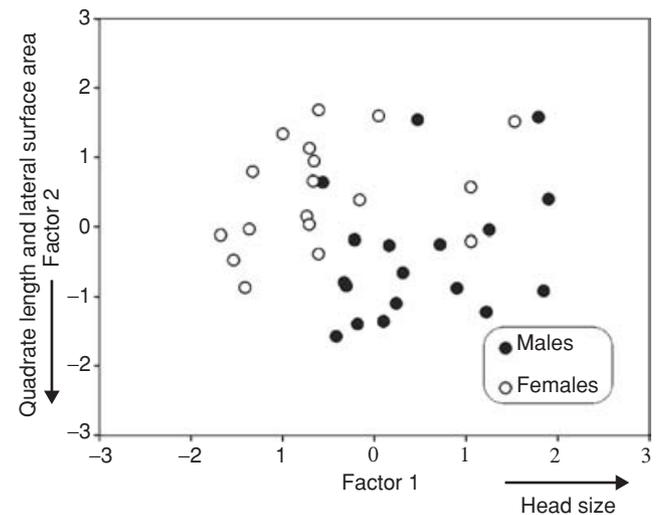


Fig. 2. Plots of factor loadings of a principal component analysis of the digitized ('detailed') head shape variables for male and female *Agkistrodon piscivorus*. Male and female snakes are significantly different in overall head size (all variables correlated positively with principal component 1) and lateral length 2 as well as the lateral surface area (these two particular variables exhibited a strong negative correlation with principal component 2). Males correlated positively with PC 1 and negatively with PC 2.

differences in the first axis became non-significant, but differences between sexes on the second axis became even more significant ($F_{1,37} = 14.08$, $P = 0.001$). Therefore, from this more rigorous analysis of head shape, it is clear that male and female cottonmouths differ in aspects of head shape associated with both the lateral surface area of their heads, as well as an indicator of quadrate length (see Fig. 2).

Snake–prey relationships

As previously reported, the cottonmouth seems to be a dietary generalist that feeds on a wide variety of prey types (Table 4) (Savitzky, 1989). In our sample, 39.3% of all snakes had prey in their stomachs, equally distributed between males (38%) and females (41%). The average number of prey consumed was 1.8 prey items for male and 1.4 prey items for female snakes. From simple counts of individual prey types, males consumed fish as their main dietary item, followed in importance by arthropods, amphibians, reptiles, mammals and molluscs (Fig. 3a). Based on frequency counts, females also consumed fish as their primary dietary item, followed by reptiles, amphibians, molluscs and arthropods. When diet was analysed relative to the total mass of prey consumed (Fig. 3b), reptiles become the principal dietary item for females and fish for males. Moreover, the KS tests of the % mass relative to total prey mass in diet revealed that the sexes are sexually dimorphic in the consumed % mass of most of the prey types observed here (fish, $P = 0.001$, $D_{\max} = 0.97$; reptiles, $P = 0.003$, $D_{\max} = 0.97$; amphibians, $P = 0.01$, $D_{\max} = 0.92$; arthropods, $P = 0.02$, $D_{\max} = 0.90$; molluscs, $P = 0.20$, $D_{\max} = 0.67$; mammals, $P = 0.50$, $D_{\max} = 0.50$). Thus, the sexes are sexually dimorphic for most of the consumed prey types observed here. Overall, males consume significantly more fish, amphibians and arthropods than females, whereas females consume significantly more reptiles and molluscs than males. When expressing dietary preferences using the relative mass of the prey, arthropods, molluscs, and mammals are no longer important prey sources for either males or females relative to the overall mass of prey consumed (all individually < 10% of the total mass of all consumed prey).

The MANCOVA testing for differences in average consumed prey dimensions, independent of body size, between the sexes showed significant differences between the sexes (Wilks' lambda = 0.50, $P < 0.01$). On inspection

Table 4. Numbers of different prey items found in stomachs of adult male and adult female *Agkistrodon piscivorus*

Prey type	Male	Female
Vertebrata		
Pisces		
<i>Lepomis macrochirus</i>	3	0
<i>Lepomis</i> sp.	9	0
<i>Fundulus</i> sp.	0	1
Unidentifiable fish	8	12
Amphibia		
Anura		
<i>Rana sphenoccephala</i>	5	1
<i>Hyla cinerea</i>	0	2
<i>Acris crepitans</i>	0	1
Unidentified tadpoles	0	2
Caudata		
Unidentifiable salamander	1	1
Unidentified amphibians	1	0
Reptilia		
Sauria		
<i>Scincella lateralis</i>	3	0
<i>Eumeces inexpectatus</i>	1	0
Unidentifiable lizards	0	3
Serpentes		
<i>Nerodia fasciata</i>	0	2
<i>Thamnophis</i> sp.	0	1
<i>Farancia abacura</i>	1	0
<i>Agkistrodon piscivorus</i>	1	3
Unidentifiable snakes	0	2
Testudines		
<i>Macrolemys temminickii</i>	1	0
Mammalia		
Rodentia		
<i>Sigmodon hispidus</i>	1	0
Invertebrata		
Arthropoda		
Coleoptera	7	0
Diptera	2	0
Hymenoptera	0	1
Blattoidea	2	0
Gastropoda	1	2
Total	47	34

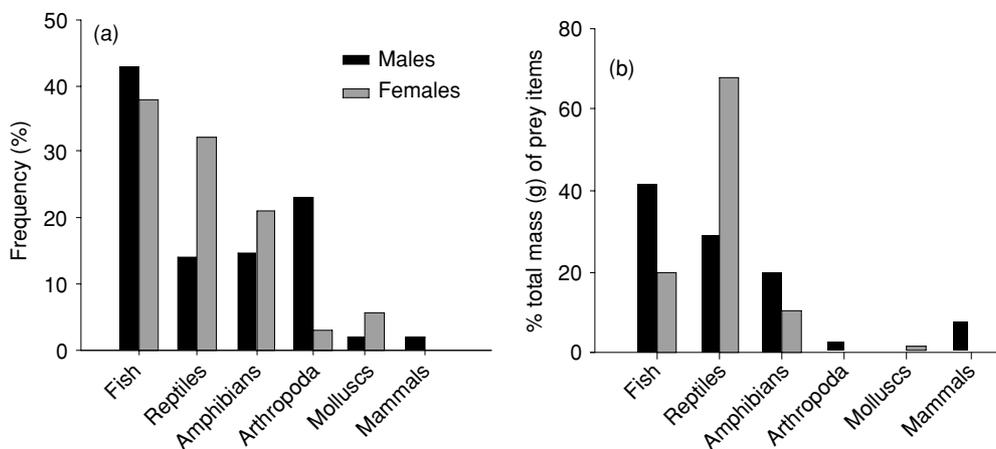


Fig. 3. (a) Frequency of particular prey items taken by male and female *Agkistrodon piscivorus*. (b) Frequency mass of particular prey items consumed by males and females.

Table 5. Maximum prey dimensions consumed by adult male and female *Agkistrodon piscivorus*

Variable	Males	Females
Prey mass (g)	52.4	33.4
Prey length (mm)	380.0	239.0
Prey width (mm)	33.8	16.2
Prey height (mm)	38.0	28.1

of the univariate F -tests, however, only average prey height remained significantly different between the sexes ($F_{1,29} = 7.40$, $P = 0.02$). Thus, average prey mass ($F_{1,29} = 0.256$, $P = 0.64$), width ($F_{1,29} = 1.89$, $P = 0.18$) and length ($F_{1,29} = 0.607$, $P = 0.44$) did not significantly differ between the sexes. Thus, male cottonmouths consumed taller prey on average (mean = 16.4 ± 7.4 mm) than similarly sized females (mean = 9.84 ± 4.0 mm), but males and females of similar size consumed similarly shaped prey in all other regards. The KS tests performed on maximum consumed dimensions revealed that males consumed significantly larger maximum dimensions than females (Table 5) (maximum prey mass, $P < 0.01$, $D_{\max} = 0.93$; maximum prey width, $P < 0.01$, $D_{\max} = 0.92$; maximum prey height, $P < 0.01$, $D_{\max} = 0.87$; maximum prey length, $P < 0.001$, $D_{\max} = 0.98$).

DISCUSSION

Sexual dimorphism in animals is typically believed to have arisen by sexual selection via female choice or male–male combat. Several studies, however, have shown that natural selection acting to reduce resource competition between the sexes may also be a major evolutionary force driving sexual dimorphism (e.g. Slatkin, 1984; Shine, 1989; Shine, Harlow *et al.*, 1998). Whereas sexual selection should lead to overall differences in size, natural selection is expected to result in distinct shape differences in the trophic apparatus (e.g. beaks in birds) that allow the sexes to exploit differently shaped prey (Camilleri & Shine, 1990). Although many studies have documented differences in overall size between male and female snakes, and concomitant differences in prey size (e.g. Shine, 1991), few studies have explicitly shown that head shape differences are related to differences in consumed prey type or prey shape (but see Camilleri & Shine, 1990; Houston & Shine, 1993). Here we demonstrated that adult male and adult female cottonmouth snakes are sexually dimorphic in not only body size, but also in some aspects of head shape. In turn, this head shape dimorphism is associated with sexual differences in consumed prey type and shape.

Intersexual differences in head shape

As male–male combat is common in pit vipers (e.g. Shine, 1994), and has been documented in cottonmouths as well

(Burkett, 1966), sexual selection most probably lies at the basis of our observed body size dimorphism. Because cottonmouths are gape-limited predators, the larger overall size of males (Table 2) enables them to ingest overall larger prey than smaller females (see Results; Table 5). However, if sexual selection were the only agent driving the observed dimorphism, no additional differences in head or prey shape would be expected (for an overview see Shine, 1991). Our results from the detailed analysis of head shape, though, revealed a significant sexual difference in head shape. Specifically, our results suggest that male cottonmouths may possess longer quadrate bones (i.e. lateral length 2), and have greater lateral surface areas than females (Fig. 2, Table 3). Additionally, our data indicate that on average male cottonmouths consume relatively taller prey than females. Therefore, although the morphological differences between male and female cottonmouths are subtle, they are none the less associated with the differences in the type and shape of the prey consumed.

One possible explanation for the observed dimorphism in head shape is that the longer quadrate bones in males enables the consumption of taller prey than similarly sized females, thus potentially reducing intraspecific resource competition between the sexes. We suggest that the greater lateral surface area in males, though, is indicative of regional changes in head height (at the posterior end) and thus, this particular component of the observed head shape dimorphism may also reflect the dimorphism in quadrate length. Indeed, these two variables scale isometrically with one another in both males (slope = 0.47, $r = 0.94$, 95% CI = 0.43–0.52) and females (slope = 0.45, $r = 0.91$, 95% CI = 0.43–0.51), when regressing lateral surface area (x -axis) vs lateral length 2 (y -axis) using reduced major axis regression. Within many snake species, the ability to successfully transport a prey item through the oral cavity depends on the capacity of the lower jaw and quadrate bones to move relative to the prey. Not only do longer quadrates allow the lower jaws to be rotated open further (all else being equal; see Gans, 1974), they presumably also allow greater lateral distension over a prey item (Gans, 1961; Kardong, 1977; Throckmorton & Clarke, 1981; Cundall & Greene, 2000). However, it should be noted that the distension of the intermandibular soft tissues during prey transport and swallowing is equally important (Cundall, 1987; Young, 1998). As the swallowing process involves the independent movements of the lower jaw and quadrate bones relative to the rest of the skull (i.e. cranial kinesis), longer quadrates may also be more effective for the transport of particularly bulky prey through the oral cavity. Therefore, we suggest that a relatively longer quadrate in male cottonmouths could increase the maximum expansion of the jaws, and may enable male cottonmouths to manipulate better and swallow taller prey than similarly sized females. Further studies using cineradiography to examine the ability of similarly sized male and female cottonmouths to manipulate and transport prey of different shapes are crucial to test this hypothesis.

The generality of our findings is difficult to assess because relatively few studies have examined differences

in head shape between different sexes, or correlated such differences with consumed prey type and/or shape (but see Camilleri & Shine, 1990). Interestingly, distinct sexual differences in diet have been reported for the sister taxon to the cottonmouth (*Agkistrodon contortrix*; Garton & Dimmick, 1969; Fitch, 1982), suggesting that head shape dimorphism may be present in this species as well. Sexual size dimorphism is, however, also present in this species. Thus, the documented differences in diet may simply reflect sexual body size dimorphism since the larger size of males will enable the consumption of overall larger prey, not natural selection for ecological divergence between the sexes. None the less, comparative data on sexual differences in head shape for a variety of snakes would be welcome to test the generality of our results, and could shed light on whether ecological divergence and head shape dimorphism in snakes evolves in parallel, or if they can evolve independently of one another.

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