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The fitness advantage of a high-performance weapon

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Weapons used in combat between males are usually attributed to sexual selection, which operates via a fitness advantage for males with weapons of better 'quality'. Because the performance capacity of morphological traits is typically considered the direct target of selection, Darwin's intrasexual selection hypothesis can be modified to predict that variation in reproductive success should be explained by variation in performance traits relevant to combat. Despite such a straightforward prediction, tests of this hypothesis are conspicuously lacking. We show that territorial male collared lizards with greater bite-force capacity sire more offspring than weaker biting rivals but exhibit no survival advantage. We did not detect stabilizing or disruptive selection on bite-force capacity. Taken together, these results support the hypothesis that superior weapon performance provides a fitness advantage through increased success in male contests. Sexual selection on weapon performance therefore appears to be a force driving the evolution and maintenance of sexual dimorphism in head shape.

ADDITIONAL KEYWORDS: bite force – lizard – sexual dimorphism – sexual selection.

INTRODUCTION

Males of many animal species possess exaggerated structures that do not appear to serve a purpose in survival but that play a significant role during intrasexual conflicts over access to mates by inflicting injuries on rivals (Andersson, 1994; Berglund, Bisazza & Pilastro, 1996). Such structures constitute weapons. Subsequent to Darwin, the evolution of weapons has been hypothesized to be the result of sexual selection; a fitness advantage is enjoyed by males with higher 'quality' weapons due to an increase in the likelihood of success during conflicts (Darwin, 1871; Andersson, 1994). Classic studies of presumed sexually-selected traits have typically focused on the intensity of sexual selection on measures of weapon anatomy (Andersson, 1994), leaving the term 'quality' ambiguous in an evolutionary context (Lailvaux & Irschick, 2006; Irschick *et al.*, 2007). Recent work, however, has revealed that the performance capacity of complex structures (i.e. 'whole-animal performance'; Arnold, 1983) is a direct target of selection, and the evolution of morphology underlying performance traits occurs secondarily (Arnold, 1983; Le Galliard, Clobert & Ferrière, 2004; Irschick *et al.*, 2008). Thus, sexual selection on performance traits, and, indirectly, their underlying morphology, may ultimately contribute to the evolution and maintenance of sexual dimorphism.

We propose that appropriately chosen measures of performance provide a quantitative metric of weapon 'quality' in a biologically relevant context (Lailvaux & Irschick, 2006). We note that how weapon performance is quantified will depend on the specific weapon for a given species. For example, the performance of an antler may be measured either as stiffness (Blob & LaBarbera, 2001), which could reflect susceptibility to breaking during male combat, or as its ability to pierce tough skin. Key to an appropriate performance measure of quality is knowledge of how the weapon is used. Quantification of the 'quality' of a weapon should be based on a metric(s) of its capacity to function as a weapon, namely its potential to injure and incur costs on rivals. We suggest that measures of

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*Corresponding author. Current address: Department of Biological Sciences, Virginia Tech, Blacksburg, VA 24061, USA. E-mail: husak@vt.edu performance, which by definition are specific to a given weapon, can provide this metric (Lailvaux & Irschick, 2006). Using such an approach to study the evolution of sexual dimorphism, Darwin's intrasexual selection hypothesis can be modified to predict that increased reproductive success should result from superior weapon performance.

Although weapons are typically thought to function solely during male combat, it is possible that they may play roles in other contexts, such as predator evasion or prey acquisition or processing (Andersson, 1994). Thus, it is important to distinguish between hypotheses based on a model of sexual selection versus those based on natural (viability) selection. If natural selection favours such traits in males, one would predict that males with higher quality traits should enjoy a survival advantage and perhaps have higher reproductive success because of that survival advantage. However, if sexual selection alone favours superior weapon performance, then higher quality weapons should afford greater reproductive success but not necessarily provide a survival advantage. Thus, two components of fitness, survival and reproductive success, can be analysed separately to test these two hypotheses. We provide a test of each of these hypotheses in a polygynous lizard that uses biting both for prey consumption (i.e. capture and processing) and as the primary means of inflicting costs on rivals during territorial conflicts.

For animals that bite during fights (e.g. over territorial boundaries and access to mates), the head (i.e. cranial musculo-skeletal anatomy, jaws, teeth, etc.) functions as a weapon. Iguanian lizards are a lineage typified by polygynous mating systems and pronounced male-biased sexual dimorphism associated with territoriality and male combat (Stamps, 1983; Lappin & Husak, 2005) (Fig. 1). When engaged in combat, the head serves as the primary weapon, and biting can result in serious injury (Baird, Sloan & Timanus, 2001; Lappin & Husak, 2005). Recent studies have shown that bite-force performance is a strong predictor of dominance (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Husak *et al.*, 2006a) and territory size and access to females (Lappin & Husak, 2005). Studies are distinctly lacking that directly link weapon performance capacity to mating success in nature.

Recent molecular techniques have shown that behavioral estimates of fitness can prove to be unreliable indicators of the genetic structure of mating systems (Westneat, 1987; Morton, Forman & Braun, 1990; Hughes, 1998; Petrie & Kempenaers, 1998). In the present study, we build upon our previous work (Lappin & Husak, 2005) and combine field studies with a molecular genetic approach to test the hypothesis that males with a stronger bite sire more offspring in a breeding season relative to weaker biting rivals. We also tested the hypothesis that males with a stronger bite have a survival advantage over weaker biters. To investigate the potential for a complex fitness surface, we tested linear directional selection as well as nonlinear forms of selection (stabilizing and disruptive) on bite-force performance in both natural and sexual selection contexts.

Figure 1. Sexual dimorphism and male weapon morphology. Male (upper panel) and female (lower panel) collared lizards showing pronounced sexual dimorphism in head size. Biting is the primary means of fighting when males compete for access to territorial space and mates. The two images are to scale. Photographs by A. K. Lappin.

MATERIAL AND METHODS

FIELD METHODS

The study site (Lappin & Husak, 2005; Husak, Fox & Lovern, 2006b), Sooner Lake Dam in Pawnee County, Oklahoma, USA, was approximately 2 ha in area. We captured adult (≥ 2 years of age) and yearling (approximately 1 year of age) male and female lizards with a noose and permanently marked them with unique toe-clip combinations. Individuals that were captured and marked the previous year as hatchlings were considered yearlings, whereas those that were captured the previous year before hatchlings emerged were considered ≥ 2 years of age (*sensu* Baird, Acree & Sloan, 1996; Husak *et al.*, 2006b). Clipped toes were saved in lysis buffer for genetic analysis. Adult males were bled from the postorbital sinus with a microcapillary tube so that blood could be used for genetic analysis. Hatchlings emerge in late summer to early fall in this part of Oklahoma. We intensively sampled the study site and surrounding area daily until the cessation of activity in late autumn to ensure that we captured most of the hatchlings. We also sampled during the next breeding season to confirm that we did not miss any hatchlings. At the end of the breeding season, we intensively sampled the study area daily to determine which territorial males survived from the beginning of the breeding season to the end of the breeding season. To avoid mistaking death for dispersal or inactivity, we sampled all surrounding areas of suitable habitat and re-sampled the study area at the beginning of the following breeding season.

MORPHOLOGY AND PERFORMANCE

Territorial adult males were captured (> 90% of the individuals in the population) early in the breeding season when biting is most relevant and significant to territory defense (i.e. fighting is most frequent) and taken back to the laboratory where we measured snout–vent length (SVL), head length, width, and depth, and maximum bite-force performance, *sensu* Lappin & Husak (2005). Bite-force performance was measured with lizards at their field-active body temperature (approximately 37 °C) using a custom piezoelectric isometric force transducer (Herrel *et al.*, 1999) with its bite plates padded with leather strips. Three trials per individual were performed with 1 min of rest between trials, and each bite was standardized for the position along the jawline at which the lizards bit the bite plates (Lappin & Husak, 2005). All lizards aggressively bit the bite plates. For each individual, the greatest standardized bite-force measurement among the three trials was used in the analyses.

PATERNIY ASSIGNMENT

Blood or toes were collected from sexually mature males and hatchlings as described above. Laboratory and analytical techniques used for paternity determination are described in detail elsewhere (Husak *et al.*, 2006b). Briefly, genomic DNA was extracted from approximately 50 μL of whole blood or two phalanges (Longmire, Maltbie & Baker, 1997). We amplified ten microsatellite loci in 15-μL volumes using the polymerase chain reaction with previously published primers (Hutchison *et al.*, 2004; Husak *et al.*, 2006b). We used an automated DNA sequencer (model 377; Perkin-Elmer Biosystems) to visualize variation at individual microsatellite loci. Genotypes were visualized using GENESCAN and GENOTPYER (Perkin-Elmer Biosystems). We then used CERVUS, version 2.0 (Marshall *et al.*, 1998) to assign fathers ($N = 10$) to hatchling ($N = 37$) lizards at 80% confidence (LeBas, 2001; Husak *et al.*, 2006b).

Table 1. Loadings of morphological variables for the first two axes in a principal components analysis

	Axis 1	Axis 2
Eigenvalues	3.10	0.61
Percent variation explained	77.55	15.25
Snout–vent length	0.85	0.50
Head length	0.95	0.25
Head width	0.87	–0.37
Head depth	0.85	–0.40

Scores from these two axes were used in a multiple regression with bite-force performance to determine what best predicts reproductive success in male collared lizards. We interpreted the first axis to represent overall body size, whereas the second to represent head shape.

STATISTICAL ANALYSIS

We used a multivariate approach to examine how well body size, head morphology, and bite-force performance predicted reproductive success. We conducted a principal components analysis (PCA) that included SVL and head length, width, and depth as variables. The PCA produced two axes that cumulatively explained 92.8% of the variance. Given the loadings of the variables on these two axes (Table 1), we interpreted axis 1 to represent overall size, with larger values along axis 1 representing larger lizards. The loadings of variables on axis 2 led us to interpret axis 2 to represent head shape. Specifically, higher scores along axis 2 represent larger lizards with longer heads, whereas lower scores represent smaller lizards with deeper and wider heads. We used stepwise multiple regression to test whether body size (scores from PCA axis 1), head shape (scores from PCA axis 2), and/or bite-force performance predicted number of offspring sired. The first regression included only linear terms to test for directional selection, whereas the second regression included both linear and quadratic terms to test for stabilizing or disruptive selection (Lande & Arnold, 1983). We then used logistic regression to determine whether body size (scores from PCA axis 1), head morphology (scores from PCA axis 2), and/or bite-force performance predicted survival among territorial males (Janzen & Stern, 1998). In the first model, we included only linear terms to

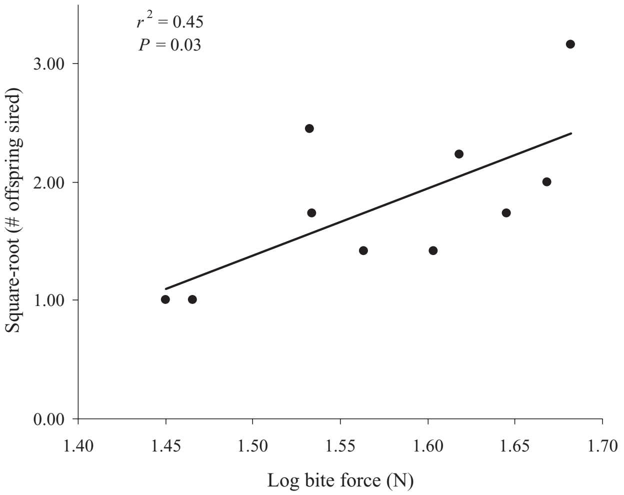

Figure 2. Relationship between maximum bite-force performance and annual reproductive success in territorial male collared lizards. The number of offspring sired was in the range 1–10 offspring per male. Multiple regression analysis showed that only bite-force performance predicted reproductive success, whereas multivariate measures of body size and head shape did not.

test for directional selection, and, in the second model, we included both linear and quadratic terms to test for stabilizing or disruptive selection (Janzen & Stern, 1998). We also examined Pearson Product-moment correlation coefficients to test for relationships between head size dimensions and bite-force performance. The goal of the correlation analyses was to determine which traits may be evolutionarily influenced by selection on bite-force performance.

RESULTS

Multiple regression analysis examining linear selection on traits of territorial males showed that bite-force performance was the only significant predictor of reproductive success ($F_{1,8} = 6.52$, $P = 0.03$, $R^2 = 0.45$, $\beta = 0.68$; Fig. 2), whereas PC scores representing body size (axis 1) and head shape (axis 2) were not. Multiple linear regression including quadratic terms, examining stabilizing and disruptive selection, did not result in a significant model when all variables were included ($F_{6,3} = 2.27$, $P = 0.27$), and a stepwise model only included the linear term for bite-force performance.

Logistic regression with survival as the dependent variable and PC scores representing body size (axis 1) and head shape (axis 2) and bite-force performance as independent variables did not produce a significant linear model for directional selection ($\chi^2 = 1.90$, d.f. = 3, $P = 0.60$), nor a significant quadratic model for stabilizing or disruptive selection ($\chi^2 = 5.84$, d.f. = 6, $P = 0.44$). This suggests that a survival advantage is not afforded by greater body size, a more robust head, or superior bite-force performance.

Among territorial males, which do not vary greatly in body size, body size did not significantly predict bite-force performance ($r = 0.27$, $P = 0.46$; Lappin & Husak, 2005). However, a positive correlation between bite-force performance and head width was detected ($r = 0.41$, $P = 0.04$). This morphometric reflects the size of the jaw-adductor musculature of males, which may be expected to influence bite force.

DISCUSSION

To our knowledge, this is the first demonstration of a direct link between the performance capacity of a weapon and genetically determined annual reproductive success. Sexual selection on bite-force performance was directional, but we found no evidence for stabilizing or disruptive selection. Our test of a natural selection hypothesis revealed that bite-force performance did not predict survival in adult males, nor did we detect directional, stabilizing, or disruptive selection on this gauge of performance in a survival context. It is important to note that bite-force performance and biting are key components of male–male interactions in this species. Escalated aggression involving fighting becomes rare later in the breeding season (Baird *et al.*, 2001; Husak & Fox, 2003), when the use of signals and indices that convey information about bite-force capacity (Lappin *et al.*, 2006) and aggressive intent (Husak, 2004) become central to interactions among males. Taken together, these results suggest that directional sexual selection for a weapon of superior quality (i.e. high performance) influences the evolution of weapon morphology (i.e. enlarged robust heads of males), and that this evolutionary trend is not driven by a survival advantage in adult males.

The results obtained in the present study showing that bite-force performance did not predict survival provide evidence that a performance characteristic, clearly important in the realm of sexual selection, appears not to play a significant role in survival. It is our view that, when feasible, future studies should simultaneously test the effects of key performance measures on survival and fecundity. This allows comparisons with other studies to examine the strength and direction of selection in nature (Kingsolver *et al.*, 2001; Kingsolver & Pfennig, 2007; Irschick *et al.*, 2008). By explicitly comparing the effects of performance on genetic reproductive success and survival, the selection mechanisms (i.e. natural versus sexual selection) operating directly on performance traits can begin to be distinguished. Our data add to a small but growing database of studies quantifying selection on performance traits in natural populations. The present analysis is noteworthy in that we detected significant directional sexual selection on bite-force performance in adult males, but not natural selection on the same trait. Furthermore, our test for stabilizing and disruptive selection, which is one of only a few, is in agreement with previous studies indicating that selection on performance is often directional (Husak & Fox, 2008; Irschick *et al.*, 2008).

Darwin's sexual selection hypothesis predicted that male traits used to impose fitness costs on rivals in the form of injury during contests over resources and mates, and which apparently do not function to increase survival, serve to give one male a reproductive advantage over other males. Our results support this hypothesis, and extend it to emphasize that weapon performance (i.e. quality) can be particularly important in determining variation in male reproductive success. This likely applies across animal taxa with mating systems in which males are territorial or otherwise compete for females, as well as to both generalized and specialized weapons. Candidate taxa range from insects to mammals with weapons ranging from invertebrate mandibles and claws to vertebrate horns and jaws (Harvey, Kavanagh & Clutton-Brock, 1978; Brown & Bartalon, 1986; Crespi, 1986; Hansen *et al.*, 1999; Sneddon *et al.*, 2000; Derocher, Andersen & Wiig, 2005; Kelly, 2006; Lee & Bass, 2006; Wilson *et al.*, 2007). We suggest that an integrative approach toward studying both the morphology and performance of weapons will shed light on the evolution and maintenance of weapons and sexual dimorphism in a diversity of taxa.

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REFERENCES

Andersson MB. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.

Arnold SJ. 1983. Morphology, performance, and fitness. *American Zoologist* **23:** 347–361.

Baird TA, Acree MA, Sloan CL. 1996. Age and gender-related differences in the social behavior and mating success of free-living collared lizards, *Crotaphytus collaris*. *Copeia* **1996:** 336–347.

Baird TA, Sloan CL, Timanus DK. 2001. Intra- and inter-seasonal variation in the socio-spatial behavior of adult male collared lizards, *Crotaphytus collaris* (Reptilia, Crotaphytidae). *Ethology* **107:** 15–32.

Berglund A, Bisazza A, Pilastro A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* **58:** 385–399.

Blob R, LaBarbera M. 2001. Correlates of variation in deer antler stiffness: age, mineral content, intra-antler location, habitat, and phylogeny. *Biological Journal of the Linnean Society* **74:** 113–120.

Brown L, Bartalon J. 1986. Behavioral correlates of male morphology in a horned beetle. *American Naturalist* **127:** 565–570.

Crespi BJ. 1986. Size assessment and alternative fighting tactics in *Elaphrothrips tuberculatus* (Insecta: Thysanoptera). *Animal Behaviour* **34:** 1324–1335.

Darwin C. 1871. *The descent of man and selection in relation to sex*. London: Murray.

Derocher AE, Andersen M, Wiig O. 2005. Sexual dimorphism of polar bears. *Journal of Mammalogy* **86:** 895–901.

Hansen CR, Vie JC, Vidal N, Keravec J. 1999. Body measurements on 40 species of mammals from French Guiana. *Journal of Zoology, London* **247:** 419–428.

Harvey PH, Kavanagh M, Clutton-Brock TH. 1978. Sexual dimorphism of primate teeth. *Journal of Zoology, London* **186:** 475–485.

Herrel A, Spithoven L, Van Damme R, De Vree F. 1999. Sexual dimorphism of head size in *Gallotia galloti*; testing the niche divergence hypothesis by functional analyses. *Functional Ecology* **13:** 289–297.

Hughes C. 1998. Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology* **79:** 383–399.

Husak JF. 2004. Signal use by collared lizards, *Crotaphytus collaris*: the effects of familiarity and threat. *Behavioral Ecology and Sociobiology* **55:** 602–607.

Husak JF, Fox SF. 2003. Adult male collared lizards (*Crotaphytus collaris*) increase aggression towards displaced neighbours. *Animal Behaviour* **65:** 391–396.

Husak JF, Fox SF. 2008. Sexual selection on locomotor performance. *Evolutionary Ecology Research* **10:** 213–228.

Husak JF, Fox SF, Lovern MB, Van Den Bussche RA. 2006b. Faster lizards sire more offspring: sexual selection on whole-animal performance. *Evolution* **60:** 2122–2130.

Husak JF, Lappin AK, Fox SF, Lemos-Espinal JA. 2006a. Bite-force performance predicts dominance in male Venerable Collared Lizards (*Crotaphytus antiquus*). *Copeia* **2006:** 301–306.

Hutchison DW, Strasburg JL, Brisson JA, Cummings S. 2004. Isolation and characterization of 11 polymorphic microsatellite loci in collared lizards (*Crotaphytus collaris*). *Molecular Ecology Notes* **4:** 554–556.

Huyghe K, Vanhooydonck B, Scheers H, Molina-Borja M, Van Damme R. 2005. Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology* **19:** 800–807.

Irschick DJ, Herrel A, Vanhooydonck B, Van Damme R. 2007. A functional approach to sexual selection. *Functional Ecology* **21:** 621–626.

Irschick DJ, Meyers JJ, Husak JF, Le Galliard J-F. 2008. How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research* **10:** 177–196.

Janzen FJ, Stern HS. 1998. Logistic regression for empirical studies of multivariate selection. *Evolution* **52:** 1564–1571.

Kelly C. 2006. Fighting for harems: assessment strategies during male-male contests in the sexually dimorphic Wellington tree weta. *Animal Behaviour* **72:** 727–736.

Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gibert P, Beerli P. 2001. The strength of phenotypic selection in natural populations. *American Naturalist* **157:** 245–261.

Kingsolver JG, Pfennig DW. 2007. Patterns and power of phenotypic selection in nature. *Bioscience* **57:** 561–572.

Lailvaux SP, Herrel A, Vanhooydonck B, Meyers JJ, Irschick DJ. 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society of London Series B, Biological Sciences* **271:** 2501–2508.

Lailvaux SP, Irschick DJ. 2006. A functional perspective on sexual selection: insights and future prospects. *Animal Behaviour* **72:** 263–273.

Lande R, Arnold SJ. 1983. The measurement of selection on correlated characters. *Evolution* **37:** 1210–1226.

Lappin AK, Brandt Y, Husak JF, Macedonia JM, Kemp DJ. 2006. Gaping displays reveal and amplify a mechanically-based index of weapon performance. *American Naturalist* **168:** 100–113.

Lappin AK, Husak JF. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalist* **166:** 426–436.

Le Galliard J-F, Clobert J, Ferrière R. 2004. Physical performance and darwinian fitness in lizards. *Nature* **432:** 502–505.

LeBas NR. 2001. Microsatellite determination of male reproductive success in a natural population of the territorial ornate dragon lizard, *Ctenophorus ornatus*. *Molecular Ecology* **10:** 193–203.

Lee JSF, Bass AH. 2006. Dimorphic male midshipman fish: reduced sexual selection or sexual selection for reduced characters? *Behavioral Ecology* **17:** 670–675.

Longmire JL, Maltbie M, Baker RJ. 1997. Use of 'lysis buffer' in DNA isolation and its implications for museum collections. *Occasional Papers Museum of Texas Tech University* **163:** 1–3.

Marshall TC, Slate J, Kruuk LEB, Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* **7:** 639–655.

Morton ES, Forman L, Braun M. 1990. Extrapair fertilizations and the evolution of colonial breeding in Purple Martins. *Auk* **107:** 275–283.

Petrie M, Kempenaers B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology and Evolution* **13:** 52–58.

Sneddon LU, Huntingford FA, Taylor AC, Orr JF. 2000. Weapon strength and competitive success in the fights of shore crabs. *Journal of Zoology, London* **250:** 397–403.

Stamps JA. 1983. Sexual selection, sexual dimorphism, and territoriality. In: Huey RB, Pianka ER, Schoener TW, eds. *Lizard ecology: studies of a model organism*. Cambridge, MA: Harvard University Press, 169–204.

Westneat DF. 1987. Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. *Animal Behaviour* **35:** 877–886.

Wilson RS, Angilletta MJ Jr, Navas RS, James C, Seebacher F. 2007. Dishonest signals of strength in male slender crayfish (*Cherax dispar*) during agonistic encounters. *American Naturalist* **170:** 284–291.