

Sexual Shape Dimorphism in Tuatara

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The tuatara, *Sphenodon punctatus*, is known to exhibit a male-biased sexual size dimorphism, often attributed to the territorial behavior of males. Our data based on preserved specimens from museum collections also show a previously undocumented dimorphism in head and limb shape in *Sphenodon*, with males having bigger heads and longer limbs for a given body size than females. A review of the existing literature on the ecology and behavior of these animals suggests that this may provide males with a greater sprint speed capacity relevant to territory defense. Differences in head shape, on the other hand, may be related to ecological niche differentiation as males have been suggested to eat larger prey than females, but this remains to be tested. An additional role for sexual selection in driving the divergence in head shape between males and females is likely but cannot be confirmed at present.

SEXUAL size and shape dimorphisms are common among squamates (Vincent and Herrel, 2007). The evolutionary processes driving the dimorphisms in morphology between sexes of the same species can be broadly subdivided into two groups. The first and most commonly invoked mechanism is sexual selection acting to change the size or shape of one of the two sexes. For example, fecundity selection has been invoked to explain large abdomen size in females (Olsson et al., 2002). Additionally, male–male competition has been suggested as driving the evolution of weapons and ornaments in males (Darwin, 1871; Maynard-Smith and Harper, 2003). Alternatively, natural selection may act to minimize resource competition between the sexes and thus lead to the evolution of sexual size or shape dimorphisms (Schoener, 1967; Slatkin, 1984). For example, it has been argued that differences in head size in male and female *Anolis* lizards may allow them to exploit different trophic resources (Schoener, 1967). Similarly, differences in limb dimensions between the sexes may allow them to specialize on different microhabitats (Butler et al., 2007). Clearly, both selective pressures are not mutually exclusive and may act in concert or oppose each other depending on the ecological circumstances and the relevant mating system.

Differences in body size or shape often give rise to sex-based differences in performance between the sexes (Herrel et al., 1999, 2001a, 2001b; Lailvaux and Vincent, 2007). In lizards, males are typically better at physical performance (e.g., sprinting, biting) and show dimorphisms in traits associated with defense of territories, females, or other resources. For example, male lizards typically have bigger heads and higher bite forces for their body size compared to females (Vincent and Herrel, 2007). Bite force is relevant to male lizards as it allows them to win territorial contests (Huyghe et al., 2005; Lappin and Husak, 2005) and may allow them to force copulations with females (Herrel et al., 1999). Additionally, males typically run faster and jump further than females (Lailvaux et al., 2003; Husak et al., 2006; Lailvaux and Irschick, 2007; Husak et al., 2008) and have longer limbs (Lailvaux, 2007; but see Peterson and Husak, 2006). Again, being able to run faster or jump further may allow males to better patrol, or chase intruders from their territories (Husak et al., 2008).

Although the evolution of male-biased differences in physical performance and associated morphology has been relatively poorly documented, available data suggest that it may be ancestral for squamates in general (Lailvaux, 2007; Vincent and Herrel, 2007). Interestingly, the Tuatara, *Sphenodon punctatus*, the closest living relative to squamates (Rest et al., 2003) is also known to exhibit a male-biased sexual size dimorphism. The larger size of males is often thought to be associated with the strong territorial behavior displayed by males (Gillingham et al., 1995). However, whether Tuatara also show differences in head or limb dimensions independent of body size remains unknown. Here we test for differences in functionally relevant traits (i.e., head size and limb dimensions) between male and female Tuatara that could potentially give rise to sex-based differences in performance. Further, we explore the potential selective basis of the observed differences in the light of existing ecological and behavioral data, and comment on the evolution of male-biased shape dimorphisms in lepidosaurians.

MATERIALS AND METHODS

Specimens.—Twenty adult and sub-adult male and eight adult female preserved *Sphenodon punctatus* from the collection at the National Museum in Prague were measured (NMP6V 5512–5529, NMP6V 6276–6277, and NMP6V 32861–32868). An additional four adult preserved specimens (two males and two females) housed at the Museum for Comparative Zoology at Harvard University (MCZ6752, MCZ4701, MCZ143830, MCZ143829) were measured to increase the sample size. Sub-adults were removed from the final analyses resulting in a total of 19 male and ten female specimens.

Morphometrics.—For each specimen we measured its snout–vent length using a tape-measure to the nearest millimeter. Additionally we took the following head and limb measurements (Vanhooydonck and Van Damme, 1999; Herrel et al., 2006) to the nearest 0.1 mm using digital calipers (Mitutoyo CD-15DC): head length (measured from the back of the parietal bone to the tip of the snout), head width (measured as the widest point of the head), head depth (measured at the tallest part of the head), lower jaw length (measured from the back of the retro-articular process to the tip of the lower jaw), and snout length (measured from the back of the maxillary

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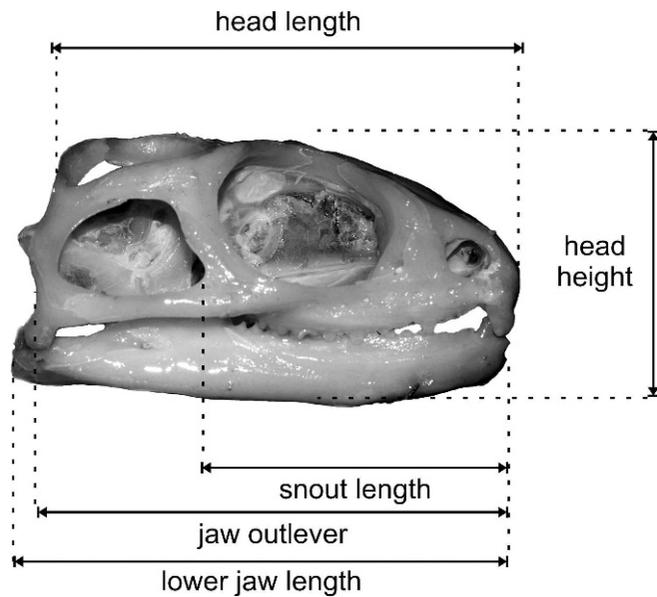


Fig. 1. Schematic representation of the cranial measures determined for each specimen, taken on intact animals only. Relevant bony landmarks for measures can easily be detected by palpation in intact specimens.

bone to the tip of the upper jaw). Additionally, the distance from the back of the quadrate to the tip of the lower jaw was measured and used as an estimate of the jaw out-lever length (Fig. 1). Based on these measurements, two additional values were calculated: the in-lever for jaw opening, being the lower jaw length minus the jaw out-lever length; and the in-lever for jaw closing, being the jaw out-lever length minus the snout length. For each specimen we also measured femur length, tibia length, metatarsus length, length of the second toe of the hind foot, humerus length, radius length, metacarpus length, the length of the fourth toe of the front foot and tail length. However, we did not analyze sexual

differences in tail length due to the high incidence of regenerated tails in this species (Seligman et al., 2008).

Analyses.—All morphometric data were \log_{10} -transformed before analysis to meet the assumptions of homoscedasticity and normality required for parametric analysis. First we tested for differences in size between males and females using a univariate analysis of variance. Given that males reached greater lengths than females, and since we were specifically interested in size-independent differences in morphology, we used analyses of co-variance with snout-vent length (SVL) as a co-variate to test for shape differences in head and limb dimensions between the two sexes. First we ran a MANCOVA coupled to univariate ANCOVAs on the cranial dimensions to test whether males and females differed in head shape. Next we ran similar analyses for forelimb and hind limb dimensions separately as different selective pressures may be operating on fore versus hind limbs. All univariate tests were corrected using a sequential Bonferroni correction (Rice, 1989).

RESULTS

Male and female *Sphenodon* in our sample differed significantly in snout-vent length ($F_{1,27} = 12.24$; $P = 0.002$; Table 1). Males also reached greater lengths than females (largest male: 250 mm; largest female: 225 mm). A MANCOVA on the head measures indicated significant differences in head shape between the sexes (Wilks' Lambda = 0.45; $F_{8,19} = 2.88$; $P = 0.028$). Univariate ANCOVAs demonstrated that differences between sexes were most prominent in head height ($F_{1,26} = 5.74$; $P = 0.02$) and the jaw out-lever ($F_{1,26} = 4.21$; $P = 0.05$), with males having relatively taller heads and relatively longer jaw out-levers than females (Figs. 2, 3). Note, however, that none of these differences remained significant after Bonferroni correction.

ANCOVAs testing for differences in overall front and hind limb length indicated significant differences in fore ($F_{1,26} = 5.26$; $P = 0.03$) and hind ($F_{1,26} = 8.73$; $P = 0.007$) limb

Table 1. Morphometric Characterization of the 19 Male and Ten Female *Sphenodon* Specimens Included in Our Study. All measurements are means in mm. SE = standard error; SVL = snout-vent length.

	Male	SE	Female	SE
SVL	219.5	4.0	195.8	5.5
Head length	56.7	1.2	49.9	1.6
Head width	43.1	0.8	38.7	1.1
Head height	35.2	0.8	29.0	1.1
Lower jaw length	58.7	1.0	52.1	1.3
Jaw out-lever	55.5	1.0	48.6	1.3
Opening in-lever	3.2	0.2	3.5	0.3
Snout length	40.3	0.6	35.6	0.9
Closing in-lever	15.2	0.5	12.9	0.7
Hind limb length	117.6	1.8	102.6	2.4
Femur length	42.0	0.8	35.5	1.1
Tibia length	32.5	0.6	29.3	0.8
Metatarsus length	22.5	0.6	20.3	0.8
Length longest toe hind	20.6	0.4	17.5	0.5
Front limb length	92.3	1.5	81.1	2.1
Humerus length	34.6	0.7	30.1	0.9
Radius length	26.6	0.6	23.4	0.8
Metacarpus length	16.6	0.5	14.4	0.7
Length longest toe front	14.4	0.3	13.2	0.4

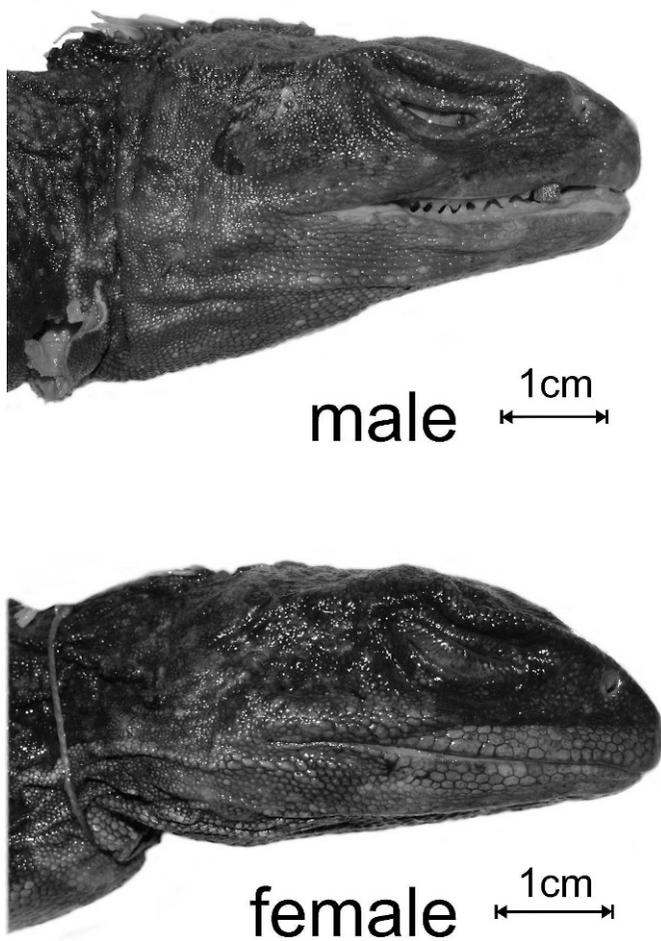


Fig. 2. Lateral view of the head of a male (top) and female (bottom) *Sphenodon punctatus* scaled to the same head length. Scale bar = 1 cm.

length, with limbs being significantly longer in males than in females. A MANCOVA on the individual hind-limb segments showed significant differences between the sexes (Wilks' Lambda = 0.66; $F_{4,23} = 3.02$; $P = 0.04$). Subsequent univariate ANCOVAs indicated differences in the longest toe on the hind limb ($F_{1,26} = 13.22$; $P = 0.001$) and the femur ($F_{1,26} = 8.47$; $P = 0.007$), both being significantly longer in males after Bonferroni correction (Fig. 3). A MANCOVA on the forelimb segments showed no difference between the sexes (Wilks' Lambda = 0.78; $F_{4,23} = 1.60$; $P = 0.21$).

DISCUSSION

Our analyses indicate significant differences in size independent head and limb dimensions between the sexes, with males having bigger heads and longer limbs than females. These differences in functionally relevant traits (Herrel et al., 1999, 2001a, 2001b; Husak et al., 2006, 2008) suggest that performance differences between the sexes likely exist as well, with males potentially being better biters and faster runners.

Interestingly, and in contrast to data published for lizards, head height is the variable that differs most strongly between the two sexes (Herrel et al., 1999, 2001a, 2001b; but see Lappin and Swinney, 1999). Moreover, differences in head dimensions are relatively subtle compared to those observed in lizards (see Vincent and Herrel, 2007 for an overview). Given the unique cranial morphology of *Sphen-*

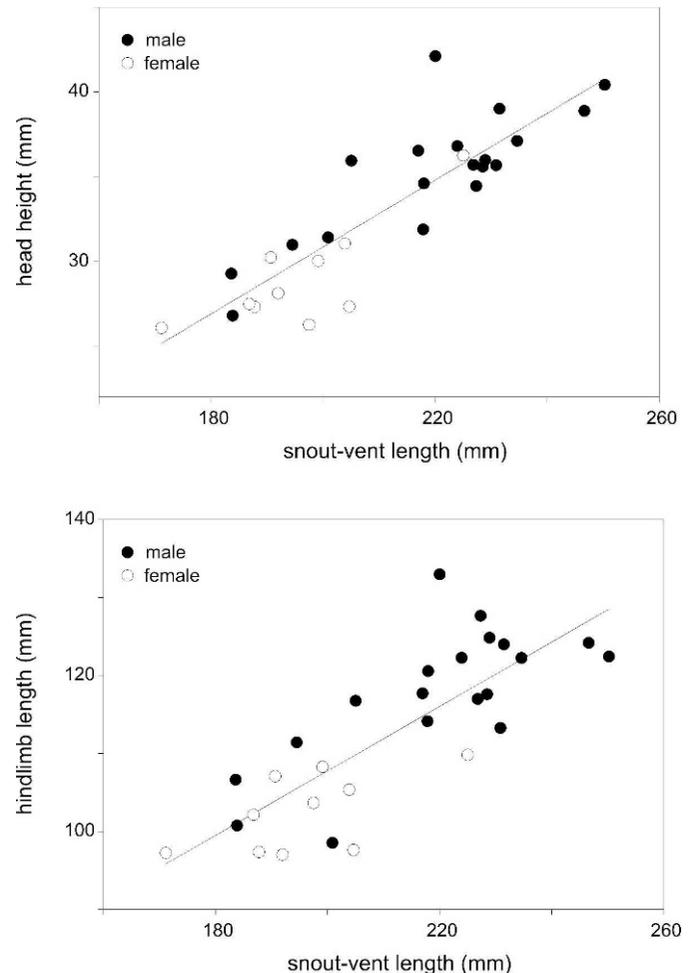


Fig. 3. Differences in head height (top) and hind limb length (bottom) between male and female *S. punctatus*. Filled symbols: males; open symbols: females.

odon with an intact lower temporal bar, the development of the external adductors may be spatially constrained. In lizards, on the other hand, the superficial part of the adductor externus muscle is positioned laterally onto the lower jaw, thus allowing for a significant increase in jaw muscle mass and head width (Schaerlaeken et al., 2008). However, the dorsal temporal opening in *Sphenodon* does allow for some bulging of the jaw adductors (Fig. 1), which may help explain the difference in head height between the sexes.

The jaw out-lever, or the part of the mandible in front of the quadrato-mandibular joint, is also longer in males compared to females. In *Sphenodon*, this may be particularly relevant during feeding, as the muscle principally responsible for the forward movement of the lower jaw during the power stroke attaches on the inside of the lower jaw anterior to the quadrato-mandibular joint (Gorniak et al., 1982). The observed difference between the sexes in jaw out-lever could thus also imply an increase in shearing efficiency in males compared to females. Alternatively, the longer jaw out-lever could give males a performance advantage during territorial disputes when males bite each other with their jaws opened widely.

Although sexual selection in relation to male-male combat is often invoked to explain inter-sexual differences in head size in lizards, this may not be the only explanation

in *Sphenodon*. Although data on inter-sexual differences in diet in *Sphenodon* are scarce, available data suggest that these animals do eat large and hard prey including large darkling beetles, giant weta, and nestling birds (Walls, 1981; Markwell, 1998; Ussher, 1999). Consequently, any differences in bite force between the sexes could be relevant in generating a niche divergence and thus reducing competition between males and females. Interestingly, the one paper that does list dietary differences between the sexes indicates that males do eat larger prey, especially juvenile seabirds (Cree et al., 1999). If the taller heads of males allow for an increased jaw muscle mass, this could potentially allow them to eat large prey more efficiently, but this remains to be tested experimentally.

Clearly, biting in male Tuatara is also relevant in male-male competition as fights often escalate and involve males biting each other, resulting in frequent tail loss (Seligman et al., 2008). Interestingly, female Tuatara also engage in vigorous territorial disputes that commonly involve biting and may lead to injury (Gillingham et al., 1995; Seligman et al., 2008). If sexual selection has driven an increase in bite force relevant to territorial disputes, then this should be reflected mainly in the external adductor, a muscle ideally suited for biting at large gapes (Herrel et al., 1998). One way to test this would be to measure bite forces in adults at different gape angles or by dissecting the jaw adductor muscles in male and female *Sphenodon* to look for differences in muscle allocation.

Besides the differences in head shape, our data also indicate significant inter-sexual differences in limb dimensions: males have longer front and hind limbs than females. In lizards, limb length is often positively correlated to sprint speed, with males often having longer limbs and higher sprint speeds than females (Gifford et al., 2008). In *Sphenodon*, previously published data show that larger juveniles do indeed run faster, but unfortunately no data were provided on the correlation between sprint speed and limb dimensions (Nelson et al., 2006). However, given the similarity in the mechanics of locomotion in lizards and Tuatara (Reilly et al., 2006), we would expect that Tuatara with longer limbs, and especially longer hind limbs, do indeed run faster. In lizards, sprint speed has been shown to be correlated to a male's ability to defend territories (Husak et al., 2006, 2008), suggesting a potentially important role for sexual selection in driving sex-based differences in relative limb dimensions.

Alternatively, the observed differences in limb dimensions could be associated with the unusual male courtship display which involves an erect type of locomotion termed the 'stolzer Gang' (Gans et al., 1984). Given that both front and hind limbs are longer in males compared to females, this may be an important contributor to the observed differences in morphology. Finally, males and females may differ in microhabitat use or foraging mode which would also place different demands on the locomotor system (Miles et al., 2007). However, these hypotheses are difficult to evaluate given the lack of ecological data for the two sexes. Measurements of performance are clearly needed to test whether the observed differences in morphology between the sexes are indeed translated into male-biased differences in performance. If this is the case, *Sphenodon* would appear to follow the typical lizard trend, suggesting that male-biased sexual differences in physical performance may be a basal trait for lepidosaurs in general.

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