

Bite-force performance and head shape in a sexually dimorphic crevice-dwelling lizard, the common chuckwalla [*Sauromalus ater* (= *obesus*)]

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The Common Chuckwalla [*Sauromalus ater* (= *obesus*)] is a large, sexually dimorphic lizard with a flattened head that takes refuge from predators in rock crevices. Males use their relatively large heads to bite competing males during territorial fights and to restrain females during copulation. Flattened heads with an antipredator function (i.e. seeking refuge in crevices) and enlarged heads with intrasexual competition and reproductive functions suggest possible antagonism between selective pressures on head morphology in males. To examine this hypothesis, we performed a morphometric analysis and measured the bite-force performance of 49 adult chuckwallas. Males had disproportionately wider heads than females, but did not have deeper heads. Males bit with nearly four times the force of females, consistent with the notion of sexual selection for high bite force in males. Although constrained by crevice-wedging behaviour, head depth was a good predictor of bite force in both sexes. In males, however, osteological head width also was a good predictor of bite force. These results are consistent with the hypothesis that head shape in males is under antagonistic selective pressures, which may partly explain the pattern of head shape dimorphism. The disproportionately wide head of males may reflect anatomical modifications to enhance bite force in response to sexual selection in spite of presumed constraints on head shape for crevice-wedging behaviour © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, 88, 215–222.

ADDITIONAL KEYWORDS: antagonistic selection – bite force – crevice-dwelling – sexual dimorphism.

INTRODUCTION

Animal traits are often under conflicting selection pressures. One form of such antagonism is that between natural selection for survival (viability) and sexual selection for mating opportunities (Andersson, 1994). This pattern has been demonstrated in many taxa with respect to conspicuous colouration, which is often favoured by sexual selection but disfavoured by viability selection due to increased visibility to predators (Endler, 1983, 1992; Grether & Grey, 1996; Macedonia, Brandt & Clark, 2002; Macedonia *et al.*, 2004). In addition, this pattern has been demonstrated in sexually dimorphic morphological traits, such as tail

size in birds (Pryke, Andersson & Lawes, 2001) and snakes (Shine & Shetty, 2001), and head and body size in lizards (Wikelski & Trillmich, 1997).

The Common Chuckwalla, *Sauromalus ater* (= *obesus*; Hollingsworth, 1998), represents a case in which antagonistic selective pressures may be influencing head morphology. Chuckwallas are saxicolous (rock-dwelling) and use rock crevices as refugia from predators. As a result, chuckwallas exhibit morphological and behavioural specializations for retreating into narrow crevices and maintaining their position therein. These include notably flattened heads (Fig. 1) and bodies (Hollingsworth, 1998), as well as defensive lung inflation (Deban, O'Reilly & Theimer, 1994) to resist the efforts of predators trying to extract them from crevice refugia.

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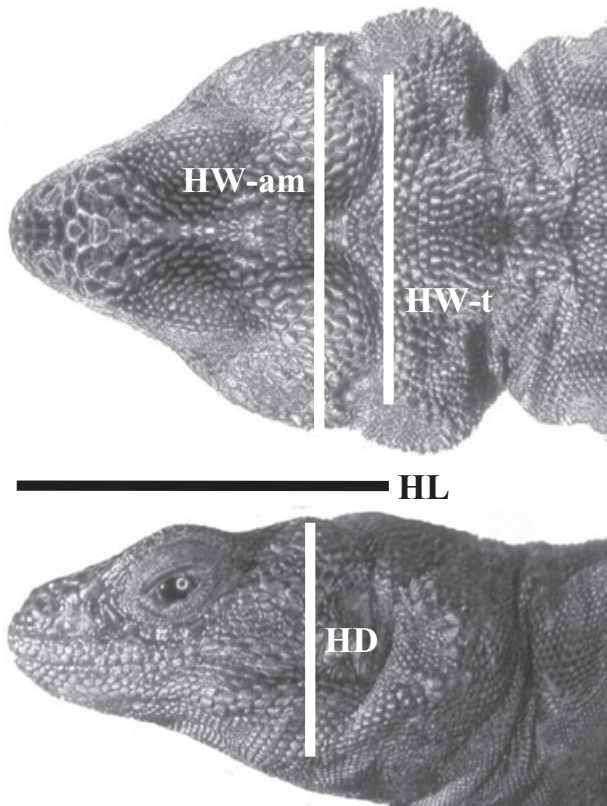


Figure 1. Images of an adult male *Sauromalus ater* (= *obesus*) showing the head measurements made in this study. An explanation of abbreviations and landmarks used in making the measurements is provided in the text.

Most lizards of the genus *Sauromalus* also exhibit the sexually dimorphic condition typical of iguanians in which males attain greater body size and head size than females (Carothers, 1984; Petren & Case, 1997; Tracy, 1999). As is the case with many other taxa, this pattern in chuckwallas is correlated with territoriality (Kwiatkowski & Sullivan, 2002b). Although a number of potentially related factors likely play a role in determining the outcomes of agonistic territorial interactions among male lizards (e.g. biomechanics, muscle physiology, condition, and hormones), large size, especially of the head, has been demonstrated as particularly advantageous (Hews, 1990; Molina-Borja *et al.*, 1998; Perry *et al.*, 2004; but see Lappin & Husak, 2005). In *Sauromalus*, intense agonistic intrasexual interactions can lead to violent biting when skirmishes over territory boundaries escalate into fights (M. A. Kwiatkowski, pers. comm.), and this is demonstrated by direct observations as well as the presence of scars on males consistent with the dental arcade of conspecific males (Kwiatkowski, 2001). Because the jaws comprise the lizard's weapon for fighting, the

ability to deliver forceful and potentially damaging bites during direct physical confrontations should be favoured by sexual selection (Gvozdik & Van Damme, 2003). Furthermore, bite force in a highly territorial lizard (*Crotaphytus*) has been shown to be predictive of estimates of reproductive success (Lappin & Husak, 2005). A large and robust head increases bite-force performance (Herrel *et al.*, 1999, 2001b; Lappin, 1999), which in turn is expected to increase fighting prowess and may enhance a male lizard's ability to maintain a large territory with access to many females (Vitt & Cooper, 1985; Hews, 1990; LeBas, 2001; Kwiatkowski & Sullivan, 2002a). A strong bite also may be advantageous when males restrain females by biting the head, neck, or forebody with their jaws during copulation (forced copulation), which is a typical behaviour among iguanian (Rodda, 1992) and other (Herrel, De Grauw & Lemos-Espinal, 2001a) lizards. Finally, there is evidence in lizards that head size may be under intersexual selection via female choice (Hews, 1990), and therefore there may be a multifaceted advantage to large head size in males.

Previous investigations of the relationship between head morphology and bite-force performance in several species of lizards provides further evidence that chuckwallas may experience antagonistic selection pressures on head shape. To date, the most unifying result in these studies has been that head depth is a strong predictor of bite-force performance (Herrel, De Grauw & Lemos-Espinal, 2001a; A. K. Lappin, unpubl. data), although other head dimensions (e.g. head width) can contribute to bite force (Herrel, De Grauw & Lemos-Espinal, 2001a; Lappin & Husak, 2005). This pattern makes good biomechanical sense because, although an increase in any head dimension (length, width, depth) can increase bite force by providing greater cranial volume to house musculature (Herrel *et al.*, 2001b), an increase in head depth further enhances bite force by lengthening the in-levers of the jaw-adductor muscles. Furthermore, as Herrel, O'Reilly & Richmond (2002) described for turtles, a deeper head will have the fibres of its major temporal jaw muscles (i.e. mm. adductor mandibulae complex) orientated with a more vertical line of action, thus increasing the efficiency of muscle force transmission in adducting the lower jaw.

The specialized crevice-wedging habit of chuckwallas, combined with large body size, large heads with a strong bite, and territorial behaviour in males, provides a natural experiment to investigate the idea that antagonistic selection pressures have shaped head form in this species. Territorial and mating behaviour are predicted to favour large head size to enhance bite-force capacity in disputes among males and during copulation with females. The use of rock crevices as refugia from predators, however, should constrain

head morphology by favouring a shallow head, thus potentially compromising bite-force performance. In this context, we examined the two predictions: First, despite the biomechanical implications of head depth on bite force, head depth will not be the head dimension that best predicts bite-force performance in chuckwallas. Head width, which is not constrained by crevice-wedging behaviour, should be a better predictor of bite force. Second, this effect will be more pronounced in males because they have large heads that are presumably beneficial during territorial disputes and mating behaviour, but they also seek refuge in crevices in which their heads must fit.

MATERIAL AND METHODS

STUDY POPULATIONS AND SPECIMENS

We studied two populations of chuckwallas in south-central Arizona separated by ~25 km (South Mountains ~12 km south of Phoenix; Phoenix mountains ~12 km north of Phoenix). Both populations were the subject of previous research on territoriality and sexual selection (Kwiatkowski & Sullivan, 2002a, b). Although of different geological origin (Kwiatkowski & Sullivan, 2002b), the terrain at the two sites is similar in that rock crevices are readily available, which the chuckwallas use as refugia from predators.

In the spring and summer of 2003, we collected adult chuckwallas by hand at both localities and promptly transported them to the laboratory for data collection. Each specimen was assigned a unique number, flagging tape was used to mark capture locations, and each subject was released at the precise location of its capture within 48 h of being removed.

MORPHOMETRICS

Snout-vent length (SVL) and mass were measured as indices of body size. To quantify head size and shape, four measurements were taken from each lizard, which represent major osteological and myological features of the skull and jaws (Fig. 1). These include head length from the quadrate-articular jaw joint to the tip of the snout (HL), head width at the quadrate-articular jaw joints (HW-t), head width at the maximum lateral extent of the temporal jaw-adductor musculature (HW-am), and maximum head depth from the quadrate processes of the parietal bone to the ventral extent of the mandible (HD). All measurements were made parallel or perpendicular to the anterior–posterior or dorsal–ventral axis of the head to avoid the potentially confounding effects of angular measurements. Linear measurements were made with digital calipers to the nearest 0.1 mm, and mass was measured to the nearest 1.0 g with a Pesola scale.

BITE-FORCE PERFORMANCE

Bite-force performance was quantified with a piezoelectric isometric force transducer (Type 9203, Kistler Inc.) custom fitted with two 25-mm wide stainless steel bite plates and connected to a charge amplifier (Type 5995, Kistler Inc.). Bite plates were attached to the transducer such that squeezing the two plates together caused the upper plate to pivot about a centred bolt that served as a fulcrum, thus generating tension on the transducer (for a detailed diagram, see Herrel *et al.*, 2001a). Prior to calibration and bite-force trials, the transducer was prepared by gluing a strip of leather (1 mm thick \times 3 mm wide \times 25 mm long) to the outer surface at the end of each beam. This provided a point near the end of each beam that allowed simple measurement of the lever length of the transducer beam so that calibration and bite-force measurements were comparable. It also provided a penetrable surface to avoid damage to the lizards' teeth. To calibrate the transducer, a series of weights was suspended from the top bite bar using fishing line. The assembled bite-force transducer produced a linear relationship ($r^2 = 0.999$, five weights).

Prior to bite-force trials, lizards were warmed under a spotlight in a holding tank to their active body temperature in the field (36–39 °C; Kwiatkowski, 2001; B. K. Sullivan, unpubl. data), which was verified for each animal immediately following the last trial using a cloacal thermometer. For measurement of bite force, transducer plates were precisely placed into the lizard's open mouth such that bites were straight with the jaws centred and orientated evenly on the beams of the transducer. Chuckwallas from the two focal populations readily gape their mouths when threatened; if necessary, a light squeeze of the snout elicited gaping. The charge amplifier was set to register the peak force attained during each trial, which we recorded for subsequent analysis. Three trials were performed in sequence on each individual with ~1 min of rest between trials.

Following each trial, the distance from the bite point on the lower jaw to the quadrate-articular jaw joint (bite moment arm) was measured to the nearest 0.1 mm with digital calipers. To standardize for variation in the bite point among and within individuals, bite forces were calculated for the midpoint of the lower jaw [standardized bite force = calibrated amplifier output (bite moment arm/0.5 \times head length)]. All statistical analyses of bite force were performed on these standardized values. For each individual, only the greatest standardized bite force value among the three trials was used in the statistical analyses.

STATISTICAL ANALYSES

Statistical analyses were done using JMPIN vs. 4.0.2 for Windows (SAS Institute, Inc.). Except for calcula-

tion of descriptive statistics, all data were log-transformed for analysis. To test for sexual dimorphism of body and head size, morphological variables and bite force were compared between the sexes using unpaired *t*-tests with a sequential Bonferroni test. To test for differences in head form between the sexes, we used a series of one-way analysis of covariances (ANCOVAS). First, we compared head morphometrics between the sexes with SVL as the covariate to test whether or not head dimensions differed between the sexes with the effect of body size removed. Second, we examined sexual dimorphism of head shape (robustness) by comparing head width and head depth (HW-t, HW-am, and HD) between the sexes with head length (HL) as the covariate. By removing the effect of head length in this way, head shape could be compared without the influence of sexual differences in body morphology and body size (e.g. females have small heads on large bodies compared to males).

To compare bite-force performance between the sexes, we used a one-way ANCOVA. To remove the effect of body size, SVL and mass were used as covariates. To compare bite force between the sexes with respect to head form, each head dimension (HL, HW-t, HW-am, and HD) was used as the covariate.

To infer which morphological variables best predict bite force, we performed a series of multiple regressions (standard least squares and stepwise) for each sex separately with bite force as the dependent variable. First, all morphological measures were included as independent variables to decipher which are the best predictors of bite force. Second, to specifically examine the relationship between head morphology and bite force, only head morphometrics were included as independent variables. Third, to examine the effect of head robustness on bite force, residuals from head width and head depth (HW-t, HW-am, and HD)

regressed on head length (HL) were entered as the independent variables.

RESULTS

In this sample of adult chuckwallas, males were significantly larger (~12%) and heavier (~26%) and had larger heads (all dimensions 25–40% greater) than females (Table 1). Males also had larger heads than females relative to body size; ANCOVA with SVL as the covariate gave highly significant sex effects for all head dimensions ($P < 0.0001$). Using HL as an index of head size (i.e. covariate) to compare head robustness gave significant sex effects. Males have relatively wider heads than females, both osteologically (HW-t) and myologically (HW-am) (Fig. 2A, B). However, males and females were virtually identical in HD relative to HL (Table 2, Fig. 2C). In both sexes, HD increased disproportionately relative to HL (Fig. 2C).

Males bit an average of 3.7 times harder than females (Table 1), which amounts to 2.3 N of bite force per mm of HL for males, vs. 0.8 N per mm of HL for females. ANCOVA showed that males bite harder than females for a given body size (Tables 1, 3), and that bite force increases disproportionately in males with respect to mass (significant interaction). Relative to head size, sexual differences in bite force depend on which head dimension is considered. Relative to HL, and especially HD, males bit considerably harder than females. However, there was no difference between the sexes in bite-force performance with respect to HW-t or HW-am (Table 3). Body temperature immediately after bite-force trials was in the range 28.5–38.0 °C, but was not correlated with bite force (ANCOVA with sex as factor: $F = 91.41$, $P < 0.0001$; body temperature as covariate: $F < 0.0087$, $P = 0.926$).

Table 1. Summary statistics (mean \pm SE) and results of unpaired *t*-tests (d.f. = 47) comparing morphological variables and bite-force performance between male and female chuckwallas

Variable	♂ ($N = 34$)	♀ ($N = 15$)	Unpaired <i>t</i> -test	<i>P</i>
SVL (mm)	168.9 \pm 2.4	151.3 \pm 3.9	3.98	0.0002**
Mass (g)	191.3 \pm 7.8	151.7 \pm 13.5	2.83	0.0069*
HL (mm)	32.8 \pm 0.5	26.2 \pm 0.5	8.58	< 0.0001**
HW-t (mm)	25.7 \pm 0.4	18.4 \pm 0.4	10.40	< 0.0001**
HW-am (mm)	28.6 \pm 0.4	21.5 \pm 0.3	11.25	< 0.0001**
HD (mm)	15.7 \pm 0.3	11.8 \pm 0.4	7.37	< 0.0001**
Bite force (N)	76.6 \pm 5.0	20.7 \pm 2.0	9.69	< 0.0001**

Significance levels following sequential Bonferroni test for seven variables: ** $P < 0.01$, * $P < 0.05$. SVL, Snout-vent length; HL, head length from the quadrate-articular jaw joint to the tip of the snout; HW-t, head width at the quadrate-articular jaw joints; HW-am, head width at the maximum lateral extent of the temporal jaw-adductor musculature; HD, maximum head depth from the quadrate processes of the parietal bone to the ventral extent of the mandible.

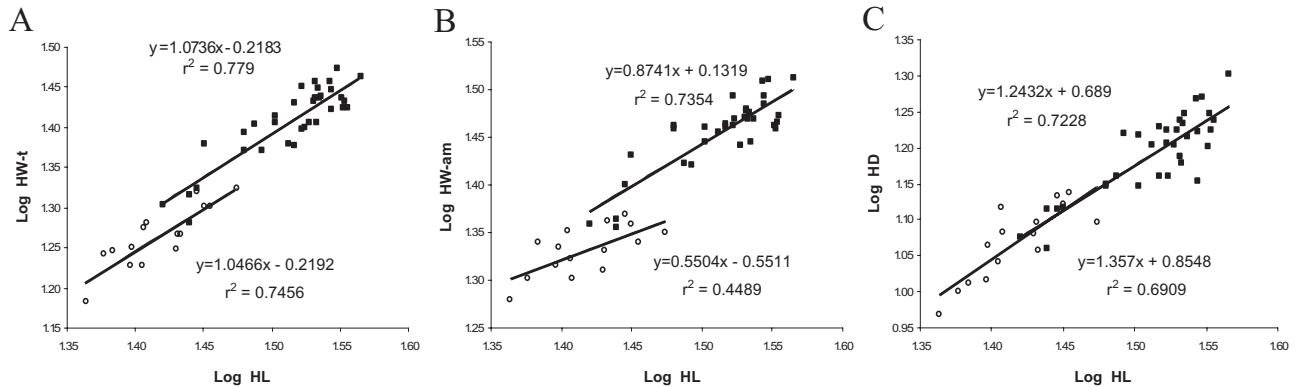


Figure 2. Log-log regressions illustrating sexual differences in head robustness for adult *Sauromalus ater* (= *obesus*). Head length was used as an index of head size. A, males have disproportionately wider heads than females at the jaw joints. B, males have disproportionately wider heads than females at the maximum lateral extent of the jaw-adductor musculature. Note that the sexual difference in this measure of robustness increases with size, albeit not significantly (Table 2). C, the sexes do not differ in relative head depth, thus supporting the hypothesis that head depth is constrained by antipredatory crevice-wedging behaviour.

Table 2. Results of one-way analysis of covariance comparing head shape (robustness) between male and female chuckwallas

	HW-t		HW-am		HD	
	<i>F</i> -ratio	<i>P</i>	<i>F</i> -ratio	<i>P</i>	<i>F</i> -ratio	<i>P</i>
Sex	8.20	0.0063	20.96	< 0.0001	0.02	0.8723
HL	104.45	< 0.0001	53.63	< 0.0001	82.23	< 0.0001
HL × sex	0.02	0.8972	2.77	0.1030	0.16	0.6933

HL, head length from the quadrate-articular jaw joint to the tip of the snout; HW-t, head width at the quadrate-articular jaw joints; HW-am, head width at the maximum lateral extent of the temporal jaw-adductor musculature; HD, maximum head depth from the quadrate processes of the parietal bone to the ventral extent of the mandible.

Standard least squares multiple regression showed that HD and HW-t were similarly predictive of bite force in males, whereas only body size (SVL, mass) was predictive in females (Table 4). A standard least squares model that included only head dimensions supported the full model results for males and, for females, HD emerged as marginally insignificant. Significant forward and reverse stepwise models retained (in order of significance) HD, HW-t, and HL for males but only HD for females. The model that specifically focused on measures of head robustness (residuals from HW-t, HW-am, and HD regressed on HL) demonstrated sexual dimorphism in the relationship between head shape and bite force (Table 4). Based on full models, residual HW-t and residual HD were strong predictors of bite force in males, and only forward and reverse stepwise models that retained these two variables were significant. For females, however, retention of only residual HD produced significant full and forward and reverse stepwise models.

DISCUSSION

Our results concur with those of other studies (Petren & Case, 1997; Tracy, 1999), which showed that male common chuckwallas achieve greater body size (SVL, mass) and have larger heads than females. Males also have larger heads than females relative to body size. These sexual size differences support the view that male chuckwallas experience intrasexual selection for large size, which is presumed to be advantageous during territorial interactions between males (Kwiatkowski & Sullivan, 2002b) and copulation with females. Alternative explanations for sexual size dimorphism include intersexual selection (i.e. female choice) and niche partitioning between the sexes (Herrel *et al.*, 1999). The role of female choice in *Sauromalus* is unclear, but the occurrence of forced copulation suggests that it has not played a primary role in driving the evolution of sexual size dimorphism in this group. There is no evidence of dietary divergence

Table 3. Results of one-way analysis of covariance comparing bite-force performance between male and female chuckwallas with each morphological variable as the covariate

Model	<i>F</i> -ratio	<i>P</i>
Sex	88.96	< 0.0001
SVL	80.51	< 0.0001
SVL × sex	1.21	0.2762
Sex	177.29	< 0.0001
Mass	113.80	< 0.0001
Mass × sex	8.90	0.0046
Sex	4.47	0.0400
HL	44.06	< 0.0001
HL × sex	0.04	0.8523
Sex	1.07	0.3073
HW-t	69.44	< 0.0001
HW-t × sex	0.27	0.6088
Sex	0.76	0.3889
HW-am	22.58	< 0.0001
HW-am × sex	0.01	0.9339
Sex	15.80	0.0003
HD	104.33	< 0.0001
HD × sex	0.35	0.5557

SVL, Snout-vent length; HL, head length from the quadrate-articular jaw joint to the tip of the snout; HW-t, head width at the quadrate-articular jaw joints; HW-am, head width at the maximum lateral extent of the temporal jaw-adductor musculature; HD, maximum head depth from the quadrate processes of the parietal bone to the ventral extent of the mandible.

between male and female chuckwallas (Kwiatkowski, 2001), and their feeding behaviour (described below) indicates that a large head is unlikely to confer an advantage in food procurement or processing in this species.

On average, male chuckwallas bit nearly four times as hard as females, and the sexual difference in bite-force performance increases as chuckwallas grow due to a relatively greater increase in performance as a function of body size in males compared with females. These results all suggest sexual selection for high bite force in males, which is expected to confer an advantage during intrasexual agonistic encounters and possibly mating with females.

Our comparison of head robustness showed that males have disproportionately wider heads than females but that the sexes are similar in relative head depth. This result suggests that selection for a shallow head, to increase the density of crevices available as refugia from predators, has constrained head shape in males. Because males have significantly larger heads

than females, and the density of refugia available to them is expected to be lower, selection for a flattened head may be stronger in males with respect to predation pressure from mammalian and avian predators capable of subduing adults of either sex.

With respect to the relationship between bite force and the integrated functional unit that generates it (i.e. head), sexual differences in bite force depend on which head dimension is considered. Males bit considerably harder than females for a given head length or head depth but there were no sexual differences in bite force with respect to head width. This relationship between head form and bite-force performance reflects the performance consequences of the disproportionately wide heads of males. Predation pressure that favours a shallow head well-suited for crevice-wedging behaviour appears to have resulted in a disproportionate increase in other head dimensions to give males high bite-force performance. The high bite-force performance of males relative to females, specifically after size-correction, suggests that antagonistic selection pressures have influenced head form in chuckwallas and lends further support to the hypothesis of sexual selection for high bite force in males. Determination of whether an increase in other head dimensions has allowed males to entirely escape the constraint that a shallow head imposes on bite-force performance would require a biomechanical analysis that facilitates sensitivity tests or, possibly, a broad comparative study.

The relative increases in head length and head width (at the jaw joints) in males provide a means to house a greater volume of jaw musculature in the temporal region (i.e. mm. adductor mandibulae complex) when head depth is constrained. In addition, Herrel *et al.* (1999) hypothesized that large pterygoideus muscles may play an important role stabilizing the jaw joint, which is likely to experience unpredictable and potentially large stresses during biting when males fight and when males hold females with their jaws during copulation. An osteologically-based increase in head width at the jaw joints provides the framework for larger pterygoideus muscles. Thus, male chuckwallas retain the ability to bite much harder than females (both absolutely and relative to size), which provides an advantage during intense agonistic intrasexual interactions, within the constraints of their specialized antipredatory behaviour.

Herrel, Aerts & De Vree (1998) and Herrel & De Vree (1999) argued that herbivory in squamates should be correlated with a deep skull and high bite forces to shear tough plant material (i.e. leaves). Therefore, the herbivorous diet of *Sauromalus* (Nagy, 1973) would appear to suggest an advantage of deep heads and high bite force in both sexes. However, our results on the relationship between head shape and

Table 4. Summary of multiple regression analyses comparing the relationship between morphology and bite-force performance between male and female chuckwallas

Variables in model	♂ (<i>N</i> = 34)		♀ (<i>N</i> = 15)	
	<i>F</i> -ratio	<i>P</i>	<i>F</i> -ratio	<i>P</i>
SVL	1.09	0.3056	6.42	0.0350
Mass	2.38	0.1343	6.41	0.0351
HL	3.16	0.0869	1.00	0.3463
HW-t	6.51	0.0167	3.59	0.0948
HW-am	1.12	0.3011	0.59	0.4646
HD	6.80	0.0146	0.23	0.6433
HL	2.20	0.1489	0.54	0.4802
HW-t	10.69	0.0028	0.22	0.6486
HW-am	0.63	0.4354	0.14	0.7129
HD	14.50	0.0007	4.74	0.0545
Residual HW-t on HL	11.06	0.0023	0.24	0.6319
Residual HW-am on HL	0.65	0.4275	0.16	0.6989
Residual HD on HL	15.00	0.0005	5.21	0.0433

SVL, Snout-vent length; HL, head length from the quadrate-articular jaw joint to the tip of the snout; HW-t, head width at the quadrate-articular jaw joints; HW-am, head width at the maximum lateral extent of the temporal jaw-adductor musculature; HD, maximum head depth from the quadrate processes of the parietal bone to the ventral extent of the mandible.

bite force in chuckwallas indicate that only males exhibit some degree of antagonism between natural and sexual selection pressures. As with most vertebrates examined to date, it is unlikely that sexual dimorphism in *Sauromalus* is related to dietary divergence because there is no evidence of dietary differences between the sexes (Kwiatkowski, 2001). In addition, the means by which chuckwallas process their herbivorous diet further indicates that feeding biology is not related to sexual dimorphism in *Sauromalus*. Whereas most herbivorous lizards, including the agamid (*Uromastix*) as studied by Herrel & De Vree (1999), process tough leaves by reducing them into small pieces, *Sauromalus* typically bite and swallow soft leaves and flowers with little if any processing (A. K. Lappin, P. S. Hamilton & B. K. Sullivan, pers. observ.; M. A. Kwiatkowski, pers. comm.).

Despite their relatively shallow heads, head depth in common chuckwallas remains a strong predictor of bite force in males and is the only head dimension predictive of bite force in females. This pattern holds even though other head dimensions are relatively greater in males than in females, which is likely a compensatory means for increasing bite-force performance in males experiencing sexual selection pressures. An increase in head depth is predicted to enhance bite-force performance by providing cranial volume to house jaw-adductor musculature (Herrel *et al.*, 2001b), as well as through an increase of the length of

the jaw-adductor muscle in-levers. Herrel *et al.* (2001a) showed that head depth is the best predictor of bite force among three species of crevice-dwelling xenosaurids (multiple regression of both sexes and of females for all species combined) that exhibit considerable interspecific variation in head depth compared with head length or width, which is a morphological pattern opposite to that found in our intersexual comparison of chuckwallas. Despite differences in variation in head shape in relation to bite-force among lizards, our results complement those of Herrel *et al.* (2001a), and they lend further support to the view that head depth contributes significantly to bite-force performance even when the dimension is constrained by other selective forces.

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