



Sexual dimorphism, body size, bite force and male mating success in tuatara

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Sexual dimorphisms in body size and head size are common among lizards and are often related to sexual selection on male fighting capacity (organismal performance) and territory defence. However, whether this is generally true or restricted to lizards remains untested. Here we provide data on body and head size, bite performance and indicators of mating success in the tuatara (*Sphenodon punctatus*), the closest living relative to squamates, to explore the generality of these patterns. First, we test whether male and female tuatara are dimorphic in head dimensions and bite force, independent of body size. Next, we explore which traits best predict bite force capacity in males and females. Finally, we test whether male bite force is correlated with male mating success in a free-ranging population of tuatara (*Sphenodon punctatus*). Our data confirm that tuatara are indeed dimorphic in head shape, with males having bigger heads and higher bite forces than females. Across all individuals, head length and the jaw closing in-lever are the best predictors of bite force. In addition, our data show that males that are mated have higher absolute but not relative bite forces. Bite force was also significantly correlated to condition in males but not females. Whereas these data suggest that bite force may be under sexual selection in tuatara, they also indicate that body size may be the key trait under selection in contrast to what is observed in squamates that defend territories or resources by biting. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **100**, 287–292.

ADDITIONAL KEYWORDS: head size – performance – sexual selection – territoriality.

INTRODUCTION

Sexual dimorphism in body size is commonly observed among vertebrates and is thought to be related to fecundity selection on females resulting in females being larger than males, or male–male interactions resulting in males being the larger sex (e.g. Andersson, 1994; Fairbairn, Blanckenhorn & Szekely, 2007). In the case of male–male competition, large male body size is thought to be favoured by selection as it gives males a competitive advantage over others in combat or resource defence (Fairbairn *et al.*, 2007).

Despite the ubiquity of sexual dimorphisms in vertebrates and the importance of sexual selection as a key concept in evolutionary biology (Andersson, 1994; Maynard-Smith & Harper, 2003), relatively little is known about the relationship between mate choice, male–male competition and organismal performance traits. Functional approaches to sexual selection may, however, provide insights into the evolution of male secondary sexual traits, male quality and male mating success and the role of body size therein (Lailvaux & Irschick, 2006; Irschick *et al.*, 2007; Vanhooydonck *et al.*, 2007).

Central to this approach is the incorporation of performance measures (*sensu* Huey & Stevenson,

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1979) as indicators of male quality or the ability of a male to acquire and defend key limiting resources, including access to space, food and sexual partners (Irschick *et al.*, 2007). Indeed, several studies on lizards have provided evidence that physical performance capacity is correlated to dominance or the ability of an individual to defend a territory (Robson & Miles, 2000; Perry *et al.*, 2004; Husak, Fox & Van Den Bussche, 2008), may predict the outcome of contests between males (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Husak *et al.*, 2006) and may be linked directly to actual mating success and fitness (Lappin & Husak, 2005; Husak *et al.*, 2006; Husak, Lappin & Van Den Bussche, 2009). However, the generality of these results to other vertebrate groups remains to be tested.

Here, we explore sexual dimorphism in body size, head size and bite force in tuatara (*Sphenodon punctatus*) and its potential correlates with mating success. Tuatara are long-lived reptiles and are the sole remaining representatives of the Rhynchocephalia. These animals have a seasonally monogamous mating system but do not exhibit long-term pair bonding (Moore *et al.*, 2009a). Tuatara are sexually dimorphic in body size, with males being larger than females, and mating involves an elaborate courtship ritual followed by copulation (Gillingham, Carmichael & Miller, 1995). Fights between males are common and may involve biting (Gillingham *et al.*, 1995). Body size appears to be the primary indicator of male mating success, as prior studies indicate that as little as 25% of the male population mates successfully (predominantly the large males; see Moore *et al.*, 2009a). Multiple paternity occurs at very low frequencies in the wild (Hay & Lambert, 2008; Moore *et al.*, 2009a) and male reproductive success is highly skewed, with a few males siring most of the offspring (Moore *et al.*, 2008, 2009a). Currently, there is no evidence for alternative strategies, suggesting that selection on the ability to defend and patrol territories, and on traits related to territory defence, is likely high. Although the principal trait under selection may be body size, a distinct dimorphism in head shape is present in tuatara (Herrel *et al.*, 2009) and, consequently, male bite force capacity may also play an important role in determining mating success. To test this hypothesis, we measured bite force for a large number of individuals in a natural population and correlate performance data for known, individually marked males, to whether males were mated or not (Moore *et al.*, 2009a, b).

MATERIAL AND METHODS

FIELD SITE AND MEASUREMENTS

We studied tuatara on Stephens Island, a 150-ha Island in the Cook Strait, New Zealand. Mating activ-

ity was monitored during the peak of three mating seasons (2005–2007). Measurements of bite force took place during the mating season in March 2009. Although measurements of performance did not coincide with measurements of male mating success, territories and male mating success are relatively stable in these long-lived animals (Miller *et al.*, 2009; Moore, Daugherty & Nelson, 2009b). Animals were captured in the forest during their active period between 21:00 and 04:00 h, measured and released before 05:00 h the same night. For all animals, we measured body mass, snout-vent length (SVL), tail length, head length, head width, head height, lower jaw length, the distance from the jaw joint to the tip of the jaw (i.e. the jaw out-lever) and the distance from the back of the jugal to the tip of the jaw (CT), and took a picture of the head in dorsal and lateral views. Based on these measurements, we calculated two additional biomechanically relevant variables related to biting: the in-lever for jaw opening (as lower jaw length minus the jaw out-lever) and the in-lever for jaw closing (as the jaw out-lever minus CT). A total of 85 males and 70 females were captured and measured in the field.

BITE FORCES

In vivo bite forces were measured using an isometric Kistler force transducer (9311B, range ± 5.000 N, Kistler, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5995A, Kistler, Switzerland; see Herrel *et al.*, 1999; Anderson, McBrayer & Herrel, 2008 for a more detailed description of the set-up). When the free end of the holder was placed between the jaws of an animal, prolonged and repeated biting resulted. The place of application of bite forces was standardized for all animals. Bite forces were measured at the back of the jaw and measurements were repeated three times for each animal. The maximal value obtained during such a recording session was considered to be the maximal bite force for that individual.

MATING SUCCESS

Mating activity was established in previous studies for a focal study group of animals (Miller *et al.*, 2009, Moore *et al.*, 2009a, b). Detailed methodology of how these data were collected are described in Moore *et al.* (2009a) and Moore *et al.* (2009b). Briefly, focal study plots were established in 2004 and all individuals in the plots were permanently marked by passive integrated transponder (PIT) tagging. Mating activity was monitored during March of 2005, 2006 and 2007.

Focal males were determined to be 'unmated' if they were monitored for >2 mating seasons and were never observed mating.

ANALYSES

All data were \log_{10} transformed before analysis to meet the assumptions of normality and homoscedasticity for parametric analyses. First, we tested for differences in body size (SVL) between adult males and females. As differences in body size were significant, we then used multivariate analyses of covariance (MANCOVAs) with SVL as covariate to test for differences in head dimensions and bite force between the two sexes. Regression analyses were used to explore which traits best explained the observed variation in bite force across all individuals and for each sex separately. Given the tendency of stepwise models to inflate type-I error rates, we decided to run a full regression models with all variables included. We use the standardized partial regression coefficients to judge the strength of the variables in the model in explaining variation in bite force (Whittingham *et al.*, 2006; Mundry & Nunn, 2009). Next, the data set was separated by sex and we calculated the residuals of the regression of bite force on SVL. Given that body condition may be related to mating success, we calculated condition as the residuals of the linear regression of body mass on SVL for each sex separately (both \log_{10} transformed; see Moore *et al.* 2007 for the rationale to use this metric as an indicator of condition). We then used Pearson correlations to explore whether body condition was related to bite force, independent of body size (i.e. residual bite force).

Finally, we used analyses of covariance (ANCOVAs) with either SVL or condition as a covariate to test whether males that were mated had higher absolute bite forces, relatively high bite forces for their body size and relatively high bite forces given the condition they are in. All analyses were performed using SPSS (ver. 15.0 for Windows).

RESULTS

SEXUAL DIMORPHISM

Males and females included in our sample were significantly different in body size (SVL: $F_{1,142} = 65.77$; $P < 0.001$), with males being bigger than females on average (Table 1). A MANCOVA with SVL as a covariate testing for differences in head shape between the sexes was highly significant (Wilks' $\lambda = 0.47$; $F = 11.74$; $P < 0.001$). Subsequent univariate F -tests indicated that differences between sexes are significant for all traits (all $P < 0.001$) except body mass ($F_{1,134} = 0.71$; $P = 0.40$).

Table 1. Summary of body and head dimensions and bite force for male and female tuatara

	Male	Female
Number of individuals	74	70
Snout-vent length (mm)	230.2 ± 28.0	199.5 ± 14.70
Tail length (mm)	196.7 ± 44.2	148.6 ± 39.2
Mass (g)	434.8 ± 172.6	272.7 ± 62.1
Head length (mm)	60.6 ± 6.7	51.3 ± 3.2
Head width (mm)	45.2 ± 6.0	37.9 ± 2.6
Head height (mm)	33.4 ± 4.3	27.9 ± 1.8
Lower jaw length (mm)	65.3 ± 7.2	54.5 ± 3.4
Jaw out-lever (mm)	58.9 ± 6.7	49.0 ± 3.1
Snout length (mm)	41.7 ± 4.4	35.4 ± 2.3
Jaw opening in-lever (mm)	6.4 ± 1.1	5.5 ± 0.7
Jaw closing in-lever (mm)	17.2 ± 2.7	13.6 ± 1.3
Bite force (N)	173.0 ± 46.8	120.3 ± 23.6

Table entries are means ± standard deviations.

A regression analysis of the data for both sexes combined retained a significant model with only head length, head height and the jaw closing in-lever principally predicting variation in bite force ($R^2 = 0.87$; $P < 0.001$), indicating that animals with longer ($\beta = 0.71$) and taller ($\beta = 0.40$) heads and greater jaw closing in-levers ($\beta = 0.31$) are better biters. A similar analysis run on the data for females only retained a significant model with head length and head height as the best predictors of bite force ($R^2 = 0.55$; $P < 0.001$; see Fig. 1), demonstrating that females with longer ($\beta = 0.77$) and taller ($\beta = 0.42$) heads have higher bite forces. An analysis on the data for males only retained a significant model with head length, the jaw closing in-lever and head height as significant predictors ($R^2 = 0.93$; $P < 0.001$), all positively related to bite force (head length: $\beta = 0.39$; closing in-lever: $\beta = 0.31$; head height: $\beta = 0.35$; see Fig. 1).

BITE FORCE CORRELATES

Bite force is strongly correlated to overall body size in both males (slope = 2.21; $r = 0.95$; $P < 0.001$) and females (slope = 1.55; $r = 0.61$; $P < 0.001$). Residual bite force is correlated with condition in males ($r = 0.34$; $P < 0.01$) but not females. Males that were mated also had significant higher absolute ($F_{1,31} = 7.15$; $P = 0.01$) but not relative ($F_{1,29} = 2.65$; $P = 0.11$) bite forces than males that were not mated. For a given condition, males that are mated have significantly higher bite forces ($F_{1,29} = 7.96$; $P = 0.01$) (Fig. 2).

DISCUSSION

Our data confirm previous studies in showing a distinct male-biased body size dimorphism in tuatara

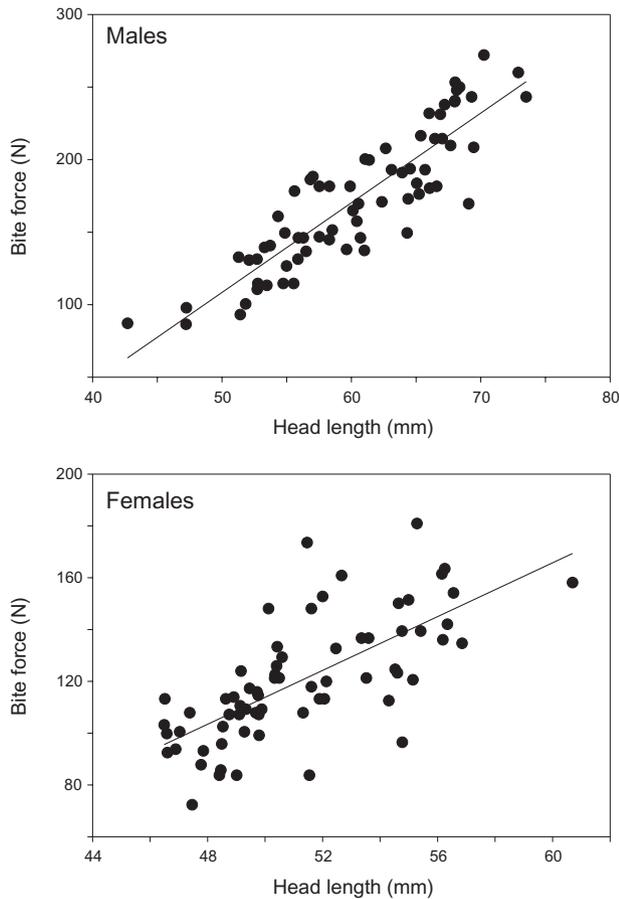


Figure 1. Correlations between head length and bite force for males (top) and females (bottom). Note how the correlation is much stronger for males compared with females.

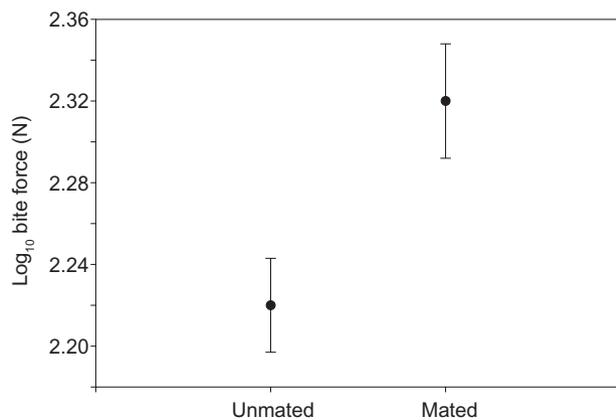


Figure 2. Graph illustrating differences in absolute bite force capacity between unmated and mated male tuatara. Note that mated males have greater absolute bite forces on average. Data points are means \pm standard deviations.

(Gillingham *et al.*, 1995). Moreover, our data based on a large number of individuals from a wild population confirm the results from a previous study using museum specimens (Herrel *et al.*, 2009) and indicate a significant head-shape dimorphism in tuatara. However, in contrast to the suggestion that sexes differ mainly in relative head height (Herrel *et al.*, 2009), our data show a significant shape dimorphism in all head dimensions, with males having a bigger head for their body size than females. The observed dimorphism in head size results in a significant difference in both absolute and size-corrected bite force, with males being better biters than females, as predicted previously (Herrel *et al.*, 2009) and observed in a recent study providing data for one female and one male captive specimen (Jones & Lappin, 2009). Interestingly, our data indicate that different aspects of head morphology are responsible for differences in bite force among individuals. Whereas in females head length is the best predictor of bite force, in males traits related to the mechanics of biting appear to be important. Specifically, the in-lever for jaw closing was among the traits best explaining variation in bite force in males but not females. Strikingly, whereas variation in these traits explained over 90% of the variation in bite force in males, head length explained only approximately 55% of the variation in bite force in females. The slope of the regression line relating SVL to bite force was different for males and females (male: 2.21; female: 1.55), suggesting slight positive allometry in males but negative allometric scaling of bite force to body size in females (the predicted slope for isometry is 2 as force is proportional to area). Although suggestive of stronger selection on bite force and head morphology in males than females, these analyses remain purely correlative. Interestingly, these slopes do differ from the slopes predicted by Jones & Lappin (2009) based on data for captive individuals (see Schaerlaeken *et al.*, 2008; Jones & Lappin, 2009), suggesting that there may be distinct differences in performance between wild-caught and captive specimens.

Our data also suggest that bite force is also related to aspects of mating success in males. The clearest evidence thereof is provided by the significant difference in bite force between mated and unmated males. However, as bite force covaries strongly with body size, body size is likely an important mediator of bite force and fighting capacity in these animals. Yet, body size itself may also be the target of selection, with higher bite forces evolving as a by-product of body size. Indeed, when correcting for body size, differences between mated and unmated males disappeared, suggesting that the principal trait under selection may be overall body size. However, the observation that in males, but not females, condition was related to bite force, the fact that bite force in

males is accurately predicted by functional traits related to biting (Fig. 1), and the fact that bite force increases with positive allometry vs. body size, suggests that bite force itself may be under selection. Indeed, when bite force measurements are corrected for the condition the animal is in, the mated males have much stronger bite forces than unmated males. Thus, even although body size may be the means by which bite force is selected for, if males in poorer condition can invest in bite force capacity, this may give them an additional advantage and may allow them to increase their fitness. In summary, whereas our data suggest that bite force may be under sexual selection in a Rhynchocephalian reptile, they also indicate that body size may be the means by which an increase in bite force is achieved. This stands in contrast to what is typically observed in squamates that defend territories or resources by biting, where selection appears to be acting directly on aspects of head size and shape (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Lappin & Husak, 2005).

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