

Bite-Force Performance Predicts Dominance in Male Venerable Collared Lizards (*Crotaphytus antiquus*)

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The evolution of exaggerated structures that function as weapons in sexually dimorphic species is often explained by intra-sexual selection related to male combat, as these structures are used in fights among males and can determine dominance during such interactions. In many lizard species, males have a larger head than females, a condition attributed to intra-sexual selection. Although head size has been shown to predict dominance in lizards, the way that head size influences dominance remains unclear. We staged interactions between body size-matched male Venerable Collared Lizards (*Crotaphytus antiquus*) in the laboratory to test the hypothesis that harder-biting males would be dominant over males with weaker bite-force performance. Winners of staged interactions bit significantly harder than losers, but no measured morphological trait was significantly different between winners and losers. This result indicates the strong role of weapon performance, as opposed to weapon morphology, in determining dominance.

SEXUAL selection related to male combat is often invoked to explain the evolution of exaggerated weapons in sexually dimorphic species (Andersson, 1994). Evidence includes the fact that such structures are used during male combat (e.g., Silverman and Dunbar, 1980; Clutton-Brock, 1982; Zeh, 1987) and that they are often important in determining dominance in male contests (e.g., Brown and Bartalon, 1986; Crespi, 1986), which can translate to a fitness advantage (e.g., Fox, 1983; Hews, 1990). The traditional way of addressing how armaments may be molded by sexual selection has involved quantification of relationships between morphology of the trait and subsequent success in male contests. However, in many cases it is not explicitly known how weapons function to influence dominance during agonistic interactions.

Male-biased head-size dimorphism in many iguanian lizard species is a well-studied example of the potential role of weapon morphology in male contest success. Among polygynous lizards, males tend to have larger heads than females, and this dimorphism has been related to male combat (Stamps, 1983; Kratochvíl and Frynta, 2002 and references therein). Many studies have related measurements of head size to laboratory-determined dominance (e.g., Molina-Borja et al., 1998; Gvoždík and Van Damme, 2003 and references therein) as well as other estimates of fitness, such as field-measured dominance (Vitt and Cooper, 1985), territory status (Hews, 1990), and mating success (LeBas, 2001). The way that head size is relevant to these aspects of fitness, however, remains unclear.

Individual variation in fitness reflects individual variation in underlying morphological and

physiological traits. It is generally accepted, however, that this relationship is mediated by whole-animal performance, hence an hypothesized morphology to performance to fitness relationship (Huey and Stevenson, 1979; Arnold, 1983; Pough, 1989). In territorial, polygynous species, sexual selection may operate on whole-animal performance, thus facilitating the evolution of morphology underlying the relevant performance trait. In lizards, the positive relationship between bite force and head size is well known (Herrel et al., 1999, 2001; Lappin, 1999), and two of the studies relating head size to dominance in lizards suggested that the functional relationship may be due to individuals with larger heads being able to bite harder (Hews, 1990; Perry et al., 2004). Supporting this idea, Lailvaux et al. (2004) showed that bite force was predictive of dominance in staged encounters between “heavyweight morph” *Anolis carolinensis* males, but they did not evaluate the relative power of body or head size to predict dominance. Lappin and Husak (2005) demonstrated that bite-force performance, but not body or head size, predicts reproductive success in *Crotaphytus collaris*. In this study, we used *C. antiquus* to test the relative roles of body and weapon (i.e., head) size versus weapon performance (i.e., bite force) in predicting dominance in male–male agonistic encounters.

Little is known about the natural history of the Venerable Collared Lizard, *Crotaphytus antiquus*. McGuire (1996) proposed that *C. antiquus* is territorial like all other *Crotaphytus* species studied to date (e.g., Fitch, 1956; Baird et al., 1996). He based this on observations of adult males chasing rival males that intruded near an

occupied area, a common territorial defense behavior in *C. collaris* (Yedlin and Ferguson, 1973). In collared lizards, like other polygynous, territorial lizard species, agonistic interactions between males can result in fights with violent biting that can produce severe wounds (Baird et al., 2003; Lappin and Husak, 2005). Such wounds likely affect future interactions (Stamps and Krishnan, 2001; Morrell and Kokko, 2003) and may be costly in terms of fitness. Associated with territoriality and fighting in collared lizards is sexual dimorphism in which males attain greater body size and have larger and disproportionately more robust heads than females (McCoy et al., 1994; Lappin, 1999). As in other species of *Crotaphytus* (Lappin, 1999), we expected that male *C. antiquus* would have larger heads relative to body size and would be able to bite harder than females. Because biting is the means by which males of many lizard species fight, we predicted that bite-force performance would be an important predictor of male dominance during agonistic encounters.

MATERIALS AND METHODS

In May 2004, we studied a population of *C. antiquus* in the Sierra de San Lorenzo Mountains near Santa Eulalia, Coahuila, Mexico. Lizards were found on large boulders at the base of the mountains. Vegetation was a typical Creosote Bush (*Larrea tridentata*) shrubland with Ocotillo (*Fouquieria splendens*), prickly pear (*Opuntia* spp.), and Lechuguilla (*Agave lechuguilla*) also common. McGuire (1996) can be consulted for more details on the habitat and natural history of this species. Lizards were captured with a pole and noose and were held in mesh bags until data collection was completed. Each subject was released at the precise location of its capture within 30 hours of removal.

Snout-vent length (SVL) and mass were recorded as measures of body size. Following Lappin and Husak (2005), head length from the quadrate-articular joint to the snout tip, head width at the maximum lateral extent of the jaw-adductor muscles, and head depth from the quadrate processes of the parietal bone to the ventral extent of the lower jaw were measured as indices of head size. All head 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 0.25 g with a Pesola scale.

Peak bite-force performance was quantified using a piezoelectric force transducer (Type 9203, Kistler Inc., Switzerland) custom fitted with two 25-mm wide stainless steel bite plates and connected to a charge amplifier (Type 5995, Kistler Inc., Switzerland). This is a modified version of the bite-force transducer used by Herrel et al. (1999). Bite plates were prepared by gluing a strip of leather (1 × 3 × 25 mm) at the end of the outer surface of each beam to define a bite point and to protect the lizards' teeth from being damaged. The charge amplifier was set to register the peak force attained during each trial, which was recorded for subsequent analysis. Prior to bite-force trials, lizards were warmed under a spotlight in a holding tank to their approximate field-active body temperature (~37 C), which was verified with a cloacal thermometer immediately before and after bite-force trials. Three trials were performed sequentially on each individual with one minute of rest between trials.

Based on simple lever mechanics as well as empirical measurements (A. K. Lappin, unpubl. data), the bite location along the jawline influences bite force. Therefore, we recorded the position of the leather strips along the jawline during each trial and measured the distance (parallel to the mid-sagittal plane) from them to the quadrate-articular joint (bite moment arm) to the nearest 0.1 mm with digital calipers. We then calculated standardized bite forces at the midpoint of the lower jaw (not including the retroarticular process) as follows: standardized bite force = (calibrated amplifier output) × (bite moment arm/0.5 head length as defined above). For each individual, only the greatest standardized bite force value among the three trials was used in the statistical analyses.

We staged dyadic encounters in a 0.55 × 0.42 × 0.33-m neutral arena. Eight pairs of lizards used in dyadic encounters were size-matched by SVL to within 2 mm. No individuals were used in a trial more than once. The floor and back and side walls of the arena were made of painted plywood, and the front was made of glass so that we could view and videotape interactions. The top was covered with a wire-mesh lid, and two incandescent lamps were positioned overhead to provide both lizards with warmth. A wooden divider was placed down the center of the arena so that lizards could not view each other when placed inside. At the beginning of each trial, lizards of each pair were placed randomly into alternate sides of the divided arena. One of the lizards had a small dot of blue, non-toxic, acrylic paint placed at the base of his tail so that the individuals could be identified during the inter-

actions. After a 10-min acclimation period during which the lizards were not within sight of each other, the divider was removed, and the lizards were allowed to interact for 30 min. All interactions were videotaped with a tripod-mounted camera positioned in front of the glass wall of the arena. The arena was washed with ethanol and then water between trials. We reviewed the videotapes and, using the methods of Fox and Baird (1992) and Husak and Fox (2003), determined which lizard was dominant in each interaction. Dominant behavior patterns received a positive score, whereas submissive ones received a negative score (see Fox and Baird, 1992). For each interaction, we summed the scores to determine which lizard was dominant. In every case it was clear which lizard was dominant.

For each sex, summary statistics were calculated for the body and head measures and standardized bite force. Data were log-transformed for all further analyses. To examine sexual dimorphism, we conducted several tests, following Kratochvíl et al. (2003). Initially, we used *t*-tests to compare mean measurements (not size-corrected) between males and females to test for sexual dimorphism of absolute body and head size. We then performed ANCOVAs with SVL as the covariate to test for sexual differences in head size relative to body size.

To test for differences between winners and losers in the dominance interactions, we compared body and head size and bite-force performance using one-tailed paired *t*-tests (following Lailvaux et al., 2004; Perry et al., 2004). We tested for differences in head morphometrics between winners and losers using absolute head dimensions, as well as by using residual values from regressions of each head morphometric against SVL. In addition to testing each head morphometric separately, we did a principal components analysis (PCA) to obtain "head shape" values from the resultant axes. We then compared PCA scores between winners and losers to determine if head shape differed between winners and losers. We performed one-tailed hypothesis tests because we predicted *a priori* that winners would be larger (among limited size variation in size-matched pairs), have larger armaments, and/or bite harder than losers.

RESULTS

We caught a total of 30 lizards (18 males, 12 females). When absolute morphometrics were compared, males were significantly larger and heavier and had larger heads in all dimensions

TABLE 1. SUMMARY STATISTICS (MEAN \pm 1 SE) FOR BODY AND HEAD SIZE AND BITE-FORCE PERFORMANCE FOR MALE AND FEMALE *Crotaphytus antiquus* FROM THE SIERRA DE SAN LORENZO MOUNTAINS, COAHUILA, MEXICO. Values in parentheses represent the range of values.

	Males (<i>n</i> = 18)	Females (<i>n</i> = 12)
SVL (mm)	100.4 \pm 1.9 (84.7–108.6)	88.3 \pm 1.1 (82.0–93.8)
Mass (g)	40.4 \pm 2.8 (20.5–54.5)	26.0 \pm 1.2 (21.5–34.0)
Head length (mm)	27.4 \pm 0.8 (22.4–30.6)	22.7 \pm 0.4 (20.9–25.6)
Head width (mm)	23.5 \pm 0.6 (18.5–26.2)	18.6 \pm 0.2 (17.4–19.9)
Head depth (mm)	14.3 \pm 0.5 (10.9–16.0)	11.1 \pm 0.2 (10.0–12.1)
Bite force (N)	44.1 \pm 4.1 (20.0–70.6)	19.8 \pm 0.8 (13.5–23.3)

than females ($t > 5.545$, *df* = 28, $P < 0.001$ for all, Table 1). All head measurements were significantly and positively correlated with SVL ($0.91 \leq r \leq 0.97$, $P < 0.001$). ANCOVA revealed that, relative to body size, males had wider heads (test for homogeneity of slopes: $F_{1,27} = 5.92$, $P = 0.02$) and deeper heads (test for homogeneity of slopes NS; test for equal intercepts: $F_{1,27} = 5.78$; $P = 0.02$) than females, but they did not have longer heads (test for homogeneity of slopes and tests for equal intercepts both NS, $P > 0.25$). The slope differed for head width, but the intercept differed for head depth, meaning that the sexual difference in head width increases with body size, whereas the sexual difference in head depth is statistically consistent with body size. Males bit with an average of over twice the force of females ($F_{1,27} = 16.56$, $P < 0.001$).

Paired *t*-tests revealed that winners of male-male dominance interactions were not significantly greater in SVL or mass, nor in head length, width, or depth than losers ($P > 0.20$ for all, Table 2). Winners and losers also did not differ in residual head morphometrics ($P > 0.40$ for all). The PCA resulted in three axes that explained 72.8%, 15.7%, and 11.5% percent of the variation, respectively. Winners and losers did not statistically differ for any of these three axes ($P > 0.30$ for all). However, winners bit significantly harder than losers ($t = 2.256$, *df* = 7, $P = 0.026$), with the mean bite force of winners being 16.7% greater than that of losers (Table 2).

DISCUSSION

As predicted, we found significant sexual dimorphism in *C. antiquus*, with males attaining

TABLE 2. SUMMARY STATISTICS (MEAN \pm 1 SE) FOR MORPHOMETRICS AND BITE-FORCE PERFORMANCE OF WINNING AND LOSING PAIRS ($n = 8$) OF MALE *Crotaphytus antiquus* USED IN DOMINANCE TRIALS. Variables significantly different between winners and losers are indicated in bold.

	Winners	Losers
SVL (mm)	101.5 \pm 2.1	101.4 \pm 1.9
Mass (g)	42.3 \pm 3.3	40.1 \pm 3.0
Head length (mm)	27.5 \pm 0.9	27.9 \pm 0.9
Head width (mm)	23.8 \pm 0.7	23.8 \pm 0.6
Head depth (mm)	14.5 \pm 0.5	14.5 \pm 0.5
Bite force (N)	48.6 \pm 5.4	41.7 \pm 4.0

greater body size and having larger heads than females, both absolutely and relative to body size. Along with male-biased dimorphism in head dimensions, we also found that males bit considerably harder than females. These results agree with what is known about other collared lizard species (Lappin, 1999) and other iguanian lizard species (Stamps, 1983).

Bite-force performance was the only significantly different trait between winners and losers in staged interactions between males. Contrary to our expectations, the head dimensions of winners were not greater than those of losers. Other studies have found that head size predicts dominance in lizards (see references above), yet ours did not. Although the small number of interactions could be the cause of this lack of a relationship, the significant difference found in bite force between winners and losers stresses the importance of weapon performance, relative to weapon morphology, in determining dominance. It appears that, in Venerable Collared Lizards, the capacity to bite harder than a rival confers an advantage during agonistic interactions. Other investigators have found similar results, either by measuring bite force directly (Lailvaux et al., 2004) or by measuring an assumed correlate of bite-force performance, i.e., head size. Our results suggest that morphological "proxies" of bite force (e.g., head size) can sometimes be misleading if performance is not measured (Lauder, 1996). These laboratory studies tell us that outcomes of agonistic interactions among males of polygynous taxa may be important determinants of successful territory acquisition and maintenance. Individuals that can potentially inflict greater costs in the form of injury to rivals are predicted to have higher quality territories (e.g., Stamps and Krishnan, 2001; Morrell and Kokko, 2003). Therefore,

dominance, as measured in dyadic encounters, can have strong effects on fitness (e.g., Fox, 1983; Hews, 1990).

Our results revealed a positive relationship between performance and dominance, a trait that likely is an important determinant of male fitness, thus providing support for the hypothesis that sexual selection operates on whole-animal performance traits. We suggest that other territorial taxa should exhibit a similar relationship between weapon performance and dominance (e.g., Sneddon et al., 2000), even if measurements of the weapon do not predict dominance. The hypothesis that sexual selection may impact the evolution of morphological traits via selection on whole-animal performance has received increasing attention in recent years (e.g., Lailvaux et al., 2004; Perry et al., 2004; Lappin and Husak, 2005 and references therein). Our results showing considerable sexual differences in performance also are consistent with the hypothesis that intra-sexual selection has influenced the evolution of exaggerated head size in male Venerable Collared Lizards (see Berglund et al., 1996; Gvoždík and Van Damme, 2003), despite the fact that head size did not differ between winning and losing males. Future work should focus on elucidating performance gradients in different demographic groups (e.g., age classes, sexes) with the primary goals being (1) the detection of generalized patterns within and among taxonomic groups and (2) the identification of traits that underlie significant variation in performance, particularly when gross morphological variation is relatively slight.

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