

Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*

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In many species of lizards, males attain greater body size and have larger heads than female lizards of the same size. Often, the dimorphism in head size is paralleled by a dimorphism in bite force. However, the underlying functional morphological basis for the dimorphism in bite force remains unclear. Here, we test whether males are larger, and have larger heads and bite forces than females for a given body size in a large sample of *Anolis carolinensis*. Next, we test if overall head shape differs between the sexes, or if instead specific aspects of skull shape can explain differences in bite force. Our results show that *A. carolinensis* is indeed dimorphic in body and head size and that males bite harder than females. Geometric morphometric analyses show distinct differences in skull shape between males and females, principally reflecting an enlargement of the jaw adductor muscle chamber. Jaw adductor muscle mass data confirm this result and show that males have larger jaw adductors (but not jaw openers) for a given body and head size. Thus, the observed dimorphism in bite force in *A. carolinensis* is not merely the result of an increase in head size, but involves distinct morphological changes in skull structure and the associated jaw adductor musculature. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 91, 111–119.

ADDITIONAL KEYWORDS: biting – diet – dimorphism – muscle – sexual dimorphism – skull shape.

INTRODUCTION

Sexual selection has long been recognized as one of the major selective forces driving the evolution of phenotypic variation in vertebrates (Darwin, 1871). Sexual selection often leads to dimorphisms (i.e. differences in size, shape, or colour) between the sexes which are the result of a differential allocation of resources. For example, in males, those structures important in male–male combat or defense of territories will be selected for (Pratt *et al.*, 1992; Molina-Borja, Padron-Fumero & Alfonso-Martin, 1998; Emlen *et al.*, 2005). Alternatively, in females of many vertebrates, allocation of resources promoting more or larger offspring will be favoured (e.g. larger abdomen size; Gross, 1996; Bauwens & Diaz-Uriarte, 1997). Some of the most spectacular results of sexual selection are the ornaments displayed by males of many vertebrates

(e.g. peacock or swallow tails, lizard dewlaps; Berglund, Bisazza & Pilastro, 1996) that are used as status signals towards other males or females (Backwell *et al.*, 2000; Vanhooydonck *et al.*, 2005). Another class of dimorphisms that are conspicuous and have attracted broad attention is the armaments used during male–male territorial interactions, such as antlers, horns, or crests (Berglund *et al.*, 1996; Dodson, 2000; Emerson, 2000; Emlen *et al.*, 2005). However, dimorphisms between sexes often are expressed in less spectacular fashion and involve differences in body size or head size only (Shine, 1993; Andersson, 1994; Censky, 1996; Gvozdkik & Van Damme, 2003).

In lizards, sexual size dimorphisms are often striking, with males typically being the larger sex (Stamps, 1993; Olsson & Madsen, 1999). Additionally, head size dimorphisms are prominent and have been linked to male–male combat and/or resource competition (Carothers, 1984; Bull & Pamula, 1996; Lailvaux *et al.*, 2004). Often, it is implicitly assumed that the observed difference in head size results in a parallel

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difference in bite force (Hikida, 1978; Carothers, 1984; Vitt & Cooper, 1985; Gier, 2003; Hasegawa, 2003). Interestingly, the few studies that have examined the correlates of head size with bite force have confirmed this suggestion; males tend to have larger heads and do indeed bite harder than females (Herrel *et al.*, 1996, 2001a; Herrel, Van Damme & De Vree, 1999; Herrel, De Grauw & Lemos-Espinal, 2001b; McBrayer & White, 2002; Verwaijen, Van Damme & Herrel, 2002). Yet, the underlying functional causes for the relationship between head size and bite force generally remain unclear. Most often, it has been suggested that having a bigger head simply results in a larger absolute jaw muscle volume, thus conferring a bite performance advantage (Herrel *et al.*, 2001a, b). However in some lizard species, the observed increase in bite force is larger than would be predicted by the difference in head size between the sexes (Herrel *et al.*, 1999), and distinct differences in the allocation of jaw adductor muscle between the sexes have been demonstrated for others (Herrel *et al.*, 1996, 1999).

Whether or not the increase in bite force is merely the result of increases in overall head size or relative muscle volume is an important issue. It has been suggested that dimorphisms (including differences in head size) are caused by higher circulating levels of testosterone (Vitt & Cooper, 1985; Sassoon, Gray & Kelly, 1987). Indeed, in some lizards, seasonal changes in head width have been observed, with males having wider heads in the reproductive season when testosterone levels are typically high (Cooper, Mendoca & Vitt, 1987; Vitt & Cooper, 1985). Given the role of testosterone in causing muscle hypertrophy (Sidor & Blackburn, 1998), and thus increasing muscle force output (Peters & Aulner, 2000), intersexual differences in bite force could potentially be controlled by the regulation of testosterone levels. If, however, intersexual differences are more complex, including more profound changes in muscle architecture or skull shape, then simple regulation of testosterone levels would likely be inadequate to cause the observed dimorphisms.

The aims of the present study were to investigate the dimorphism in head size and bite force in a common lizard, the green anole (*Anolis carolinensis*), and to investigate the underlying functional morphological basis for these differences. We chose this species because it has been previously demonstrated that males and females are dimorphic in head size (Irschick *et al.*, 2005). First, we compared body size, head size, head shape, and bite force between the sexes for a large sample from a single population of *A. carolinensis*. Next, we analysed shape differences in the cranial structure of male and female *A. carolinensis* using geometric morphometric analyses. Finally, we tested whether differences in overall

jaw muscle mass and muscle allocation exist between sexes.

MATERIAL AND METHODS

SPECIMENS

Lizards used for morphometric analysis and bite force measurements ($N = 80$) were caught in the vegetation along a 755-m transect that follows a straight dirt road crossing Good Hope Field in St Charles Parish, south-eastern Louisiana (see Irschick *et al.*, 2005). All animals used in this analysis were caught in September and October of 2002.

BODY/HEAD MEASUREMENTS

The following measurements were taken from each animal used in the performance trials using digital calipers (± 0.01 mm; Mitutoyo, Sakato, Japan): snout-vent length, head length, head width, head height, lower jaw length, the distance from the quadrate to the tip of the jaw (i.e. the jaw out-lever), and the distance from the coronoid (estimated by the back of the jugal) to the tip of the lower jaw. Head length was measured from the tip of the snout to the posterior edge of the parietal bone, which can easily be detected by palpation. Head width was measured at the widest part of the skull and includes potential bulging of the jaw muscles. Head height was measured at the highest part of the skull just posterior to the orbit, and may again include bulging of the jaw adductors (musculus pterygoideus). Next, the in-lever for jaw opening was estimated by subtracting the jaw out-lever length from the lower jaw length; the in-lever for jaw closing was estimated by subtracting the distance from the coronoid to the tip of the jaw from the jaw out-lever. Note, however, that this can only be considered the in-lever length for the external adductors that insert onto the coronoid bone by means of the bodenaponeurosis. A summary of the morphometric data is presented in Table 1.

DISSECTIONS

Fourteen male and five female lizards from the sample described above (but not included in the performance trials) were sacrificed by administration of an overdose of ketamine. Next, animals were preserved in a 10% aqueous formaldehyde solution for 24 h, rinsed extensively, and transferred to a 70% aqueous ethanol solution. All jaw closers (i.e. the adductor externus, adductor internus and adductor posterior groups *sensu* Lakjer, 1926) and jaw openers (musculus cervicomandibularis and the musculus depressor mandibulae) were removed on one side in each individual,

Table 1. Summary of differences in body size, head size, bite force, and muscle mass in male and female *Anolis carolinensis*

| | Male (<i>N</i> = 40) | Female (<i>N</i> = 40) |
|--------------------------------|--------------------------|----------------------------|
| Snout–vent length (mm) | 62.58 ± 5.2 | 55.36 ± 2.09 |
| Mass (g) | 5.12 ± 1.24 | 3.44 ± 0.39 |
| Head length (mm) | 18.81 ± 1.27 | 15.27 ± 0.57 |
| Head width (mm) | 9.84 ± 0.9 | 8.2 ± 0.31 |
| Head height (mm) | 6.94 ± 0.72 | 5.82 ± 0.24 |
| Lower jaw length (mm) | 19.98 ± 1.61 | 16 ± 0.55 |
| Jaw outlever (mm) | 18.24 ± 1.45 | 14.6 ± 0.53 |
| Open in-lever (mm) | 1.74 ± 0.2 | 1.41 ± 0.11 |
| Close in-lever (mm) | 3.06 ± 0.35 | 2.35 ± 0.19 |
| Bite force (N) | 4.74 ± 1.46 | 2.59 ± 0.39 |
| Jaw opener muscle mass (mg) | 4.88 ± 1.75 | 2.67 ± 0.98 |
| Jaw closer muscle mass (mg) | 56.32 ± 18.54 | 16.67 ± 6.31 |

Table entries are mean ± standard deviations. For muscle mass data, sample sizes are *N* = 14 for males and *N* = 5 for females. All head dimensions are significantly greater in males even when taking into account differences in body size.

blotted dry and weighed using a Mettler MT5 microbalance (±0.01 mg).

BITE FORCE

In vivo bite forces were measured using an isometric Kistler force transducer (type 9203; Kistler Inc., Winterthur, Switzerland), mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5995, Kistler Inc.; for a more detailed description, see Herrel *et al.*, 1999, 2001a, b). Prior to, and inbetween, performance trials, the animals were placed in an incubator set at their preferred temperature. Lizards were generally eager to bite when taken out of their bags. Where necessary, lizards were induced to bite by gently tapping the sides of their jaws. The place of application of bite forces was standardized by the length of the bite plates used. Gape angle (opening of the jaws) was standardized (10 ± 5°) by moving the bite plates away from each other for larger individuals. Measurements were repeated five times for each animal with an intertrial interval of at least 30 min. The maximal value obtained during such a recording session was considered to be the maximal bite force for that animal (Table 1).

STATISTICAL ANALYSES

All data were log₁₀-transformed before analysis. After transformation, all data were normally distributed. To

test whether males were larger on average than females, a univariate analysis of variance (ANOVA) was used. Given that the difference in body size was significant, differences in head size and bite force were tested using a multivariate analysis of covariance with lizard snout–vent length as covariate, head dimensions and bite force as dependent variables, and sex as the fixed factor. To determine which of the head dimensions best explained the observed variation in bite force across all individuals, a stepwise multiple regression was performed with bite force as dependent and body size and head dimensions as independent variables. Next, differences in muscle mass between the sexes were tested using an analysis of covariance (ANCOVA) with snout–vent length as covariate. To test whether differences in jaw adductor mass were still significant for a given head size, we used an ANCOVA with head width as covariate.

SKULL SHAPE ANALYSIS

A total sample of 52 alcohol-preserved specimens of *A. carolinensis* (28 male, 24 female) were analysed for dimorphism in skull shape. All specimens were taken from the Stephen F. Austin State University Vertebrate Natural History Museum (see Appendix). Sex was determined by visual inspection of hemipenes and/or ovaries or testes. Each lizard was laid flat on film (Kodak Industrex M, Kodak, Rochester, New York) and radiographed (30 kVp, 3 mA for 90 s; Hewlett Packard Faxitron Series model 43805N, Hewlett Packard, Palo Alto, CA, USA) in dorsal view. Rubber bands were placed across the heads of the lizards and around the cardboard backing of the film to hold the mandible firmly against the surface to ensure a direct dorsal/ventral orientation of the skull. After exposure and developing, digital images of each lizard radiograph were taken and imported into a computer.

A total of ten landmarks (Fig. 1) were digitized on one side of the skull in each of the 52 specimens (tps-Dig, version 1.40; Rohlf, 2004a). Landmarks (Fig. 1) generally represent the tips or corners of processes (e.g. lateral tip of jugal, landmark 9), intersection of tissues (e.g. ectopterygoid and lower jaw, landmark 8), or maxima of curvature (e.g. tip of premaxilla, landmark 1) of structures (Bookstein, 1991). Given the variable quality of X-ray images, landmarks were chosen based on their reliability of identification in all specimens in addition to their ability to cover regions of the skull functionally related to biting. Landmark configurations for each specimen were scaled to unit (= 1) centroid size, superimposed, and aligned using the generalized orthogonal least-squares method to produce a consensus configuration (tpsRelw, version 1.39; Rohlf, 2004b). Fourteen partial warps (number of partial warps = 2*p* – 6 where *p* is the number of land-

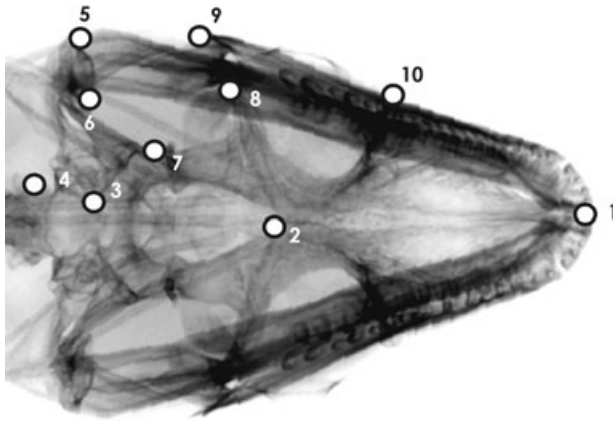


Figure 1. Radiograph of the head of a male *Anolis carolinensis* in dorsal view. Anatomical landmarks digitized to quantify head shape are illustrated (1–10).

marks) and two uniform components (calculated via the complement method; Rohlf & Bookstein, 2003) were obtained from the landmark data in the program tpsRelw (version 1.39; Rohlf, 2004b). Greater detail on the geometric morphometric methodology employed here is provided elsewhere in the literature (Bookstein, 1991; Rohlf *et al.*, 1993; Rohlf, Loy & Corti, 1996).

Two approaches were used to analyse the geometric morphometric data and test for the presence of sexual dimorphism in skull shape in *A. carolinensis*. First, the matrix of scores on the 14 partial warps plus two uniform components (i.e. the ‘weight’ matrix) was analysed using relative warps analysis (RWA); with the parameter $\alpha = 0$, the RWA simply represents a principal components analysis of the covariance matrix of partial warp and uniform component scores. Axes obtained from the RWA were plotted to look for patterns of dimorphism in skull shape between the sexes, and thin-plate spline deformation grids and vector plots depicting shape change along these axes were calculated in tpsRelw (version 1.39; Rohlf, 2004b). In the second analysis, the weight matrix was analysed using discriminant function analysis (DFA), which calculates the linear combination of variables that maximally separates a priori defined groups (i.e. sexes in the present analyses; Manly, 1986). Thus, DFA is an effective tool for examining the degree to which the sexes can be distinguished on the basis of skull shape.

RESULTS

BODY/HEAD MORPHOMETRICS

Male *A. carolinensis* in our sample are significantly larger than females, which is reflected in differences in snout–vent length ($F_{1,78} = 69.15$; $P < 0.01$) and body mass ($F_{1,78} = 76.25$; $P < 0.01$). Moreover, analyses of

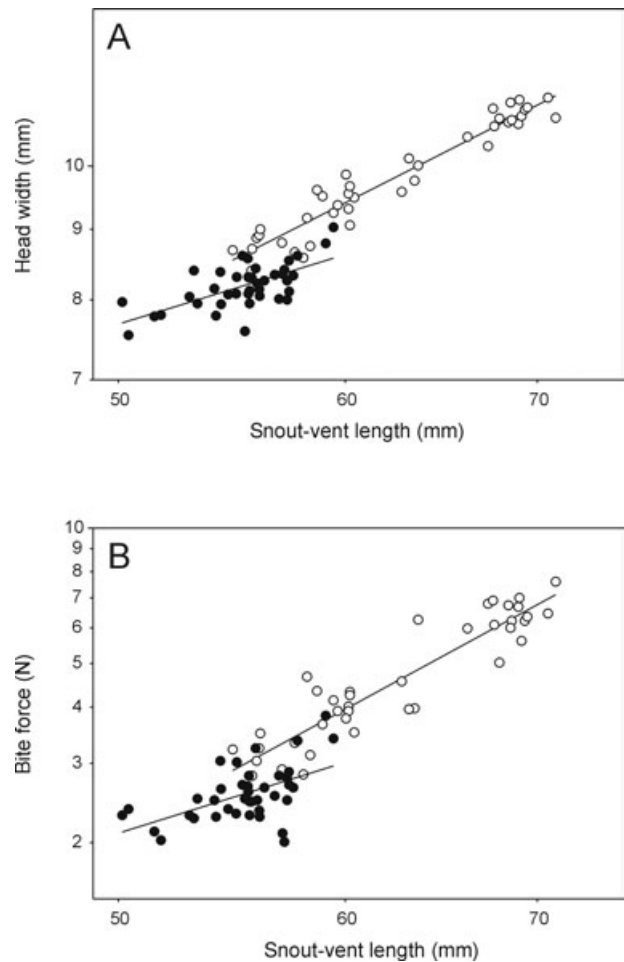


Figure 2. A, differences in head width between the two sexes in *Anolis carolinensis*. Note that females are on average smaller than males, but also have narrower heads for a given body size than males. B, females also bite less hard for a given body size than males. Note the log scale on the x- and y-axes. Open symbols, males; filled symbols, females.

covariance with snout–vent length as the covariate demonstrate that males have significantly larger heads for a given body size when compared to females (all $P < 0.01$; Table 1, Fig. 2). However, males are not significantly heavier than females for a given body size (ANCOVA: $F_{1,77} = 3.73$; $P = 0.057$).

BITE FORCES

Males bite harder than females in both absolute ($F_{1,78} = 110.89$; $P < 0.01$) and relative terms (ANCOVA: $F_{1,77} = 22.91$; $P < 0.01$; Figs 2, 3). A stepwise multiple regression analysis with bite force as dependent variable retained a significant model ($r^2 = 0.91$; $P < 0.01$) with head width, snout–vent length and head length as the only variables. Thus, lizards that are larger and that have wider and longer heads bite harder. How-

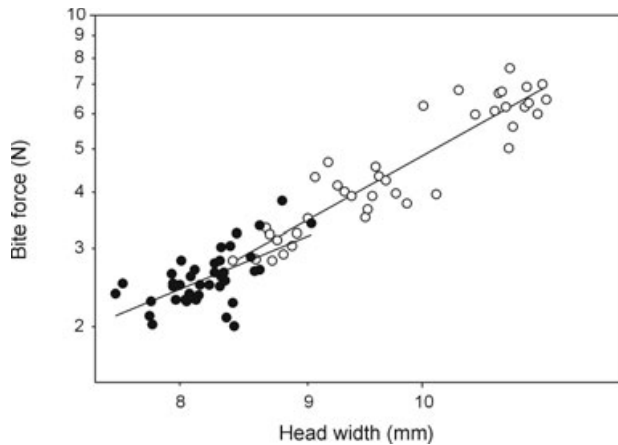


Figure 3. Scatterplot illustrating that a large amount of the intersexual difference in bite force disappears when comparing males and females of a given head width. Note the log scale on the x - and y -axes. Open symbols, males; filled symbols, females.

ever, inspection of the standardized coefficients indicates that head width is by far the best predictor of bite force in *A. carolinensis* (head width: $\beta = 0.47$; snout-vent length: $\beta = 0.27$; head length: $\beta = 0.24$).

An analyses for both sexes separately retained significant models for both males and females. Interestingly, whereas for males lower jaw length was the best predictor of bite force ($r^2 = 0.87$; $P < 0.01$), head width and the in-lever for jaw closing were the best predictors of bite force for females ($r^2 = 0.44$; $P < 0.01$). Inspection of the standardized coefficients indicated that head width ($\beta = 0.52$) is a better predictor of bite force than the in-lever for jaw closing ($\beta = 0.28$).

SKULL SHAPE

Results of the RWA on the head shape data indicate clear separation of male and female specimens (Fig. 4). In particular, the first relative warp axis, which accounted for 34.65% of the sample variance,

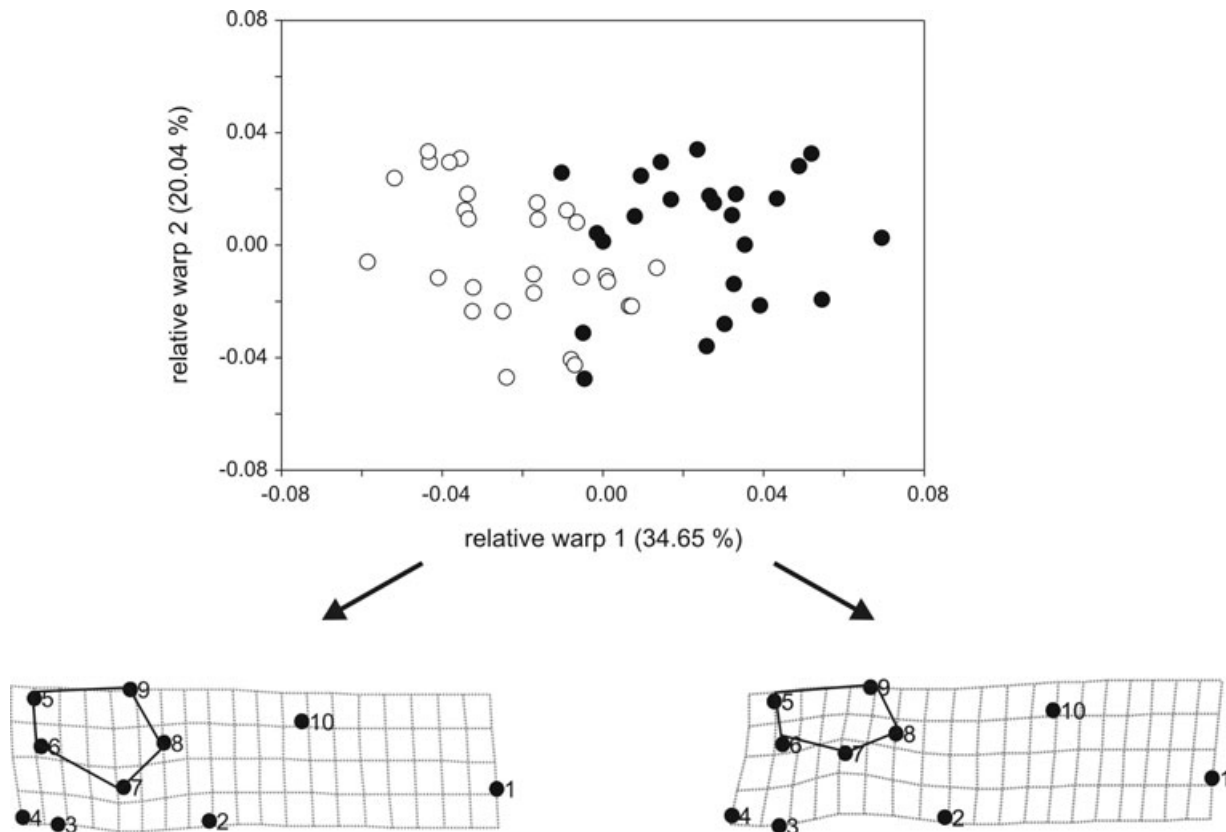


Figure 4. Scatterplot of scores on the first two axes obtained from a relative warps analysis on the skull shape data. Almost complete separation of males and females along the first relative warp axis indicates clear sexual dimorphism in skull shape. Females are characterized by a narrower adductor chamber (deformation grid on right) than males (deformation grid on the left). The percentage of variance explained by each of the relative warp axes is indicated.

Table 2. Classification count for the two sexes

| Actual | Predicted | | Total |
|--------|-----------|------|-------|
| | Female | Male | |
| Female | 24 | 0 | 24 |
| Male | 0 | 28 | 28 |
| Total | 24 | 28 | 52 |

Reduction in classification error due to sex was 100.0%.

separates males (scoring low and negative) from females (scoring high and positive), with only a slight overlap. Thin-plate spline deformation grids depicting positive and negative deviations from the consensus skull form were calculated to examine shape variation along the RWA axes (Fig. 4). Deformation grids indicate that much of the variation along RW1 involves the shape of the jaw adductor muscle chamber (i.e. landmarks 5–9, which include the quadrate, pterygoid, and ectopterygoid bones), with males scoring lower along the axis and exhibiting distinctly larger chambers. Landmark 7, at the junction of the epipterygoid and pterygoid, shows the greatest variation; it is located more medially at the negative end of the axis (males) and more laterally at the positive end (females; Fig. 4). Finally, landmark 1 is displaced posteriorly relative to the consensus form in specimens scoring high on RW1, indicating that females have a relatively shorter snout than males.

The results of a discriminant function analysis on the weight matrix of partial warp and uniform component scores demonstrate a significant difference in head shape between male and female lizards (Wilks' lambda = 0.2423; $F_{16,35} = 6.8$; $P < 0.0001$). Classification of specimens by placing them with the group mean to which they exhibited the smallest generalized distance (Mahalanobis d^2) yielded a 100% correct assignment to the appropriate sex (Table 2).

MUSCLE MASSES

Males have significantly larger jaw closer muscles (ANCOVA: $F_{1,16} = 13.33$; $P < 0.01$) but not jaw opener muscles (ANCOVA: $F_{1,16} = 0.51$; $P = 0.49$) for a given body size (Fig. 5). Remarkably, this difference in jaw closer muscle mass between the sexes remains even when taking into account the known difference in head width between the sexes (ANCOVA with head width as covariate: $F_{1,16} = 5.31$; $P = 0.035$; Fig. 6). Unexpectedly, females have larger jaw opener muscles for a given head width than males (ANCOVA with head width as covariate: $F_{1,16} = 5.12$; $P = 0.038$).

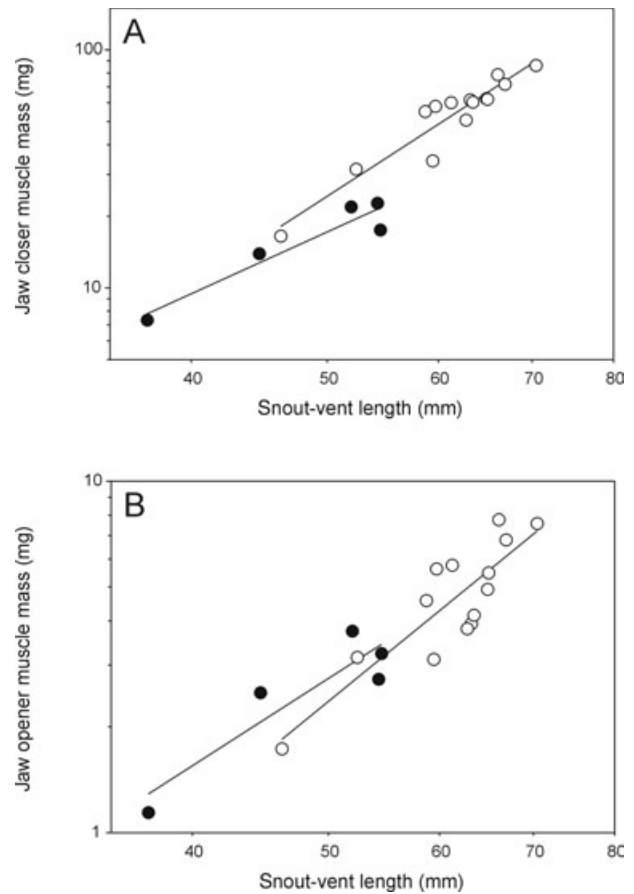


Figure 5. Scatterplots illustrating that males have significantly larger jaw adductor muscles for a given body size (A). However, this is not the case for the jaw opener muscles (B). Note the log scale on the x- and y-axes. Open symbols, males; filled symbols, females.

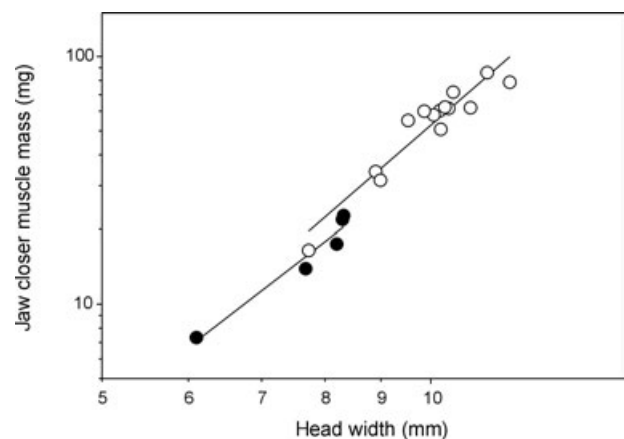


Figure 6. Scatterplot showing that even for a given head width males still have larger adductor muscles than females, which is likely the result of the enlarged adductor chamber in males (see Fig. 4).

DISCUSSION

Our results are in accordance with previous studies (Preest, 1994; Irschick *et al.*, 2005), and show that male and female *A. carolinensis* are indeed dimorphic in body and head size. Males are bigger overall, and have bigger heads than females of a similar body size. Moreover, our data show that the dimorphism in head size results in both an absolute and relative (i.e. for a given body size) dimorphism in bite force between the sexes. Again, this is in accordance with data for other lizards where sexual differences in head size are associated with sexual differences in bite force (Herrel *et al.*, 1999, 2001a, b; Verwaijen *et al.*, 2002). Given the robustness of this pattern, it appears to be a general trait that is likely to hold for all lizards that display sexual dimorphism in head size.

Interestingly, our data for *A. carolinensis* show that distinct differences in skull shape exist between the sexes that are likely directly linked to bite force potential. In males, the adductor chamber is distinctly enlarged relative to that of females (Fig. 4), thus allowing for larger jaw adductor muscles. Our data on the mass of the jaw adductors confirm this suggestion and demonstrate that males have larger jaw adductor muscles than females. Although this could potentially be the result of the bigger head size of males, even for given head width (being the best predictor of bite force across all lizards), differences in jaw adductor muscle mass between the sexes remain. Clearly, these data demonstrate that sexual differences in bite force involve distinct shape changes of the cranium that allow for a substantially larger adductor mass. Interestingly, a recent study investigating bite force capacity in male collared lizards found only weak correlations between external head dimensions and bite force (Lappin & Husak, 2005), suggesting that internal skull structure, rather than head size, might be the critical determinant for bite force capacity. Although data on sexual differences in cranial structure are not available for other lizards, this would be an interesting avenue for future research.

Recently, it was demonstrated that bite force plays an important role during male–male combat (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005) and may be a critical determinant of male fitness (Lappin & Husak, 2005). However, our data suggest that sexual differences in bite force are not caused by muscle hypertrophy alone but rather involve complex modifications of the cranial structure. Thus, simple mechanisms involving changes in testosterone levels (Vitt & Cooper, 1985; Sassoon *et al.*, 1987) are likely not entirely responsible for differences in bite force between the sexes in *A. carolinensis*. However, increased testosterone levels could still be responsible for the hypertrophy of the external jaw adductors and may thus play an impor-

tant role in regulating bite force capacity. This needs to be tested, however, using testosterone implants or castration in males of sexually dimorphic species.

Previous analyses of sexual dimorphism in head size in *A. carolinensis* have noted substantial differences in prey size between the sexes with females eating smaller prey than males (summarized in Preest, 1994). Our data on bite force suggest that females might be constrained in the maximal prey size eaten given that bite force is known to constrain diet (Herrel *et al.*, 2001a; Verwaijen *et al.*, 2002; Aguirre *et al.*, 2003). Moreover, the increased handling times observed for females (Preest, 1994) as a result of their lower bite forces (Verwaijen *et al.*, 2002) may increase the risk of predation. Thus, the difference in diet may be the result of natural selection leading to reduced niche overlap between the sexes (Schoener, 1967). Interestingly, our data indicate that female *A. carolinensis* have relatively larger jaw openers, suggesting that the jaw system might be optimized towards fast jaw movements that could allow females to specialize on evasive prey. Indeed, when comparing published dietary data for male and female *A. carolinensis*, it becomes apparent that adult males eat mostly homopterans and coleopterans (Lister, 1976), whereas females appear to specialize on dipterans (Schoener, 1968). Coleopterans are typically hard prey requiring substantial forces before fracture, and dipterans are among the most evasive arthropods available. Comparative data for other species of lizards and measurements of jaw speeds in *A. carolinensis* are clearly warranted to better understand the observed differences in diet between sexes.

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APPENDIX

Stephen F. Austin State University Natural History Collection catalogue numbers* of the specimens used to quantify skull shape.

Museum numbers

| | | | | |
|------|------|------|------|------|
| 1310 | 1326 | 1543 | 1576 | 1828 |
| 1857 | 1869 | 1906 | 1932 | 2715 |
| 2719 | 27 | 8 | 3207 | 887 |
| 1182 | 1369 | 2303 | 2475 | 2720 |
| 2749 | 956 | 1184 | 1597 | 1678 |
| 1945 | 222 | 2276 | 24 | 2717 |
| 3084 | 3794 | 865 | 2004 | 272a |
| 272b | 263 | 3010 | 886 | 889 |

*Fourteen additional specimens were uncatalogued.