

Does large body size relax constraints on bite-force generation in lizards of the genus *Uromastyx*?

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Abstract

The evolution of large body size has often been considered a key trait allowing the evolution of herbivory in lizards. Although many omnivorous lizards appear unspecialized, they typically show high bite forces, allowing them to reduce tough and fibrous plant matter. In contrast, true herbivores often show a suite of morphological and physiological specializations, allowing them to efficiently process and assimilate plant material. Moreover, many specialized herbivores have a large body size, thus likely relaxing constraints on bite-force generation given that bite force increases with increasing body mass. In this study, we test whether large herbivorous lizards of the genus *Uromastyx* have relatively lower bite forces for their body size compared with a medium-sized congener. No differences in bite force or head dimensions were observed between the two species or between both sexes in our sample. Moreover, bite force scaled with positive allometry relative to jaw length, suggesting that larger animals have disproportionately large bite forces. This suggests that even in the largest species, constraints on bite-force generation are still strong, possibly due to the demands imposed on the jaw system by the mechanical properties of the diet.

Introduction

The evolution of large body size has often been thought to be a key element in the evolution of an herbivorous lifestyle in lizards (Szarski, 1962; Ostrom, 1963; Sokol, 1967; Pough, 1973; but see Espinoza *et al.*, 2004). Indeed, large body size does not only confer an advantage through the lower mass-specific metabolic requirements but also provides for a large abdomen and thus gut volume and surface area. Moreover, the hindgut is often subdivided into compartments by means of caecal valves providing a fermenting chamber which has been suggested to allow for a more efficient digestion of the plant matter by endosymbionts (Iverson, 1980). Although the consumption of plant matter has evolved many times independently in lizards (Cooper & Vitt, 2002), omnivorous lizards have generally been considered to be relatively unspecialized opportunistic generalists. However, more recent studies have indicated distinct adaptations of the jaw and digestive system in these omnivores involving the evolution of specialized teeth, high bite forces and the development of caecal valves (Iverson, 1980; Espinoza *et al.*, 2004; Herrel, Vanhooydonck & Van Damme, 2004a; Herrel *et al.*, 2008).

Analyses of bite force in lizards have suggested that lizards that include considerable amounts of plant matter in

their diet, on average, have higher bite forces and more strongly developed jaw adductor muscles than insectivores or carnivores (Herrel, Aerts & De Vree, 1998; Herrel *et al.*, 1999a, 2004a, 2008; Herrel, 2007). Indeed, to process tough and fibrous material such as plants, high bite forces are probably necessary. Moreover, particle size is known to have an important effect on digestive efficiency in herbivorous lizards (Bjorndal, Bolten & Moore, 1990), and thus the ability to crop small bite-sized pieces from plants enabled by large bite forces is probably under strong selection. Indeed, the smaller the particles, the more of the indigestible cell wall will be exposed to the digestive enzymes of endosymbionts. In some small lacertid lizards, this has resulted in the rapid evolution of large jaw muscles and high bite forces (Herrel *et al.*, 2008). However, many true herbivores (i.e. lizards that consume nearly exclusively plant matter year round) are relatively large lizards and as such constraints on bite force may be relaxed as absolute bite forces are large due to the scaling of bite force with body size. Moreover, many of these large herbivores possess specialized teeth (e.g. Hotton, 1955; Robinson, 1976) and hindguts that function as fermenting chambers characterized by the presence of caecal valves (Iverson, 1980; Troyer, 1984; Foley *et al.*, 1992; Herrel *et al.*, 1999a).

Lizards of the genus *Uromastix* are strict herbivores (Al-Ogily & Hussain, 1938; Dubuis *et al.*, 1971; Bouskila, 1987; Robinson, 1976, but see Castilla *et al.*, 2011), inhabiting Old World deserts from northern Africa to western India (Wilms *et al.*, 2009, 2010, 2011). Moreover, the genus *Uromastix* shows a large variation in body size across different species with some species ranging up to 700 mm in total length (Wilms *et al.*, 2009). These animals have an extremely specialized morphology with cutting teeth (Robinson, 1976; Throckmorton, 1979) and specialized jaw movements (Throckmorton, 1976; Herrel & De Vree, 1999). The specialized jaw movements in this genus (streptostyly) may allow animals to optimize the line of action and moment arm of the jaw adductors relative to the jaw joint, and as such may allow for greater bite-force generation (Herrel, Aerts & De Vree, 2000). Moreover, lizards of the genus *Uromastix* have an enlarged digestive tract with fermenting chambers and caecal valves (Foley *et al.*, 1992).

Here we predict that constraints on bite-force generation will be relaxed in the larger species of this highly specialized genus as they have bite forces that are large in absolute terms and may not need to invest as much in energetically expensive tissue such as muscle. Thus, we predict that larger species will have relatively low bite forces for their body size compared with smaller congeners. We test this hypothesis by comparing previously published bite forces for the medium-sized *Uromastix acanthinurus* (Herrel & De Vree, 2009) with data collected for *Uromastix microlepis aegyptia*, one of the largest (sub)species in the genus (Wilms *et al.*, 2009).

Materials and methods

Animals

Twelve *Uromastix aegyptia* of both sexes and varying in body size (Table 1) were captured between 6 and 13 October 2012 in Rass Laffan (25°50'8"; 51°31'56"), situated in the north-east of the State of Qatar along the Arabian Gulf. Lizards were tem-

porarily housed in large outdoor terraria (10 × 3 m) while being measured. All measurements were conducted in the laboratory facilities of the Qatar Environment and Energy Research Institute (Qatar Foundation).

Morphometrics

Head dimensions and snout–vent length (SVL) were measured in all individuals. Head length was taken as the distance between the back of the parietal bone and the tip of the upper jaw; head width was measured at the widest part of the head; head height was measured as the highest point of the head just posterior to the orbits; lower jaw length was taken as the distance between the back of the retroarticular process and the tip of the lower jaw. Additionally, two morphological variables related to the biomechanics of the jaw system were estimated by measuring (1) the distance from the jaw articulation to the tip of the lower jaw (i.e. the jaw out-lever) and (2) the distance from the posterior edge of the jugal bone to the tip of the lower jaw. Based on these variables, the length of the jaw in-lever for opening was calculated by subtracting the jaw out-lever from the lower jaw length. Next, by subtracting the distance from the tip of the jaw to the back of the jugal from the jaw out-lever, the in-lever for jaw closing was calculated. Measurements were taken using digital calipers (Mitutoyo CD-20DC, Kanagawa, Japan; precision: 0.01 mm). The body mass was measured for each animal using an electronic balance (Gram MM-1200, Barcelona, Spain; precision: 0.2 g).

All measurements were taken by the same person (A. H.) and with the same equipment as used for the measurements previously published for *U. acanthinurus* (Herrel & De Vree, 2009).

Bite forces

In vivo bite forces were measured at the tip of the jaw using an isometric Kistler force transducer (type 9203, range of ±500 N; Kistler, Winterthur, Switzerland; Herrel *et al.*, 1999a,

Table 1 Bite forces and body and head dimensions of *Uromastix aegyptia* from Qatar

Sex	SVL	Mass	Head length	Head width	Head height	Lower jaw length	Jaw out-lever	Prejugal length	Open in-lever	Close in-lever	Bite force
Male	67.3	9.4	15.2	14.3	9.2	15.2	14.0	10.1	1.2	3.9	10.0
Male	146.0	106.6	25.6	25.3	16.0	28.8	26.4	19.0	2.4	7.4	47.3
Male	149.4	112.0	25.4	23.3	15.0	29.7	27.4	17.3	2.4	10.1	44.8
Male	200	241.1	31.9	31.0	20.4	37.3	32.8	25.0	4.5	7.7	89.8
Male	255	484.8	36.1	35.5	24.0	43.6	38.6	27.4	5.0	11.2	131.3
Male	290	691.3	41.5	48.6	25.7	45.7	43.8	33.8	1.9	10.0	119.9
Male	330	891.8	42.1	43.7	29.7	48.9	44.2	34.8	4.8	9.4	140.7
Female	131.7	26.5	23.7	21.3	13.6	24.8	22.9	16.7	1.9	6.2	23.5
Female	189.8	231.0	30.9	29.3	18.7	34.3	30.5	25.0	3.8	5.5	78.8
Female	245	420.0	35.2	39.2	21.7	40.4	37.4	26.5	3.0	10.9	91.1
Female	265	455.8	36.3	36.3	23.8	42.5	40.7	28.0	1.8	12.7	117.9
Female	290	716.4	43.7	45.2	25.8	49.7	46.1	34.3	3.6	11.8	101.2

All linear dimensions are indicated in millimetres, mass in grams and bite force in newtons. SVL, snout–vent length.

2001) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5995A). The place of application of bite forces was standardized for all animals by aligning the jaws with a metal stop mounted on the transducer so each individual bit at the tip of the jaws. Measurements were repeated five times for each animal, with an intertrial interval of at least 30 min during which animals were allowed to thermoregulate in the outdoor enclosure. The maximal value obtained during a recording session was considered to be the maximal bite force for that individual. Lizards are typically eager to bite when held and were stimulated to bite the transducer by gently tapping the sides of the jaws. This typically resulted in strong and prolonged biting. Again, methods and equipment were identical to those used for measurements in *U. acanthinurus* (Herrel & De Vree, 2009).

Analyses

All data were \log_{10} -transformed before analyses to meet assumptions of normality and homoscedasticity. We first tested for differences in bite force and head size between sexes using an analysis of (co)variance (AN(C)OVA). As differences were non-significant, we pooled data for all individuals in subsequent analyses. Next we used stepwise multiple regression analyses to test which variables best explained variation in bite force across individuals. Finally, we tested for differences between species (*Uromastyx aegyptia*, this study vs. *Uromastyx acanthinurus*; Herrel & De Vree, 2009) in morphology using a multivariate ANOVA. We subsequently tested for differences in absolute bite force between species using an ANOVA and in relative bite forces using an ANCOVA with either SVL or lower jaw length as covariates.

Results

An ANOVA detected no differences in size between the sexes of *U. aegyptia* in our sample (SVL: $F_{1,11} = 0.56$, $P = 0.47$; mass: $F_{1,11} = 0.22$; $P = 0.65$). Similarly, differences in head dimensions were not significantly different between the sexes (Wilks' lambda = 0.69; $F_{8,4} = 0.22$; $P = 0.97$). An ANOVA testing for differences in bite force between sexes was not significant ($F_{1,10} = 1.17$; $P = 0.79$) and neither was an ANCOVA using SVL as covariate ($F_{1,9} = 1.47$; $P = 0.26$; Fig. 1). A stepwise linear regression retained a significant model with body mass as the sole predictor of bite force in *U. aegyptia* ($R = 0.982$; $P < 0.001$). When removing body mass from the predictor variables, a significant model with lower jaw length as the only predictor of bite force was retained ($R = 0.975$; slope = 2.27; $P < 0.001$).

A multivariate analysis of variance performed on the head dimension testing for differences between the two species was not significant (Wilks' lambda = 0.56; $F_{4,14} = 2.80$; $P = 0.07$). A univariate ANOVA testing for differences in bite force between species detected no differences ($F_{1,16} = 0.37$; $P = 0.55$; Fig. 1). An ANCOVA with SVL as covariate also did not show significant differences between species ($F_{1,15} = 1.67$; $P = 0.22$). An ANCOVA with lower jaw length as covariate was only marginally non-significant ($F_{1,15} = 4.43$; $P = 0.52$).

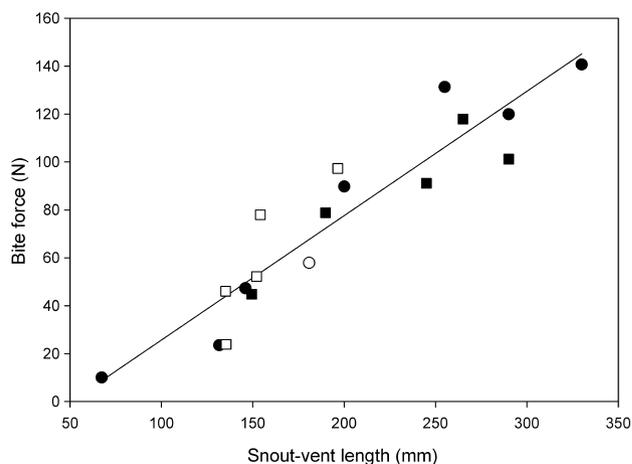


Figure 1 Graph illustrating the correlation between bite force and overall body size. Filled circles indicate *Uromastyx aegyptia*; open circles represent *Uromastyx acanthinurus*. Squares: males; circles: females. No significant differences between species in bite force relative to body size were observed. Data for *U. acanthinurus* taken from Herrel & De Vree (2009).

Inspection of the estimated marginal means suggested that *U. aegyptia* had greater bite forces for a given head length than *U. acanthinurus* (1.84 ± 0.03 vs. 1.72 ± 0.05).

Discussion

In contrast to our predictions, species differed neither in absolute or relative head size nor in bite force. Moreover, no differences between the sexes were detected in overall head shape or bite force. Indeed, in contrast to the known dimorphism in body size and weight (Wilms *et al.*, 2010), *Uromastyx* males and females in our sample did not differ in head size and bite force. This is in contrast to many other lizards where a distinct head shape and bite-force dimorphism have been observed (see Herrel *et al.*, 1999b, 2001; Vincent & Herrel, 2007, for an overview). This suggests that in both sexes, bite force appears to evolve under natural selection in direct relation to diet. As the consumption of tough and fibrous plant matter is equally important for both sexes, this may explain the observed lack of differences in head shape and bite force. Moreover, the slope of bite force versus lower jaw length was greater than the predicted slope of two for geometric similarity, suggesting selection for high bite forces in larger individuals, a feature commonly observed in lizards but rare in other vertebrates. When correcting for variation in head size, *U. aegyptia* also showed slightly higher, albeit non-significantly so, bite forces compared with *U. acanthinurus* as suggested by an inspection of the size-adjusted means. All these lines of evidence suggest that selection on bite-force capacity is high in lizards of the genus *Uromastyx*, with larger animals biting relatively more forcefully than smaller ones. Thus, in contrast to our *a priori* hypothesis, no relaxation of

the constraints on high bite-force generation due to large body size is observed in strict herbivores such as *U. aegyptia*.

This is in contrast to observations for omnivorous lizards specializing on fruits. For example, in *Anolis* lizards, frugivory is associated with the evolution of large body size, yet, independent of bite-force capacity (Herrel *et al.*, 2004b). Similarly, in *Gallotia* lizards of the Canary Islands that are known to consume considerable amounts of fruits, bite force was suggested to be evolving under sexual selection pressures rather than natural selection in relation to diet, at least in males (Herrel *et al.*, 1999a). *Uromastix* lizards are known to consume a variety of plant matter including tough and fibrous material such as leaves, stems and seeds (Al-Ogily & Hussain, 1938; Dubuis *et al.*, 1971; Grenot, 1976; Bouskila, 1987; Castilla *et al.*, 2011), items known to need high forces to be reduced (e.g. the force needed to reduce a leaf of endive can range up to 50 N; Herrel, Verstappen & De Vree, 1999c). Moreover, during the dry season, food may become limited (Wilms *et al.*, 2009, 2011) and *Uromastix* lizards will consume dry plant matter, beetles, or will even scavenge and eat vertebrate remains (Castilla *et al.*, 2011). Interestingly, our data suggest that body mass was the best predictor of bite force in *Uromastix*. Given that our data were collected in autumn when body mass decreases dramatically (Wilms *et al.*, 2009), this suggests that, rather than a direct effect of overall size, this may be an effect of body condition, where animals in a relatively better condition may be able to generate larger bite forces. Conversely, animals with higher bite forces may be able to exploit a wider range of food items and as such be in better body condition. The fact that regression models where body mass was eliminated from the model retained lower jaw length instead of SVL tends to support this hypothesis. However, it would be interesting to explore relationships between body mass and bite force in spring when food is more abundant.

Interestingly, the best predictor of bite force in *Uromastix* was lower jaw length, a variable not directly related to the space available for jaw muscles. In other species, head width, head height and jaw-closing in-lever are often much better predictors of bite force (e.g. Herrel *et al.*, 1999a, 2001; Lappin & Husak, 2005; Lappin, Hamilton & Sullivan, 2006; McBrayer & Anderson, 2007). This more common pattern is explained by the fact that these measurements are better proxies for the space available for jaw muscles which ultimately determines bite-force capacity. However, *Uromastix* lizards are characterized by the presence of an extra bundle of the pterygoideus muscle, the musculus pterygoideus externus, which wraps around the lower jaw and attaches to the temporal bar (Herrel *et al.*, 1998). Given that the insertion of this muscle is on the lateral side of the lower jaw, external to the jaw adductor fossa, this may explain why lower jaw length was the best predictor of bite force in this species.

In conclusion, our data suggest that large body size does not relax selection on bite force in *Uromastix*. This may be due to the extreme nature of its habitat where food is scarce and animals are forced to eat dry and extremely tough, fibrous plant material. However, additional data for this genus and

other herbivorous lizards inhabiting arid areas would be needed to test this hypothesis.

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