

Weapon Performance, Not Size, Determines Mating Success and Potential Reproductive Output in the Collared Lizard (*Crotaphytus collaris*)

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ABSTRACT: In territorial polygynous taxa, reproductive success reflects phenotypic variation. Using *Crotaphytus collaris*, a sexually dimorphic lizard in which males use the head (i.e., jaws and associated musculature) as a weapon when territorial interactions escalate to fights, we tested the hypothesis that weapon performance (i.e., bite force) is a better predictor of fitness than body or weapon size. Bite-force performance predicted the number of female home ranges overlapped, estimated mating success, and potential reproductive output. However, no body or weapon size measure correlated with these estimates of fitness, and only one weapon dimension (head width) correlated with bite force. These results indicate that weapon performance has far stronger effects on fitness than body or weapon size, likely because it directly influences fight outcomes. As such, it is desirable that the use of morphology as a proxy for performance and its presumed extensions to fitness be based on empirical morphology-performance relationships.

Keywords: weapons, performance, territoriality, mating success, sexual selection.

In sexually dimorphic species, the evolution of exaggerated structures serving as weapons is usually attributed to sexual selection pressures related to male combat (Andersson 1994). There is a great deal of evidence that such structures are used during male combat (e.g., Eberhard 1979; Silverman and Dunbar 1980; Clutton-Brock 1982; Zeh 1987; Conner 1988; Poole 1989; Carrier et al. 2002) and that

they are often important in determining dominance (e.g., Brown and Bartalon 1986; Crespi 1986). One well-studied example of the potential role of weapon morphology in determining fitness involves head size in lizards. Among polygynous lizards, males tend to have larger heads than females, and male-biased head dimorphism is associated with male combat (Stamps 1983; Carothers 1984; Vitt and Cooper 1985; Kratochvíl and Frynta 2002). Studies have related head size to laboratory-determined dominance (e.g., Molina-Borja et al. 1998; Alberts et al. 2002; López and Martín 2002; Gier 2003; Perry et al. 2004), field-measured dominance (Vitt and Cooper 1985), territory status (Hews 1990), and mating success (LeBas 2001). Studies relating morphology and performance to dominance assume that dominance, as determined in the laboratory, is an important component of fitness in nature (e.g., Garland et al. 1990; Robson and Miles 2000; Perry et al. 2004).

It has largely been accepted that, in many instances, selection acts upon whole-animal performance, which is determined by lower levels of biological organization (Huey and Stevenson 1979; Arnold 1983; Pough 1989). By extension, it is expected that in territorial species with polygynous mating systems, individual variation in mating success and reproductive output should reflect individual variation in morphological and physiological traits. Two studies that have shown a positive relationship between dominance and head size in lizards suggested that it may be due to individuals with larger heads being able to bite harder and thus having superior fighting ability (Hews 1990; Perry et al. 2004). In several lizard taxa, a positive relationship between bite force and head size has been demonstrated (Herrel et al. 1999, 2001*b*; Lappin 1999), and bite force has been correlated with dominance in laboratory-staged encounters in lizards (Lailvaux et al. 2004; J. F. Husak, A. K. Lappin, S. F. Fox, and J. A. Lemos-Espinal, unpublished manuscript). However, despite the establishment of links among head size, bite force, and dominance, there has been no test of the hypothesis that bite-force performance is significantly correlated with any measure of potential fitness in nature. Here, we empirically test the hypothesis that a direct measure of weapon per-

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formance is a better predictor of estimates of fitness than either body size or weapon size.

The collared lizard (*Crotaphytus collaris*) is a territorial, polygynous lizard in which adult males defend exclusive territories. Females, whose entire home ranges are usually encompassed by one male's territory, also are defended, presumably for exclusive mating access. Agonistic interactions between males over territorial boundaries can escalate to fights with violent biting that can produce serious wounds (Baird et al. 2003; Husak and Fox 2003a; fig. 1). Such injuries may incur a fitness cost because they likely affect future interactions by reducing fighting ability (Stamps and Krishnan 2001; Morrell and Kokko 2003). Associated with strong territoriality in collared lizards and the role of biting in male-male agonistic interactions is notable sexual dimorphism, with males being larger and having disproportionately large and robust heads (Fitch 1956; McCoy et al. 1994; Lappin 1999; fig. 2).

Because the head (i.e., jaws and associated musculature) constitutes the weapon used by male *C. collaris* during fights, and because bites can inflict significant damage to conspecifics, we predicted that bite-force performance would play an important role in a male's ability to establish and maintain a large territory overlapping the home ranges of many females. By extension, we predicted that estimates of annual mating success and potential reproductive output in male *C. collaris* would be positively related to their bite-force capacity (i.e., weapon performance) and that bite force would be a better indicator of these estimates of Darwinian fitness than either body size or weapon (i.e., head) size. We tested these predictions by combining morphometric and bite-force data with spatial and behavioral data in a population of collared lizards.

Methods

Study Species and Population

From April through July of 2003, we studied a population of *Crotaphytus collaris* at Sooner Lake Dam, 24 km south of Ponca City, Oklahoma. This population is well suited for studies involving the spatial distribution of individuals (e.g., Husak and Fox 2003a, 2003b) because the entire contiguous population is surrounded by unsuitable habitat, specifically a reservoir on one side and thick grassland devoid of rocks suitable for perches and refugia on the other.

In April and May of 2003, lizards were captured with a pole and noose, and each lizard was assigned a unique toe clip combination. A unique sequence of color spots was applied to the hind limbs for identification from a distance. Lizards were held in mesh bags until after morphometric and bite-force data were collected. Each subject

was released at the precise location of its capture within 30 h of removal.

Following Baird et al. (1996), each male lizard was categorized as territorial or nonterritorial (i.e., yearling) on the basis of territory-holding status, identifiable by the extremely low degree of overlap among territorial males and the high levels of advertisement at territory boundaries (Fox and Baird 1992; Baird et al. 2001; Husak and Fox 2003a). In contrast, yearling male home ranges show considerable overlap (Baird et al. 1996). As is typical for this species in Oklahoma, all adult males were territorial. All yearling males from which we collected data (14) were not territorial, except one (see "Discussion"), which we included in the analyses. Sample sizes thus consisted of 11 territorial males and 47 females (sexually mature yearlings and adults), for which we determined home range areas and their overlap with the territories of the males in the sample. The sample of females was also used to calculate estimates of mating success and the potential reproductive output of the territorial males, which is described below.

Territories, Home Ranges, and Potential Fitness

To determine territory and home range areas, we walked through the site daily in May and June and recorded lizard locations on a scale map of the study area. Lizard locations were mapped relative to triangulated landmarks so that minimum convex polygon territories could be delineated (Rose 1982; Stone and Baird 2002). Territory and home range areas were determined with a minimum of 20 sightings per lizard, the sample size at which these areas asymptote in this population (J. F. Husak, unpublished data), and calculated using the animal movement extension in ArcView GIS (Environmental Systems Research Institute, Redlands, CA).

The first estimate of annual mating success of territorial male lizards was simply the number of sexually mature females whose home ranges overlapped the territory of each male. All females whose home ranges overlapped a male's territory were included in that male's estimated mating success. For this estimate, we did not adjust for the number of male territories overlapped by each female's home range, which was always one or two.

Our second estimate of annual male mating success was based on the proportion of courtship encounters initiated with each female (Baird et al. 1996). Ten 20-min focal observations were conducted on each territorial male, and the number of courtship encounters between individuals was recorded. For each female, we determined the proportion of courtships accounted for by each male and recorded that as each male's probability of inseminating that female. For each male, the probabilities were summed to yield the estimated number of females inseminated (for

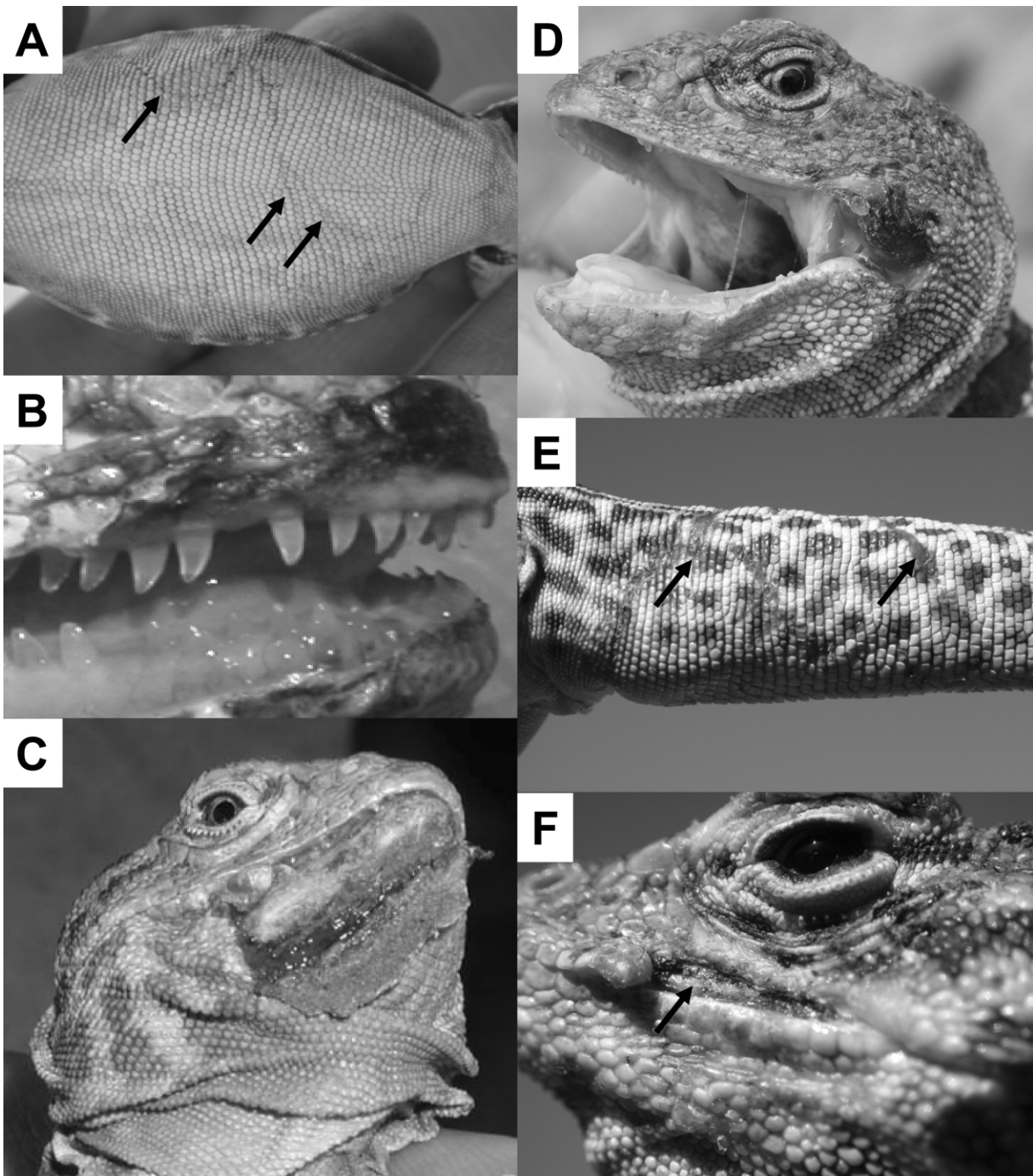


Figure 1: Examples of wounds incurred by adult male collared lizards via fighting. *A*, *Crotaphytus collaris* (Sooner Lake) with scars on ventral torso that match the dental arcade of a large male conspecific (arrows). *B*, *Crotaphytus bicinctores* (southwestern Arizona) with several labial scales and most of rostral scale torn away, exposing the anterior teeth (adult male neighbor had the same wound, suggesting that the two locked jaws). *C*, *Crotaphytus collaris* (Glass Mountains, Oklahoma) with skin of lower jaw torn away, exposing lower jaw bones. *D*, *Crotaphytus collaris* (Sooner Lake) with fresh wound on mouth corner that penetrates the jaw adductor musculature. *E*, *Crotaphytus dickersonae* (Kino Bay, Sonora, Mexico) with scars on tail that match the dental arcade of a conspecific (arrows). *F*, *Crotaphytus dickersonae* (Kino Bay, Sonora, Mexico) with bite wounds on head and jaw and upper labial scale row torn away, exposing the maxilla (arrow). More serious wounds can include broken bones, including those of the limbs and jaws. Color version of figure available in the online edition of the *American Naturalist*.

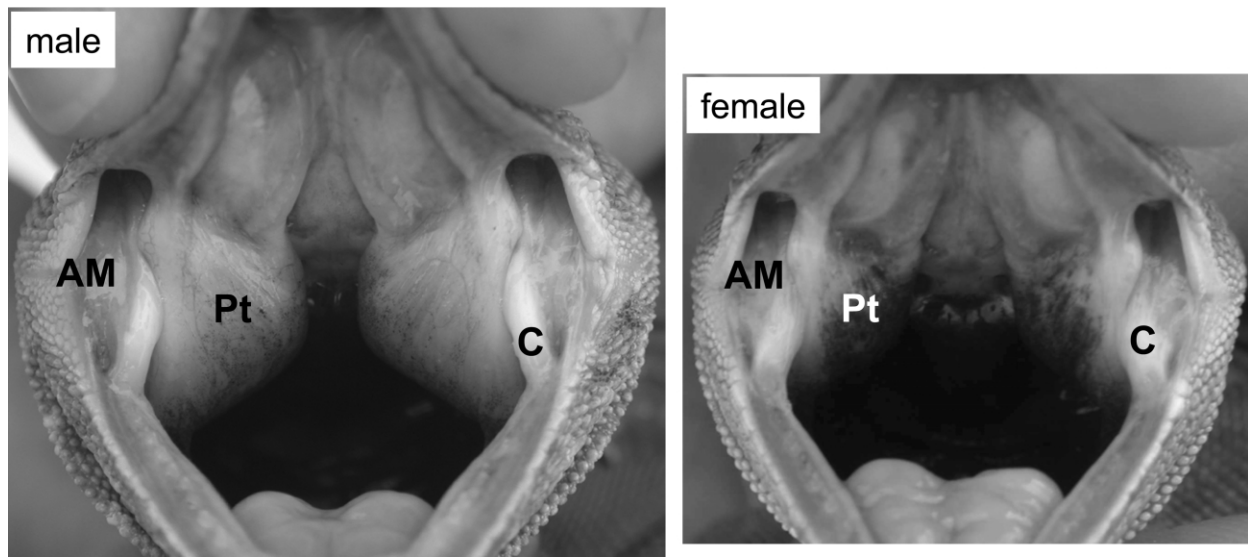


Figure 2: Gaping adult male and adult female *Crotaphytus collaris* from Sooner Lake. Note relatively enlarged jaws and jaw adductor muscles of male, which constitute a formidable weapon used in intrasexual combat. Abbreviations as follows: AM = muscles of adductor mandibulae complex, Pt = pterygoideus muscle, C = coronoid bone (insertion of components of adductor mandibulae complex). Color version of figure available in the online edition of the *American Naturalist*.

similar indices, see Clutton-Brock et al. 1982; Baird et al. 1996).

The potential reproductive output of each territorial male (an approximation of fitness taking into account variation in both female fecundity and spatial relationships) was estimated by summing the potential reproductive output of all the females whose home ranges overlapped with that male's territory. The potential reproductive output of females was estimated using the average of two similar relationships between female snout-vent length (SVL) and clutch size (CS) in *C. collaris* (Arkansas: Trauth 1978; Texas: Ballinger and Hipp 1985): $CS = 0.2105(SVL) - 11.45$. When a female's home range overlapped two males' territories, her potential reproductive output was divided between those males. Further, yearling females at Sooner Lake produce one clutch late in the year, whereas adults produce two to three clutches per year (J. F. Husak, unpublished data; see also McCoy et al. 2003). Therefore, we doubled the potential reproductive output for adult females and incorporated this into the potential reproductive output of each male.

Our measures of mating success and reproductive output of male collared lizards, used as estimates of fitness, were indirect. Ideally, quantification of the realized reproductive success of males in a population would be determined via genetic analysis of paternity. However, spatial and behavioral criteria have been applied in many estimates of reproductive success in male lizards (e.g., Trivers

1976; Ruby 1981, 1984; M'Closkey et al. 1990; Hews 1993; reviews: Stamps 1983; Abell 1998, 1999), and there is confirmation of their valid application (Abell 1997; Haenel et al. 2003). However, we are aware of their potential shortcomings (see LeBas 2001), and future empirical work will reveal to what general extent behavioral estimates of fitness predict true reproductive success in lizards. Unpublished data (J. M. Hranitz and T. A. Baird, personal communication) suggest that the estimates used in our study positively correlate with genetically determined paternity in a population of collared lizards in Oklahoma that inhabits a structurally similar habitat. That is, females are rarely inseminated by males that do not overlap their home ranges. The extremely low overlap of male territories in *C. collaris* populations studied to date suggests that adult males are unlikely to mate frequently with females in another male's territory, and, during our focal observations, we observed males interacting only with females whose home ranges they overlapped.

Morphometrics

Snout-vent length (SVL) and mass were recorded as measures of body size. 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 indexes of head

size (i.e., weapon size in adult males). 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.

Bite-Force Performance

Peak bite-force performance was measured using a piezoelectric isometric force transducer (type 9203, Kistler, Switzerland) custom fitted with two 25-mm-wide stainless steel bite plates and connected to a charge amplifier (type 5995, Kistler, Switzerland). This bite-force transducer is a modified version of that used by Herrel et al. (2001a).

Transducers were prepared by gluing a strip of leather (1 mm × 3 mm × 25 mm) at the end of each plate's outer surface. This defined a bite point such that calibration and bite-force measurements were comparable. A series of weights suspended at the strip with fishing line was used to calibrate amplifier output to reflect the force applied during bites to the same area.

Lizards were warmed to their field-active body temperature (~37°C), verified using a cloacal thermometer. Three bite-force trials per individual were performed in sequence with 1 min of rest between trials. All lizards vigorously bit the transducer during all trials. During each bite, the position of the leather strips along the jaw line was recorded from lateral view, and the saggital distance from the strips to the quadrate-articular joint (bite moment arm) was measured to the nearest 0.1 mm with digital calipers. Lever mechanics predict and data show (A. K. Lappin, unpublished data) that the position along the jaw line at which bites occur significantly influences bite force. To standardize for this variation, bite forces were calculated at the lower jaw midpoint (not including the retroarticular process; calibrated amplifier output [bite moment arm/0.5 × head length as defined above]). For each individual, the greatest standardized bite-force value among the three trials, assumed to represent maximum voluntary bite-force performance (see Losos et al. 2002), was used in the analyses.

Statistical Analyses

Statistical analyses were performed using JMPIN version 4.0.2 for Windows (SAS Institute). For all analyses, all data were log transformed, except for number of female home ranges overlapped and estimated number of females inseminated, which were square root transformed. Our sample is representative of the population. The number of territorial males in the entire contiguous population has ranged from 11 to 19 over the last 6 years, and we were able to collect all data from 11 of the 15 territorial males present in the population in 2003.

To evaluate the power of body and head size versus bite force in predicting territory area and our estimates of fitness, we performed three correlation analyses. First, we calculated Pearson product moment correlations (r) among all of the variables to examine relationships among absolute measures. Second, we calculated correlations using residuals from bite force regressed on each morphometric to examine the relationship between size-adjusted performance and the estimates of fitness. Third, we calculated correlations using principal component scores from two principal components analyses (PCAs) of the morphometrics (all and head only) to assess the relationship between overall size (body plus weapon and weapon only) and the estimates of fitness. Next, we ran a series of standard least squares and stepwise (forward and reverse) multiple regressions with territory area, number of female home ranges overlapped, estimated number of females inseminated, and potential reproductive output as the dependent variables. The six independent variables were SVL, mass (body size), head length, head width, head depth (weapon size), and bite force (weapon performance).

To evaluate the predictive power of body and weapon size on weapon performance, we calculated correlations between absolute measures as well as between morphometric principal component scores and bite force (see above). We then ran a series of standard least squares and stepwise (forward and reverse) multiple regressions with bite-force performance as the dependent variable and the measures of body and head size as the independent variables. For full multiple regression models, we assessed the degree of multicollinearity with the Durbin-Watson statistic (D-W) and external predictive power with the PRESS statistic, and we assessed goodness of fit of the stepwise models with Mallow's C_p statistic (Neter et al. 1996).

Results

Territory areas (mean = 1,827.5 m²; SE = 318.7) spanned nearly an order of magnitude (431–3,557 m²). The number of female home ranges overlapped by a male's territory ranged from two to nine (mean = 5.4; SE = 0.6). Thirty-five females (74%) had their home ranges exclusively contained within one male's territory, and 12 (26%) overlapped the territories of two males. Estimates of the number of females inseminated by each territorial male ranged from one to eight (mean = 4.4; SE = 0.7). Males were observed to court only females whose home ranges they overlapped. The potential reproductive output of territorial males ranged from 12.6 to 49.0 offspring sired per year (mean = 33.5; SE = 3.8).

Bite-force performance was significantly and positively correlated with territory area ($r = 0.656$, $P = .028$; fig. 3A), the number of female home ranges overlapped

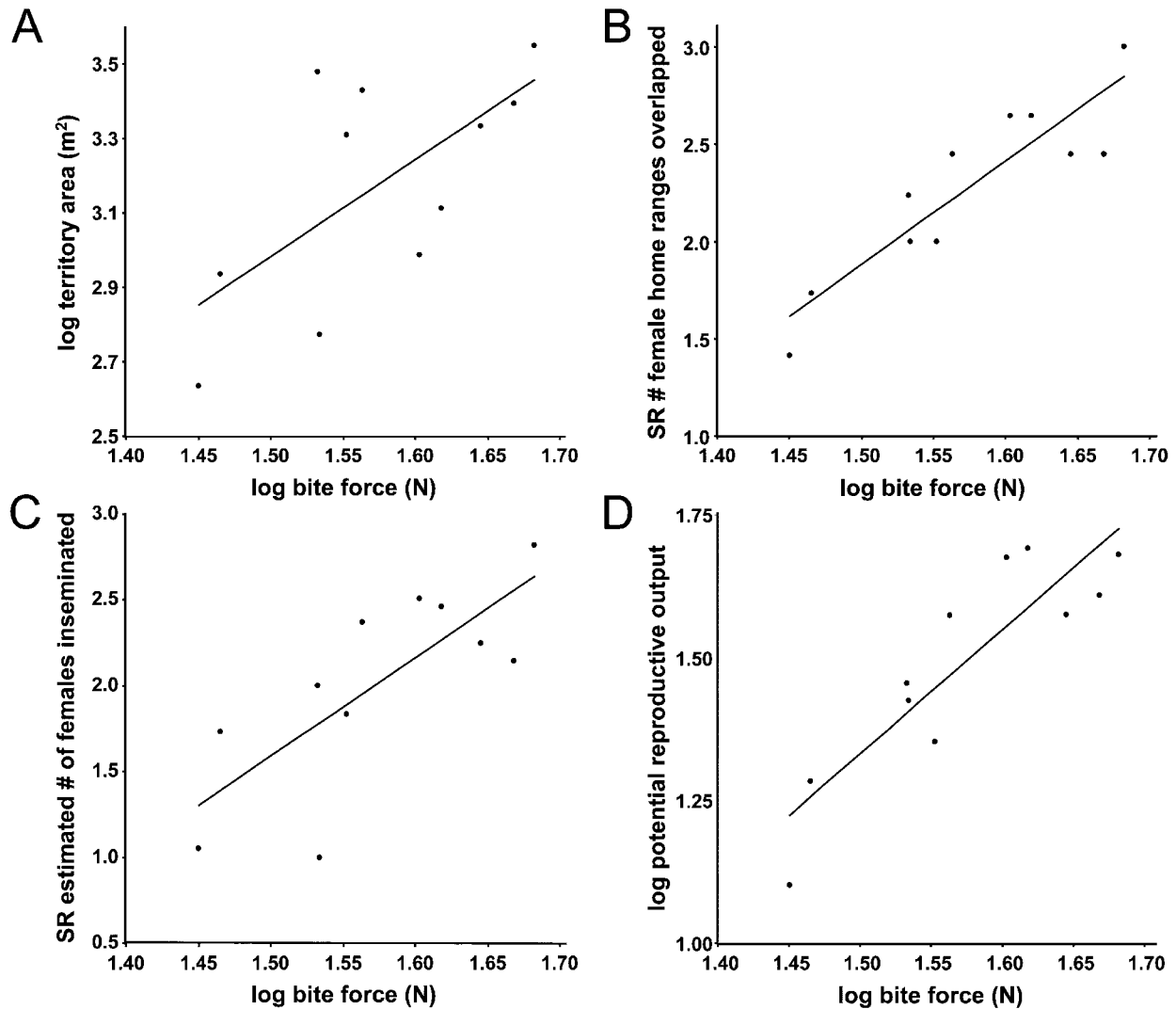


Figure 3: Relationships between weapon performance and territory size (A), estimated mating success (B, C), and potential reproductive output (D) in territorial male collared lizards at Sooner Lake, Oklahoma. Weapon performance is a strong predictor of these estimates of fitness, particularly the number of female home ranges overlapped ($r^2 = 0.810$) and potential reproductive output ($r^2 = 0.781$).

($r = 0.891$, $P < .001$; fig. 3B), estimated number of females inseminated ($r = 0.782$, $P = .005$; fig. 3C), and potential reproductive output ($r = 0.884$, $P < .001$; fig. 3D). Notably, the individual with the greatest bite-force performance maintained the largest territory, overlapped the most females, accounted for the highest estimated number of inseminated females, and had the second highest potential reproductive output (48.1 N, 3,557 m², 9 females, 8.0 inseminated females, 47.9 offspring/year), whereas the individual with the lowest bite-force performance had the smallest territory, overlapped the fewest females, accounted for the lowest estimated number of inseminated females, and had the lowest potential reproductive output

(28.2 N, 431 m², 2 females, 1.1 inseminated females, 12.6 offspring/year). No measure of body or head size was correlated with territory area or any estimate of reproductive success. Size-corrected bite force (i.e., residuals from bite force regressed on each morphometric) was significantly and positively correlated with the estimates of reproductive success in most cases (table A1 in the online edition of the *American Naturalist*), suggesting that territorial males that bite relatively hard for their size (body or weapon) have higher fitness.

Multiple regression (standard least squares) did not produce a significant model with territory area as the dependent variable ($P = .270$). A significant model was gen-

erated with number of female home ranges overlapped ($P = .026$, D-W = 2.52, PRESS = 1.92) as the dependent variable. Marginally nonsignificant models resulted with estimated number of females inseminated and potential reproductive output as the dependent variables ($P = .060$, D-W = 2.22, PRESS = 3.59 and $P = .062$, D-W = 2.97, PRESS = 0.12, respectively). All models showed little multicollinearity and high external predictive power. In all models, bite force was the only significant predictor of the estimates of fitness (table 1). With the removal of bite force as an independent variable, all full multiple regression models lost statistical significance ($P > .60$). Forward and reverse stepwise regression resulted in significant models that retained only bite force: number of female home ranges overlapped ($F = 34.628$, $df = 1, 9$, $P < .001$, $C_p = 3.36$), estimated number of females inseminated ($F = 14.145$, $df = 1, 9$, $P = .004$, $C_p = 5.36$), and potential reproductive output ($F = 32.004$, $df = 1, 9$, $P < .001$, $C_p = .94$).

With respect to the relationship between body and weapon size and performance, bite force was significantly correlated only with head width ($r = 0.635$, $P = .035$; fig. 4). Principal component scores from the morphometrics PCAs did not correlate with bite force (table A2 in the online edition of the *American Naturalist*). Multiple regression did not generate a significant model relating size to performance.

Discussion

The outcomes of agonistic interactions among males of many polygynous taxa are a primary determinant of successful territory acquisition and maintenance as well as mating success; therefore, they are predicted to have strong effects on fitness (e.g., Le Boeuf 1974; Eberhard 1979; McCann 1981; Clutton-Brock et al. 1988; Hews 1990). In such taxa, males often possess weapons used in agonistic interactions (Andersson 1994). The robust heads of adult male collared lizards, used in combat, are such a weapon (figs. 1, 2). The consequence of weapon performance in this species is revealed by strong, positive relationships between bite-force performance and estimates of mating success and potential reproductive output.

Weapon Performance versus Size

The results of this study support the hypothesis that the performance of a weapon, rather than its size or the size of the animal possessing it, is what determines the outcome of conflicts over territory boundaries. Previous studies have revealed that weapon size (see the first section of the article) and, more recently, weapon performance can be correlated with laboratory measures of dominance (Sned-

Table 1: Results of multiple regression models (standard least squares)

Model and independent variable	<i>F</i> ratio	<i>P</i>	Mean squared error
Territory area	1.944	.270	.060
Snout-vent length	.074	.798	
Mass	.132	.734	
Head length	.095	.773	
Head width	.853	.408	
Head depth	4.352	.105	
Bite force	2.166	.215	
No. females overlapped	8.435	.029	.038
Snout-vent length	6.312	.065	
Mass	.745	.436	
Head length	1.518	.285	
Head width	.478	.527	
Head depth	2.623	.180	
Bite force	28.393	.006	
Estimated no. females inseminated	5.515	.060	1.254
Snout-vent length	6.928	.058	
Mass	2.104	.220	
Head length	.900	.396	
Head width	4.722	.095	
Head depth	5.028	.088	
Bite force	17.409	.014	
Potential reproductive output	5.367	.062	.010
Snout-vent length	1.315	.315	
Mass	1.755	.255	
Head length	.349	.586	
Head width	<.001	.987	
Head depth	1.210	.333	
Bite force	16.438	.015	

Note: Models evaluate body and head size and bite force as predictors of territory size, number of female home ranges overlapped, estimated number of females inseminated, and potential reproductive output of territorial male collared lizards at Sooner Lake Dam, Oklahoma.

don et al. 2000; Lailvaux et al. 2004). This study demonstrates the prominent influence of weapon performance over both weapon size and body size in determining components of fitness measured in the field. Our results are strengthened by the fact that they are based on data from most of the territorial males in a population.

Additional evidence of the importance of weapon performance comes from the single territorial yearling male in our sample, representative of the rare occasion when a male collared lizard manages to establish a territory in its first year (J. F. Husak, unpublished data; T. A. Baird, personal communication). This individual, although of typical size for a large yearling, generated the greatest bite force by a large margin, 20% greater than the second-best-performing yearling, 55% greater than the largest (SVL) yearling, and 37% greater than the mean for yearling males

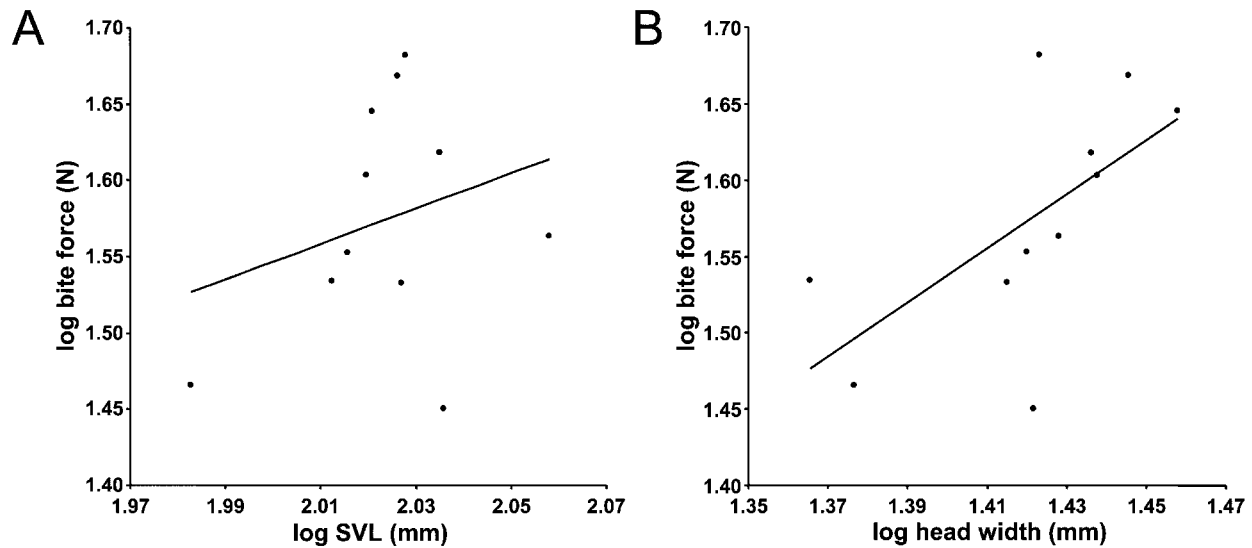


Figure 4: Relationships between size and weapon performance in territorial male collared lizards at Sooner Lake, Oklahoma. *A*, Body size (SVL) was a poor predictor of bite-force performance. *B*, Head width was the only morphometric that was significantly correlated with bite-force performance ($r^2 = 0.403$).

(A. K. Lappin and J. F. Husak, unpublished data). The fact that the only yearling male to establish a territory was not distinctly large but was by far the strongest biter emphasizes the key role of weapon performance in establishing and defending a territory.

The model of Morrell and Kokko (2003) predicts that winners of fights will acquire better territories. Our results demonstrate that relatively hard-biting males secure larger territories that overlap more female home ranges than their competitors. The most parsimonious explanation for this pattern is that individuals with superior weapons win more fights. A key implication is that in studying the role of weapons in fighting and dominance, the use of weapon morphology as a substitute for measures of weapon performance should be based ideally on a mechanistic understanding of the morphology-performance gradient and minimally on empirical correlations between measures of morphology and performance. When direct measures of performance are not feasible (e.g., because of constraints imposed by study system), indirect measures of performance can be used (see Wainwright 1987; Korff and Wainwright 2004).

What Determines Weapon Performance?

Did our measures of weapon size miss the characteristics that determine weapon performance, with the result being a weak morphology-performance relationship and no apparent morphology-fitness relationship? Given that

weapon performance was a good predictor of components of fitness, the expectation is that performance differences would have a morphological basis. Head dimensions are predictors of bite force in some lizards (Herrel et al. 2001a), and head width and depth (Molina-Borja et al. 1998; Hews 1990; Perry et al. 2004) and bite force (Lailvaux et al. 2004) have been found to be predictors of dominance in staged encounters. In this study, only one weapon size measure correlated with bite force (fig. 4B), and no body or weapon size measure correlated with any estimate of fitness. One possible explanation is that territorial males in this population have a limited size range, including that of the head. Another is that head dimensions reflect only limited aspects of the morphology that determines performance. Finally, musculoskeletal redundancy of the lizard jaw adduction system (i.e., multiple jaw adductor muscles) may weaken the morphology-performance relationship (see Alfaro et al. 2004).

Despite the homogeneity of head size among territorial males at Sooner Lake, bite-force performance varied considerably (1.7-fold). This indicates that weapon characteristics other than size proximately determine weapon performance. Notably, the one weapon dimension that correlated with bite force (head width) is the only measure influenced by muscle size (i.e., muscles bulge laterally through skull fenestrations). Muscle cross-sectional area determines muscle force generation, and, in turn, jaw adductor muscle force vectors determine bite force. Although beyond the scope of this study, a biomechanical analysis

of the jaw adductor system should more accurately predict bite-force performance than external measures of head size. However, simple measures of weapon morphology are unlikely to match weapon performance in predicting fitness because many variables potentially contribute to performance (e.g., biomechanics, muscle physiology, neural control, hormones). If an extensively inclusive model was generated that accurately predicted performance, sensitivity tests could reveal which morphological characteristics best predict performance. The predictive power of even an elegant model, however, would still suffer from problems associated with the biomechanical redundancy of muscles associated with jaw adduction (Alfaro et al. 2004).

The Cost of Injury

The model of Stamps and Krishnan (2001) predicts that individuals that incur the greatest costs during territory establishment will have smaller territories, and those that incur the lowest costs will have the largest territories. We propose that injuries from fights in collared lizards can constitute a formidable cost in the form of a reduction in weapon performance. Anecdotal support demonstrating the cost of injury comes from an adult male in our sample that had its jaw broken early in the breeding season (early May, 5 weeks before bite forces were measured). This injury was likely the result of a fight, since the position of the break with no other obvious wounds makes a predation attempt an unlikely explanation. This male's bite-force performance, measured after its jaw had healed, was the lowest in the sample at 59% that of the strongest biter, though the two were nearly identical in size. This individual was relegated to the smallest territory, which was of particularly low quality since it was at the periphery of suitable habitat, largely shaded, and overlapped the fewest female home ranges (2).

Weapon Performance as a Substrate for Sexual Selection

As outlined by Arnold (1983), selection acts directly upon performance characteristics most relevant to fitness, which then drives morphological evolution. Among males of territorial species, performance characteristics that improve fighting ability should increase mating success. In collared lizards, interactions between males can escalate to injurious biting, and bite-force performance is a direct measure of the ability to wound and potentially displace a competing male and acquire access to additional females.

Our results are consistent with the hypothesis that intrasexual selection has driven the evolution of exaggerated head size in male collared lizards (similar sexual dimorphism occurs in all *Crotaphytus* studied to date; see McGuire

1996; Lappin 1999). Although we did not find weapon size to be a determinant of any estimate of fitness, sexual selection likely has created a threshold head size that males must attain in order to be competitive for territories (i.e., to enclose adequate jaw adductor musculature such that it does not limit competitive weapon performance). For most males, this threshold head size is achieved during secondary sexual maturation. Above the threshold, when males are closely matched in body and weapon size (as they are in this population), weapon performance is the factor of most importance in resolving conflicts, determining dominance, and ultimately influencing spatial distributions and fitness. In other taxa exhibiting sexual dimorphism suggestive of weapon evolution, analogous relationships between weapon performance and estimates of fitness may be expected.

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