Gaping Displays Reveal and Amplify a Mechanically Based Index of Weapon Performance

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abstract: Physical prowess, a key determinant of fight outcomes, is contingent on whole-organism performance traits. The advertisement of performance, via display, is poorly understood because it is unclear how information about performance is encoded into display characteristics. Previous studies have shown that weapon performance (i.e., bite force) predicts dominance and reproductive success in male lizards. We tested the hypothesis that gaping displays by adult male collared lizards (*Crotaphytus*) can provide an index of weapon performance by exposing the major jaw-adductor muscle complex and that white patches at the mouth corners amplify this index. For territorial adult males, the breadth of the muscle complex, which is not correlated with body size, was a strong predictor of bite force. For nonterritorial yearling males and females, however, measures of body and head size predicted bite force. The patches are highly conspicuous, exhibit UV-reflecting properties within the visual range of lizards, and provide size-independent information about bite force only in adult males. We conclude that exposure of the muscle complex during gaping displays can provide rival males with a reliable, body-size independent, biomechanically based index of weapon performance, an index that the mouth-corner patches amplify. Indexes that transmit information through mechanistic links to performance are expected to be widespread among animals.

Keywords: cues, signals, jaws, bite-force performance, *Crotaphytus*.

Intraspecific communication, via the exchange of threat displays, is a widespread feature of aggressive interactions (Huntingford and Turner 1987). Among the most important functions of such displays is to facilitate the assessment of rivals by advertising fighting ability, given that signal-based assessment strategies can expedite conflict resolution and thus reduce costs associated with escalated interactions (e.g., injury, energy expenditure, exposure to predators; Parker 1974; Clutton-Brock and Albon 1979; Enquist and Leimar 1983; Huntingford et al 2000; but see Taylor and Elwood 2003). Many aggressive displays are thought to provide an index of size (e.g., Robertson 1986; Bee et al. 1999; Hongo 2003; Reby and McComb 2003; Hurd 2004; Osborne 2005; Reby et al. 2005), as body size can be a predictor of fighting ability (Riechert 1998). However, size alone may predict neither relative fighting ability nor the winners of fights, particularly when combatants are similar in body size (Hughes 1996; Sneddon et al. 1997; Neat et al. 1998*a*, 1998*b*; Stamps and Krishnan 2001). Therefore, we expect threat displays also to advertise size-independent cues or signals that are linked to fighting ability.

Fighting ability depends on the capacity to impose fitness costs on rivals (Parker 1974). In species endowed with weapons, fighting ability is strongly influenced by the capacity of those weapons to inflict injuries on rivals, which is a function of weapon performance. Signals that advertise weapon performance may therefore constitute an important component of many aggressive display repertoires. Weapons and armaments that are directly observable, such as horns and antlers, are often displayed conspicuously by combatants (Berglund et al. 1996; Hughes 1996; Maynard Smith and Harper 2003). However, when key weapon characteristics are difficult for rivals to scrutinize (e.g.,

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muscles), specialized behaviors and structures may function to advertise the performance capacity of such weapons, specifically by revealing and highlighting characteristics that determine weapon performance. This prediction has been difficult to evaluate owing to the rarity of signaling studies in which weapon performance is measured directly.

In lizards, biting is the primary means by which injuries are inflicted on rivals, and male lizards, being more combative than females, often possess conspicuously enlarged heads and hypertrophied jaw muscles (Stamps 1983; Carothers 1984). The proposition that the biting apparatus constitutes the key weapon employed by male lizards predicts a positive relationship between weapon performance (i.e., bite force) and dominance in aggressive interactions. Consistent with this prediction are results of research showing that direct measurements of bite force predict dominance in staged contests (Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006) and field-measured reproductive success (Lappin and Husak 2005).

The strong links between bite force and dominance indicate that the advertisement of bite force, via display, would be expected to benefit contestants during agonistic interactions, particularly when there are significant risks associated with escalation (e.g., injury). The diverse repertoire of agonistic displays employed by diurnal lizards (Carpenter and Ferguson 1977) and their association with male-biased sexual size dimorphism (Ord et al. 2001) suggests that such signals may contain information about weapon performance, specifically, among individuals that engage in agonistic interactions that can escalate to dangerous levels. Various attributes of these displays and their associated structures (e.g., stereotyped postures and movements that expose colorful patches of integument to rivals) have been shown to be predictive of dominance (Thompson and Moore 1992; Carpenter 1995) and contest outcome (Olsson 1994; Molina-Borja et al. 1998). However, the mechanisms that facilitate the encoding of information about fighting ability in agonistic displays remain poorly understood (reviewed in Whiting et al. 2003; but see Brandt 2003; Hurd 2004). Recent studies of *Anolis* lizards report a positive correlation between the size of the dewlap (a conspicuous signaling structure possessed by many lizards) and bite force, thus suggesting that the dewlap could function to advertise bite force (Vanhooydonck et al. 2005*a*, 2005*b*). Nevertheless, given that none of these signaling structures have a causal (i.e., mechanical) link to weaponry, it is unclear what mechanism(s) could ensure the reliable (i.e., honest) transmission of information about weapon performance.

Here, we propose that mouth-gaping displays by adult male collared lizards (*Crotaphytus*) during agonistic interactions—a pervasive behavior among male iguanian lizards (Carpenter and Ferguson 1977; Carpenter 1978)—provide an index of weapon performance, as they reveal to rivals the size of the primary muscle complex that generates bite force. An index is a signal that is physically constrained to provide reliable information due to an incorruptible link between signal characteristics and the attribute that is advertised (Maynard Smith and Harper 1995; Hurd and Enquist 2005). Territorial encounters between adult male collared lizards, which begin with complex displays exchanged at considerable distances (>30 m), can escalate when rival males advance toward each other and engage in close-range displays (<0.5 m; Fitch 1956; Husak 2004). Close-range displays include mouth gaping (fig. 1), which exposes the adductor mandibulae complex (AMC), the jaw-adductor muscle complex primarily responsible for generating bite force (Smith 1982; Gans et al. 1985; Gans and De Vree 1986; Herrel et al. 1998; McBrayer and White 2002). Gaping displays by adult male collared lizards during agonistic interactions occur in two contexts: while directly facing each other (frontal gaping display) and while orienting their bodies laterally and facing opposite directions (lateral gaping display). During frontal gaping displays, the breadth of the AMC on each side of the jaws is clearly visible and distinctly defined, and thus the muscle complex could provide a physically constrained cue of bite-force performance (fig. 1*A*). Moreover, gaping exposes bright patches situated at the corners of the mouth, which overlay the lateral aspect of the AMC (fig. 1). Because the patches visually enhance the conspicuousness of the AMC by highlighting its lateral margin, they appear to fit the definition of an "amplifier": a signal that augments a receiver's ability to perceive and assess preexisting cues and signals (Hasson 1989, 1997; Taylor et al. 2000; Harper, 2005). During lateral gaping displays, the AMC is not observable by a rival, but the mouth-corner patch facing the combatant remains prominently visible (fig. 1*C*).

If the exposure of AMC breadth during adult male gaping displays has the potential to serve as a reliable index of weapon performance, then AMC breadth should be a strong predictor of bite force, independent of potential alternative cues of bite force, such as body size and head size. The hypothesis that the mouth-corner patches amplify this index of weapon performance (i.e., AMC breadth) predicts that the patches enhance the visibility of the index. Variation in patch characteristics also may provide information about weapon performance, although this is not required by the definition of an amplifier (Hasson 1997).

We tested the potential of gaping displays, which expose the AMC, to provide an index of bite force to receivers by examining the relationship between bite force and body size, head size, and AMC breadth. We then examined the

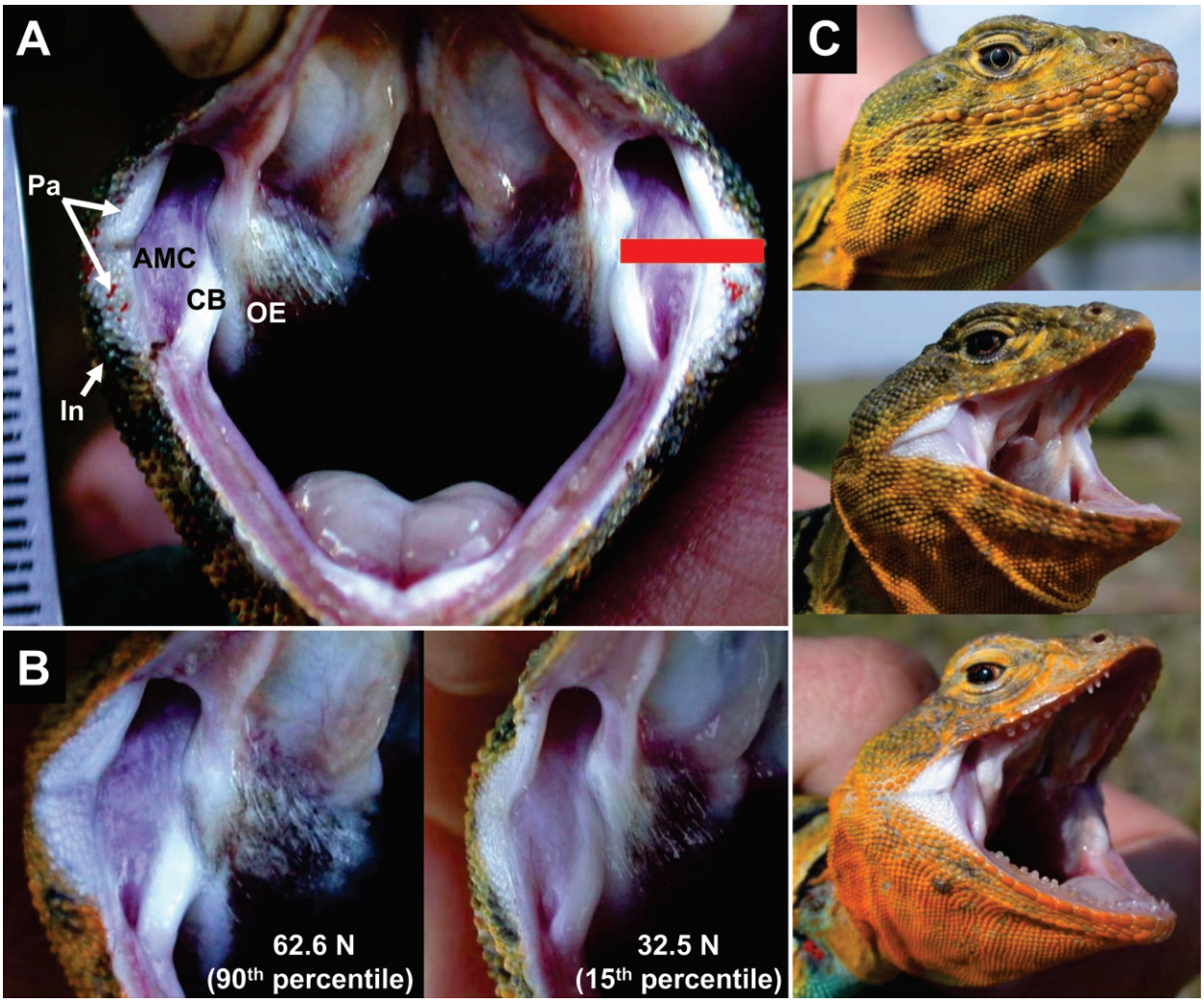

Figure 1: *A*, Anterior view of a gaping adult male *Crotaphytus collaris* as would be viewed by a competing male during a close-quarters frontal gaping display. The muscles of the adductor mandibulae complex (*AMC*) are delineated medially by the coronoid bone (*CB*), on which components of the jaw-adductor muscles insert, and laterally by the mouth-corner patches (*Pa*). The coronoid bones contrast with the melanic oral epithelium (*OE*), and the patches contrast with the adjacent integument (*In*). The horizontal bar indicates breadth of the AMC. Scale in millimeters. *B*, Comparison of the AMC and associated patch between an adult male with relatively high weapon performance (*left*) versus one with relatively low weapon performance (*right*). Although these two lizards were comparable in body size (SVL: strong biter = 110.5 mm; weak biter = 113.8 mm), they differed considerably in bite-force performance (standardized bite-force performance and bite-force percentiles relative to adult male sample provided). Note the broader muscle complex of the stronger biter, which is amplified by its prominent mouth-corner patch. Images to same scale. *C*, The mouth-corner patches of collared lizards each consist of a folded pocket of skin with reduced scales that unfolds as the mouth is opened. Photographs by A. K. Lappin.

conspicuousness of the putative index by measuring the reflectance spectra of the anatomical structures that define it, with respect to the lizard visual system. To determine whether the patches have the potential to amplify the index of weapon performance, we examined visual contrasts between the patches and the adjacent integument. Finally, we tested whether dimensions of the patches themselves could potentially provide information on weapon performance independent of size.

Methods

Study Species and Population

In June of 2003, we studied a population of collared lizards (*Crotaphytus collaris*) at the Wichita Mountains National Wildlife Refuge in Oklahoma. This population has been the subject of previous comparative studies (e.g., McCoy et al. 1994, 1997; Baird et al. 1997; Macedonia et al. 2004; Husak et al., forthcoming). Lizards were captured with a

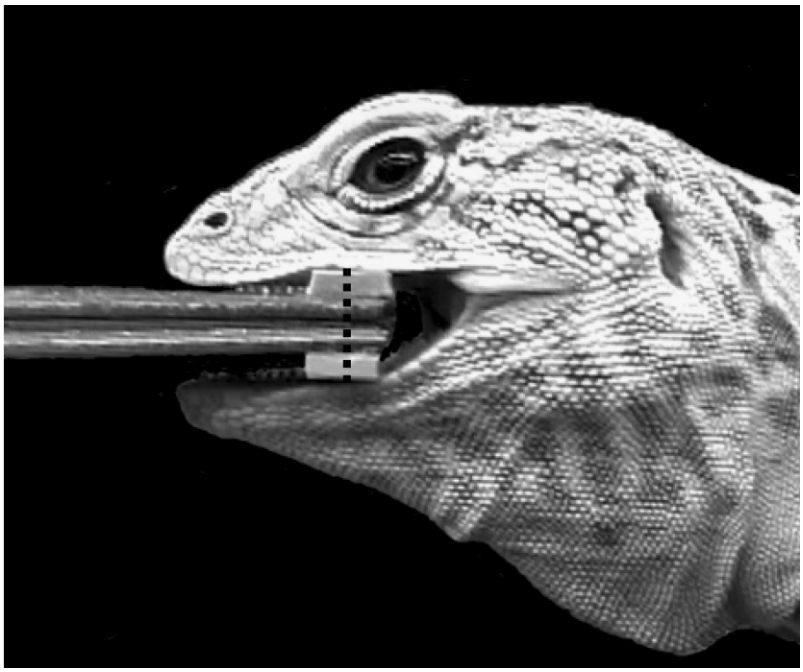

Figure 2: Video frame of a bite-force performance trial. A male *Crotaphytus collaris* bites a double-cantilever-beam force transducer with a leather strip glued to the outer end of each beam. Given that bite force is affected by the bite point along the jaw (i.e., dotted line through leather strips), trials were standardized to account for variation in bite point (see text). See the online videos for examples of two trials with different bite points.

pole and noose or by hand; each was assigned a unique number, and flagging tape was used to mark capture locations. Lizards were held in mesh bags until after data collection, and each was released within 12 h at its location of capture.

Morphometrics

Snout-vent length (SVL) and body mass were recorded as measures of body size. All 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. Head size measures included head length, width, and depth (see Lappin and Husak 2005 for details). In addition, we noninvasively quantified the size of the primary muscle complex that generates bite force (i.e., AMC) as follows. Each lizard was held and induced to gape maximally while a second person captured a close-up digital image of the gaping lizard from the anterior view. A metric ruler next to the lizard's open mouth provided a scale. Using SigmaScan software (Systat Software, Richmond, CA), we measured the breadth of the AMC (average of two sides), defined medially by the center of the coronoid bone and laterally by the extent of the bulging muscles at the corner of the mouth (fig. 1*A*). This measurement provided a correlate to the cross-sectional area of the muscle complex.

Using the imaging software, we measured the following dimensions of the mouth-corner patches from the anterior view: maximum distance between the patches as defined by their lateral edges (lateral patch distance), the minimum distance between the patches as defined by their medial edges (medial patch distance), the width of one patch as defined by its lateral and medial edge (patch width), and the area of one patch (anterior patch area). From images taken from the lateral view, we measured the area of the visible patch (lateral patch area).

Bite-Force Performance

Peak bite-force performance was measured with a piezoelectric isometric force transducer (Type 9203, Kistler, Switzerland) fitted with two 25-mm-wide stainless steel plates and connected to a charge amplifier (Type 5995, Kistler, Switzerland; Herrel et al. 2001). To define a bite point such that transducer calibration and bite-force measurements were comparable, and to avoid damaging the lizards' teeth, transducers were prepared by gluing a strip of leather (1 mm × 3 mm × 25 mm) at the end of each plate's outer surface (Lappin 1999; Lappin and Husak 2005; fig. 2; see the videos in the online edition of the *American Naturalist*). A series of weights suspended on the

strip with fishing line served to calibrate amplifier output to reflect the bite forces applied to the same area.

Lizards were warmed to their field-active body temperature (~37°C), verified using a cloacal thermometer, and three bite-force trials per individual were performed in sequence with 1 min rest between trials. All lizards bit the transducer vigorously during all trials. Given that the position along the jaw line at which bites occur significantly affects bite force, we standardized each trial by calculating the bite force at the jaw midpoint between the quadrate-articular jaw joint and the lower jaw tip (for methods, see Lappin 1999; Lappin and Husak 2005). For each individual, the greatest standardized bite-force value, assumed to represent maximum voluntary bite-force performance (see Losos et al. 2002), was used in the analyses.

Spectrometry and Analyses of Visual Contrast

Methods for spectrophotometric measurements of lizards from this study population are detailed elsewhere (see Macedonia et al. 2004). Briefly, reflectance spectra were obtained using a reflectance probe (Ocean Optics R200-7, Dunedin, FL) connected to a xenon lamp (Ocean Optics PX-2), a portable spectrometer (Ocean Optics USB2000), and a notebook computer running Ocean Optics OOIBASE32 software. We measured the reflectance spectra of the mouth-corner patches and the coronoid bones, which define the breadth of the AMC at its lateral and medial edges, respectively (fig. 1*A*). To examine the potential for the patches and coronoid bones to delineate AMC breadth visually, we also measured the reflectance spectra of the external integument (on the mandible) adjacent to the mouth-corner patches and the melanic oral epithelium adjacent to the coronoid bones. A small ruler attached to the reflectance probe maintained a constant 5-mm distance between the end of the probe and the target. To ensure that body temperature during spectral readings was comparable to that during basking (35°–40°C), subjects were warmed to ~37°C, and temperature was monitored with a cloacal thermometer.

We estimated how *C. collaris* would perceive the contrast between adjacent anatomical features inside and outside the mouth by incorporating *C. collaris* photoreceptor data (E. R. Loew, unpublished data) into the visual contrast analysis. Normalized visual pigment absorption curves were generated using spectral peak (λ_{max}) values following the method of Stavenga et al. (1993). Oil droplet transmission spectra were multiplied by their associated visual pigments to calculate the response function for each of the four photoreceptor classes. These response functions then were multiplied by the reflectance of the mouth-corner patches, external integument, coronoid bones, and melanic oral epithelium, producing one value for each photoreceptor-by-target combination. To satisfy the assumption that white light stimulates each cone class equally (Fleishman and Persons 2001), each photoreceptor-by-target sum was corrected (i.e., normalized) by multiplying it by the reciprocal of the area under the curve for the relevant visual pigment. The relative stimulation of each cone class by a given target reflectance was calculated by dividing the normalized sum for each individual cone class by the combined sum of the four cone classes. These relative stimulation values are referred to here as X_{UV} (UV-sensitive visual pigment), X_S (short-wavelength-sensitive pigment), X_M (middle-wavelength-sensitive pigment), and X_L (long-wavelength-sensitive pigment). Chromatic contrast between the mouth-corner patches and external integument and between the coronoid bones and melanic oral epithelium was calculated as

$$Cc = [(X_{UV1} - X_{UV2})^2 + (X_{S1} - X_{S2})^2 + (X_{M1} - X_{M2})^2 + (X_{L1} - X_{L2})^2]^{1/2},$$

where X is the relative stimulation of photoreceptor i (see also Fleishman and Persons 2001; Uy and Endler 2004). To determine brightness contrast between adjacent anatomical features, the brightness of each feature was calculated first by summing the four (nonnormalized) photoreceptor-by-target sums. The mathematical difference in brightness between two adjacent features then was divided by the sum of brightness for those two features. The absolute value of this quotient was our measure of brightness contrast (i.e., scale of 0 to 1).

Statistical Analyses

For statistical analyses, lizards were categorized into three exclusive groups (Baird et al. 1996; Husak and Fox 2003): adult males (>100 mm SVL, $N = 22$), yearling males (80–100 mm SVL, $N = 20$), and sexually mature females (>80 mm SVL, $N = 38$). We separated males from females because only males engage in fights during which injurious biting can occur (Baird et al. 2003; Husak and Fox 2003; Lappin and Husak 2005). In addition, we separated adult males (2+ years old) from yearling males because adult males are territorial and exhibit high levels of agonism, whereas yearling males typically are not territorial, rarely display, and avoid confrontations (Baird et al. 1996). We compared results among the three demographic groups because the behavioral differences suggest that relationships between putative morphological signals of bite force (i.e., weapon performance in adult males) and actual measures of bite force might differ. Statistical analyses were performed using JMPIN, version 4.0.2 (SAS Institute,

Cary, NC), and Statistica, version 7.1 (StatSoft, Tulsa, OK). Data were log-transformed for all analyses.

To test the hypothesis that during frontal gaping displays by adult male collared lizards, the breadth of the AMC has the potential to convey an index of bite-force performance that is more informative than cues potentially provided by body size and head size, we ran three multiple regression analyses (standard least squares and reverse stepwise for each). In the first, bite-force performance was the dependent variable, and all of the measures of body and head size and AMC breadth were the independent variables. Next, we performed the analysis with only the head size measures and AMC breadth as the independent variables. This served to compare the predictive power of traditional head measures, visible externally, to that of AMC breadth, visible only during gaping displays. Finally, we used residuals of head dimensions and AMC breadth on SVL as the independent variables specifically to examine traditional head measures versus AMC breadth as predictors of bite force (i.e., residuals of bite force on SVL) with the effect of body size removed. The latter two models can be thought of as tests designed to compare potential performance-assessment cues that describe the weapon itself (i.e., the head). For significant full models, we examined partial correlations among the variables to evaluate the predictive power of each independent variable while taking into account the others.

We performed several diagnostics to determine the validity of our multiple regression models. We determined the degree of multicollinearity among independent variables by examining the correlation matrix of independent variables and variance inflation factors (VIFs) for each variable in the regression models (Neter et al. 1996). Large correlation coefficients ($r > 0.7$) and VIFs >10 indicate that multicollinearity may be influencing model estimates (Neter et al. 1996). Because of our somewhat small sample size, we also used the PRESS statistic to determine the predictive power of our models. The PRESS statistic is based on recalculation of the regression model after deletion of the *i*th case and predicting the deleted *i*th case based on the newly fitted model. PRESS statistics are the sum of the squared prediction errors over all *i* cases. Small PRESS values and those similar to the error sum of squares (SSE) of the original model indicate that prediction errors are small (Neter et al. 1996). For stepwise models, we determined goodness of fit with Mallow's Cp (Neter et al. 1996).

Our proposal that the mouth-corner patches function as an amplifier, by enhancing the visual perception of the breadth of the AMC, does not require that the patches contain information about quality. However, due to their visual prominence during gaping displays and association with the AMC, we supposed that they might. To test the hypothesis that the mouth-corner patches themselves have the potential to convey information about weapon performance, in addition to cues provided by overall size, we constructed best-fit linear models of bite-force performance. To generate a measure of overall size, we condensed the body and head size variables into fewer orthogonal variables using principal components analysis. AMC breadth was not included in this analysis, such that the condensed size variable reflected only externally assessable measures of size. We extracted components with eigenvalues >1.0, which resulted in single components explaining 87.1% and 82.3% of the original variance in adult and yearling males, respectively, and two components collectively explaining 89.7% of the original variance in females. We then included these component(s) as model predictors, along with the five patch variables (lateral patch distance, medial patch distance, patch width, anterior patch area, lateral patch area), and found the best-fit (i.e., most informative) model of bite force based on the minimization of the Akaike Information Criterion (AIC). The AIC is an information theoretic derivative of the log-likelihood function that provides the best measure of model fit in the case of observational data (Burnham and Anderson 2002). We assessed the significance of individual variables in these models using the Wald statistic. This maximum likelihood–based modeling approach does not produce an analogue of the (least squares) R^2 value. Therefore, to illustrate the informative value of patch variables, we calculated and compared two adjusted R^2 values (least squares regression), one for the model including only the size component(s) and one for the best-fit model that included both the size component(s) and the patch dimensions. For example, if the adjusted R^2 for the model including only the size component(s) was 0.80 and that for the best-fit model including both the size component(s) and patch dimensions was 0.85, then the patch variables would explain an additional 5% of the variance in bite force beyond what could be predicted using size alone.

Results

The results of the multiple regression analyses supported the hypothesis that the breadth of the adductor mandibulae complex, visible during frontal gaping displays, is a better predictor of adult male weapon performance (i.e., bite force) than body size or external weapon (i.e., head) size. For the multiple regression that included all body and head size measures plus AMC breadth as independent variables, a significant full model was generated for adult males ($P = .0005$, SSE = 0.070, PRESS = 0.144) in which AMC breadth closely approached significance as a predictor of bite force ($P = .063$; table 1). The partial correlation between AMC breadth and bite force in adult

Table 1: Results of standard least squares multiple regression evaluating measures of body and head size and the breadth of the adductor mandibulae complex (AMC) as predictors of bite-force performance in collared lizards at the Wichita Mountains National Wildlife Refuge

Demographic group and independent variable	*F* ratio	*P* value
Adult males ($F = 8.194$, df = 6, 21, MSE = 0.005, $P = .0005$):		
SVL	.127	.726
Mass	.130	.724
Head length	.586	.456
Head width	.343	.567
Head depth	.384	.545
AMC breadth[a]	4.026	.063
Yearling males ($F = 4.429$, df = 6, 19, MSE = 0.006, $P = .0118$):		
SVL	1.495	.243
Mass	.076	.787
Head length	2.444	.142
Head width	.046	.834
Head depth	.434	.522
AMC breadth	.119	.736
Females ($F = 6.271$, df = 6, 37, MSE = 0.005, $P = .0002$):		
SVL	.673	.418
Mass	.590	.448
Head length	.328	.571
Head width	3.155	.086
Head depth	6.293	.018
AMC breadth	.361	.553

[a] SVL = snout-vent length. AMC breadth is a noninvasive measure that previously has not been used in studies of bite force in lizards. Removing AMC breadth from the adult male model, and thus including only traditional measures of body and head size, results in a significant model ($F = 10.376$, df = 6, 21, $P < .0001$) in which only head width predicts bite force ($P = .018$; others: $.110 < P < .647$).

males was distinctly greater than that between any body or head size measure and bite force (AMC breadth: 0.460; all other variables: $-0.092 \le r_p \le 0.194$). Notably, AMC breadth was not significantly correlated with any measure of body or head size in adult males, except weakly so with head width (SVL: $r = 0.163$, $P = .470$; mass: $r = 0.297$, $P = .179$; head length: $r = 0.225$, $P = .314$; head width: $r = 0.500$, $P = .018$; head depth: $r = 0.250$, $P = .263$). For yearling males, a significant full model resulted ($P = .0118$, SSE = 0.077, PRESS = 0.250), but no morphological measurement emerged as a predictor of bite force. For females, a significant full model ($P = .0002$, SSE = 0.156, PRESS = 0.221) contained head depth. This result was supported by a relatively strong partial correlation between head depth and bite force (head depth: 0.411; head width: 0.304; all other variables: $-0.137 \le r_p \le 0.146$). Stepwise models supported the results of full models: adult males—AMC breadth ($F = 26.629$, df = 1, 20, $P = .0001$, Cp = 0.550); yearling males—SVL ($F = 23.849$, df = 1, 18, $P = .0001$, Cp = 1.022); and females—head depth ($F = 15.120$, df = 1, 35, $P = .0004$, Cp = 0.662) and head width ($F = 5.202$, df = 1, 35, $P = .0288$).

For the multiple regression models that included only head size measures plus AMC breadth as independent variables, a significant full model was generated for adult males ($P < .0001$, SSE = 0.071, PRESS = 0.114), with only AMC breadth as a significant predictor of bite-force performance ($P = .0227$; table 2). AMC breadth also had a relatively large partial correlation with bite force (AMC breadth: 0.519; all other variables: $0.162 \le r_p \le 0.228$). For yearling males, a significant full model resulted ($P = .0109$, SSE = 0.103, PRESS = 0.284) with head depth as a significant predictor of bite force ($P = .0343$), which was reflected by a strong partial correlation between head depth and bite force (head depth: 0.515; all other variables: $-0.263 \le r_p \le 0.226$). For females, a significant full model ($P < .0001$, SSE = 0.159, PRESS = 0.209) contained head depth ($P = .0107$) and head width ($P = .0323$), which was supported by relatively strong partial correlations between these head dimensions and bite force (head depth:

Table 2: Results of standard least squares multiple regression evaluating measures of head size and adductor mandibulae complex (AMC) breadth as predictors of bite-force performance in collared lizards at the Wichita Mountains National Wildlife Refuge

Demographic group and independent variable	*F* ratio	*P* value
Adult males ($F = 13.662$, df = 6, 21, MSE = 0.004, $P < .0001$):		
Head length	.933	.348
Head width	.461	.506
Head depth	.790	.387
AMC breadth[a]	6.278	.023
Yearling males ($F = 4.790$, df = 6, 19, MSE = 0.007, $P = .0109$)		
Head length	1.116	.308
Head width	.806	.384
Head depth	5.422	.034
AMC breadth	.001	.971
Females ($F = 9.605$, df = 6, 37, MSE = 0.005, $P < .0001$):		
Head length	.173	.681
Head width	4.995	.032
Head depth	7.315	.011
AMC breadth	.779	.384

[a] Removing AMC breadth from the adult male model, and thus including only traditional measures of body and head size, results in a significant model ($F = 12.468$, df = 6, 21, $P < .0001$) in which only head width predicts bite force ($P = .019$; others: $.459 < P < .863$).

0.426; head width: 0.363; all other variables: $-0.152 \leq r_p \leq -0.072$). Stepwise models generated concurring results: adult males—AMC breadth ($F = 15.983$, df = 1, 20, $P = .0008$, Cp = 2.480); yearling males—head depth ($F = 19.319$, df = 1, 18, $P = .0003$, Cp = 0.477); and females—head depth ($F = 15.120$, df = 1, 35, $P = .0004$, Cp = 1.992) and head width ($F = 5.202$, df = 1, 35, $P = .0288$).

For the multiple regression models in which size-corrected measures (i.e., residuals of head dimensions and AMC breadth on SVL) were the independent variables, a significant full model was generated for adult males ($P = .0034$, SSE = 0.070, PRESS = 0.112) in which only residual AMC breadth was a significant predictor of residual bite force ($P = .0487$; table 3). Partial correlations supported these results (residual AMC breadth: 0.458; all other variables: $0.179 \leq r_p \leq 0.237$). For yearling males, a significant full model was not generated ($P = .3790$, SSE = 0.077, PRESS = 0.182). For females, a significant full model ($P = .0308$, SSE = 0.159, PRESS = 0.203) contained residual head depth ($P = .0188$) and residual head width ($P = .0446$), and partial correlations corroborated this result (residual head depth: 0.395; residual head width: 0.342; all other variables: $-0.146 \leq r_p \leq -0.094$). Stepwise models supported the results of full models: adult males—residual AMC breadth ($F = 16.013$, df = 1, 20, $P = .0008$, Cp = 2.545); yearling males—no significant model; and females—residual head depth ($F = 7.513$, df = 1, 35, $P = .0096$, Cp = 2.107).

The results of the multiple regression analyses demonstrate that AMC breadth is a strong and independent predictor of bite force in adult males but that body and head size measures are better predictors of bite force in yearling males and females. Small PRESS values, similar to the original SSEs, indicate that all of the regression models had high predictive power. Examination of the correlation coefficients for the independent variables show that absolute head size measures were highly correlated with each other and with body size in each of the three demographic groups ($r > 0.7$ for all), and VIFs were correspondingly large for several of these variables (adult males: 2.200–10.530; yearling males: 3.484–32.628; females: 2.248–12.493). However, AMC breadth was not highly correlated with body size or any of the head measures in adult males ($0.16 < r < 0.50$) or females ($0.12 < r < 0.67$), but it was for yearling males ($0.57 < r < 0.78$). The VIFs for AMC breadth gave concurring results (adult males: 2.200; yearling males: 3.833; females: 2.248). Taken together, our models using absolute measures did display some multicollinearity, as is expected for multivariate analyses that include morphometrics, but this effect was negligible for the AMC breadth variable. The fact that AMC breadth was not highly correlated with body or head size, except in yearling males, emphasizes its predictive power relative to that of the size measurements. One potential effect of multicollinearity among independent variables is that it may invalidate significance tests of their partial correlation coefficients. Therefore, our analysis using size-corrected variables was designed to determine whether multicollinearity was responsible for any head measures being nonsignificant predictors of bite force. These models were more robust, as they did not exhibit multicollinearity ($r < 0.7$ for all), and all VIFs were small (adult males: 1.189–2.454; yearling males: 1.083–1.925; females: 1.222–1.930). These results support the conclusions of the other (not size-corrected) regression models. The result that AMC breadth is a strong and independent predictor of bite force, specifically in adult males, is consistent with the hypothesis that frontal gaping displays could serve as an index of weapon performance by exposing the AMC. The lack of correlation between AMC breadth and body and head size indicates that an assessment of size cannot predict what additional information the AMC may provide about bite force during a gaping display.

The mouth-corner patches of collared lizards, a putative amplifier of AMC breadth, are extremely bright and exhibit UV-reflecting properties that are within the visual range

Table 3: Results of standard least squares multiple regression evaluating residuals of head dimensions and adductor mandibulae complex (AMC) breadth on body size (snout-vent length) as predictors of bite-force performance in collared lizards at the Wichita Mountains National Wildlife Refuge

Demographic group and independent variable	*F* ratio	*P* value
Adult males ($F = 5.990$, df = 6, 21, MSE = 0.004, $P = .0034$):		
Residual head length	1.008	.330
Residual head width	.568	.462
Residual head depth	.850	.370
Residual AMC breadth[a]	4.509	.048
Yearling males ($F = 1.131$, df = 6, 19, MSE = 0.005, $P = .3790$):		
Residual head length	2.925	.108
Residual head width	.119	.735
Residual head depth	1.771	.203
Residual AMC breadth	.061	.808
Females ($F = 3.039$, df = 6, 37, MSE = 0.005, $P = .0308$):		
Residual head length	.294	.592
Residual head width	4.356	.044
Residual head depth	6.104	.018
Residual AMC breadth	.717	.403

[a] Removing residual AMC breadth from the adult male model, and thus including only residuals of traditional measures of head size, results in a significant model ($F = 5.426$, df = 6, 21, $P = .0078$) in which only head width predicts bite force ($P = .008$; others: $.371 < P < .528$).

of iguanian lizards (fig. 3; Fleishman et al. 1993 for *Anolis*; Loew et al. 2002). The reflectance spectrum of the patches, which highlight the lateral aspect of the AMC, contrasts sharply with that of the adjacent integument. The coronoid bones, which define the medial margin of the AMC, are similar in spectral shape to the mouth-corner patches and contrast strongly with the adjacent oral epithelium.

The maximum likelihood–based modeling approach supported the hypothesis that the mouth-corner patches of adult male collared lizards have the potential to convey size-independent information about weapon performance. For adult males, the best-fit model of bite force (AIC = 141.6, $\chi^2 = 28.7$, df = 4, $N = 21$, $P < .00001$) included the size principal component (Wald = 33.69, $P < .000001$), lateral patch distance (Wald = 2.90, $P = .09$), patch width (Wald = 3.14, $P = .08$), and lateral patch area (Wald = 7.86, $P < .005$). The inclusion of patch variables in this model, especially lateral patch area (patch area from the lateral view), indicates that the patches carry information about bite force that is independent of (and in addition to) that predicted by overall size. The predictive utility of these variables is further illustrated by comparing the adjusted R^2 value (least squares regression) for the model including only the size component (0.53) with the best-fit model (as above; $R^2 = 0.71$). Thus, in the sample of adult males, the patch variables explain an additional

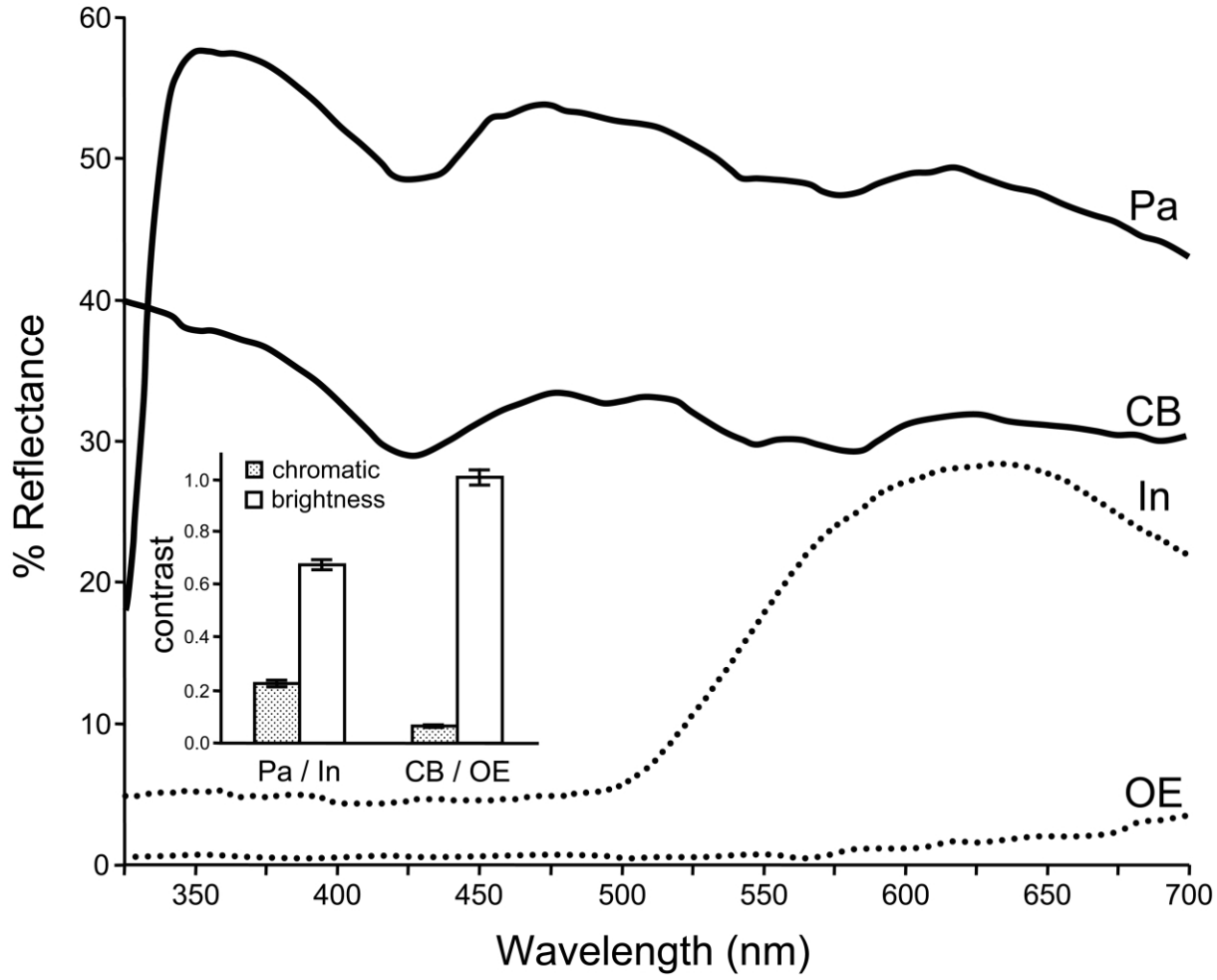

Figure 3: Reflectance spectra of mouth-corner patches (*Pa*) and coronoid bones (*CB*; *solid lines*), which define adductor mandibulae complex breadth, and adjacent anatomical features (*dotted lines*) of adult male collared lizards. Inset shows chromatic and brightness contrasts between adjacent features. Visual pigment peak absorbance values (λ_{max}) of spectral sensitivity curves used in contrast analyses: UVS = 357 nm, SWS = 459 nm, MWS = 480 nm, LWS = 556 nm (E. R. Loew, unpublished data). During frontal gaping displays, the patches contrast with the integument (*In*), and the coronoid bones contrast with the melanic oral epithelium (*OE*). During lateral gaping displays, the patches contrast with the surrounding integument. Samples sizes: Pa ($N = 22$), In ($N = 22$), CB ($N = 20$), OE ($N = 10$).

18% of the variance in bite force beyond what is predicted using size alone. In contrast, the best-fit model for bite force in yearling males (AIC = 116.0, $\chi^2 = 10.1$, df = 1, $N = 17$, $P < .005$) included size as the sole predictor (Wald = 10.84, $P < .001$). The adjusted R^2 value of this model (0.41) actually exceeded that of the four next-best-fit models, each of which included an additional patch variable ($0.37 > R^2 > 0.38$). Thus, in yearling males, the patches are no more informative of bite force than size alone. In females, the best-fit model of bite force (AIC = 159.9, $\chi^2 = 41.8$, df = 4, $N = 40$, $P < .00001$) included the two size components (Wald = 32.5 and 16.5, $P < .00005$), patch width (Wald = 4.0, $P < .05$), and anterior patch area (Wald = 5.5, $P < .05$). However, the adjusted R^2 of this model (0.51) only marginally exceeded that of a model including only the size components (0.48). Thus, although the patch variables are significantly predictive of bite force, the amount of additional variance accounted for by patch variables is only 3%. These results show that the patches are significantly and independently predictive of bite-force performance only in adult males.

Discussion

Our results show that the breadth of the adductor mandibulae complex in territorial adult male collared lizards, as visible during frontal gaping displays, is a strong predictor of bite force. In addition, AMC breadth in adult males is not predictable based on measures of body or head size. For yearling males and females, which typically are not territorial and do not engage in fights (Baird et al. 1996; Baird and Timanus 1998), bite force is statistically predicted by traditional measures of body and head size. The visually conspicuous mouth-corner patches of collared lizards, situated on the lateral aspect of the AMC and visible during both frontal and lateral gaping displays, are the most brightly reflective region of the integument (see Macedonia et al. 2004 for reflectance spectra from other parts of the integument). Together with the reflective coronoid bones, the patches contrast with adjacent tissues and delineate the breadth of the hypertrophied AMC of adult males during frontal gaping displays. The patches themselves have the potential to provide size-independent information on bite force in adult males.

We propose that the exposure of the AMC during frontal gaping displays by adult male collared lizards provides a paradigmatic example of an index. By definition, an index is a signal (i.e., evolved for a signaling function) that is uncheatable, in that its degree of expression is causally related to the attribute being signaled (Maynard Smith and Harper 1995, 2003; Vehrencamp 2000). A gaping display per se does not qualify as an index of weapon performance because it is not constrained to honestly advertise bite force (i.e., ability to gape is not limited by bite-force performance). Moreover, the AMC alone cannot be considered an index, as there is no evidence that it evolved (large size) to function as a signal of bite force. Therefore, we suggest that gaping displays (a signal) potentially serve as an index of weapon performance to rivals, specifically in the context of revealing AMC breadth (a physically constrained cue), which is predictive of weapon performance. We suggest that it is generally useful to distinguish between which aspect of a putative index qualifies it as a signal versus which aspect, constrained by physical ability, actually holds information about quality. The decomposition of indexes into these components may prove helpful in identifying mechanisms by which honest information about quality is transmitted, particularly when performance measures shown to be predictive of dominance or reproductive success are incorporated into the analysis.

The assessment of weapon performance depends on characteristics that are available to function as signals. When weapons are difficult to assess, as is the case when key effectors of performance are concealed (e.g., muscles), specialized structures and behaviors may function to expose and accentuate any available attributes that determine weapon performance. The cross-sectional area of a muscle is the principal determinant of its force-generating capacity (Eckert 1988); therefore, the cross-sectional area of a lizard's jaw-adductor musculature is expected to be the principal determinant of its bite-force performance. Because the cross-sectional area of a muscle cannot be assessed externally, the breadth of a muscle or muscle complex may be the best correlate to muscle cross-sectional area that is visibly apparent to rivals during agonistic interactions. In the case of adult male collared lizards, AMC breadth is a direct correlate of the primary mechanistic basis for weapon performance.

The breadth of the AMC is dependent on the degree of development and the condition of the jaw musculature (fig. 1*B*). In a manner similar to whole-body measures of condition commonly used in ecological studies (Abell 2000; Schulte-Hostedde et al. 2005), the condition of the jaw-adductor musculature is variable among individuals as well as temporally plastic within individuals. Therefore, during agonistic frontal gaping displays, adult male collared lizards provide each other an index of weapon performance, amplified by bright patches, that is sensitive to variation in the development and condition of the primary effector of weapon performance.

The mouth-corner patches satisfy the design criteria of amplifiers (sensu Hasson 1989, 1997; Taylor et al. 2000; Harper 2005), as they enhance the visibility of the AMC during frontal gaping displays by virtue of their spectral properties and anatomical position. Spectral analysis indicates that these bright patches, which contrast conspic-

uously with the adjacent external integument, exhibit UV-reflecting properties that collared lizards can perceive. The fact that the patches are visually so conspicuous, yet are exposed only when a lizard gapes, is consistent with a signaling function. Analogous to a lizard extending its brightly colored dewlap, gaping affords control over the use of the signal during interactions. Although not required of amplifiers, the patches also provide size-independent information about weapon performance. This is perhaps an indirect effect resulting from their physical association with the lateral aspect of the AMC. A single patch is prominently visible during lateral gaping displays, an orientation that does not permit rivals to gauge the breadth of the AMC. Interestingly, of the patch dimensions that we measured, patch area from the lateral view was the most informative of weapon performance.

Indexes of weapon performance based on jaw-adductor muscle morphology, as well as contrasting tissues that amplify the appearance of the jaw-adductor musculature, may be widespread among lizards that employ gaping during agonistic territorial displays. In particular, we expect that other iguanian lizards are good candidates for possessing such indexes and associated amplifiers. Gaping is prevalent in the territorial display repertoires of iguanians, and they typically possess acute vision that plays a prominent role in communication (Carpenter and Ferguson 1977; Fleishman 1992). Most significantly, Fleishman et al. (1993) noted the presence of bright UV-reflective spots at the mouth corners of five *Anolis* species that are visible only when the mouth is open. An ability to perceive UV wavelengths, as is the case with all iguanian lizards examined to date (Fleishman et al. 1993; Loew et al. 2002), is expected to augment the salience of signals with UV-reflective properties, especially when they contrast with surrounding tissues and/or the environment. A broad survey conducted within a phylogenetic framework would serve well to investigate the evolution of this signaling structure, particularly with respect to its association with agonistic behavioral repertoires.

Gaping displays may provide a means for conflict resolution that reduces costs for both competitors, particularly with respect to the risk of injury that goes with engaging in a fight. A gaping display by an adult male collared lizard contains information about fighting ability, as it exposes the AMC, a reliable and visually enhanced morphological cue of weapon performance. Correspondingly, by eliciting a gaping response by an opponent, information can be acquired about the capacity that opponent has to deliver damaging bites. The lack of a relationship between AMC breadth and body or head size in our sample of adult males indicates that information about weapon performance that can be garnered during a gaping display may not be otherwise available. During conflicts that are not easily resolved (e.g., between rivals similar in body size), information about weapon performance that may be conveyed during a gaping display may conclude an interaction before it escalates to a potentially costly fight.

Our results do not exclude alternative functions of gaping displays, such as preparing an animal to fight (Szamado 2003) or advertising intent to escalate (Enquist 1985). Neither of these alternatives, however, predicts the observed relationship between AMC breadth and bite force nor explains the apparent evolution of specialized structures to visually enhance the AMC. By revealing and amplifying its biomechanical basis, gaping displays have the potential to transmit information about weapon performance to rivals. If gaping displays indeed function in the advertisement and assessment of weapon performance, then experimental augmentation of the appearance of the AMC should produce appropriate changes in the responses of rivals. Moreover, given that gaping displays used in an intrasexual agonistic context are common among a diversity of vertebrates (e.g., fish, lizards, mammals [carnivores, primates]), an important role of such displays may be to advertise and facilitate the assessment of structures that predict quantifiable aspects of weapon performance.

A growing number of studies indicate that whole-organism performance variables (sensu Huey and Stevenson 1979; Arnold 1983; Pough 1989; e.g., bite force, chela strength, sprint speed, locomotor endurance) are important determinants of dominance, contest outcome, reproductive success, and prey-predator signaling in a diversity of animal taxa (Garland et al. 1990; Leal 1999; Robson and Miles 2000; Sneddon et al. 2000; López and Martín 2002; Brandt 2003; Kemp and Alcock 2003; Lailvaux et al. 2004, 2005; Perry et al. 2004; Lappin and Husak 2005). Thus, we expect display structures and associated behaviors that honestly signal whole-organism performance, particularly that of weapons, to be common across the animal kingdom. The direct measurement of whole-organism performance should be incorporated into more studies of signaling, accompanied, when possible, by explicit hypotheses of the mechanistic links between signal design and the information that signals convey.

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Adult male collared lizard (*Crotaphytus collaris*) from the Wichita Mountains National Wildlife Refuge. Photograph by A. K. Lappin.