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Losing reduces maximum bite performance in house cricket contests

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Summary

1. Whole-organism performance capacities influence male combat outcomes in many animal species. However, several species also exhibit winner and loser effects, and current theory predicts that losers are more likely to lose again due to a decrease in aggression following defeat, not because of any change in underlying maximum performance capacity.

2. To test the effect of fight experience on performance, we measured the maximum bite force of male *Acheta domesticus* crickets that were pitted against size-matched opponents in staged fights. Winners then fought a second contest against other winners while losers fought other losers, after which we measured the change in bite force in all contest crickets and in a control group that did not take part in any contests.

3. Bite force predicted fight outcomes in the first round, and losing the first fight had a significant effect on bite force, leading to a 20% decrease in relative bite force compared to crickets that won both rounds. However, winning did not increase performance as there was no difference between those that won the first round and those that never experienced a loss, nor did winning a second bout alleviate the negative effects on realized bite performance of losing an initial bout.

4. Past defeats can therefore alter the realized short-term maximal performance of traits that contribute to contest outcomes independent of maximum performance limits set by morphology.

Key-words: bite force, male combat, whole-organism performance

Introduction

The factors affecting whole-organism performance (defined as any quantitative measure of an organism performing a dynamic, ecologically relevant task such as jumping, running or biting; Bennett & Huey 1990; Lailvaux & Irschick 2006) are a key issue in evolutionary ecology given the causal link between performance and fitness (Husak & Fox 2008; Irschick *et al.* 2008). For example, male combat is ubiquitous in the animal kingdom, and individual fighting ability is often rooted in measureable whole-organism performance capacities such as sprint speed or bite force (reviewed in Lailvaux & Irschick 2006). Maximum bite force capacity in particular predicts victory in male combat in a variety of taxa, including lizards (Lailvaux *et al.* 2004; Huyghe *et al.* 2005; Husak *et al.* 2006) and crickets (Hall *et al.* 2010), and it is an important predictor of fitness in certain species (Husak, Lappin & Van Den Bussche 2009; Cespedes & Lailvaux 2015). In addition to evidence which suggests that individual performance is acted on by natural and sexual selection (Le Galliard, Clobert & Ferrière 2004; Husak 2006a), there is a growing literature showing that these maximum capacities are also subject to proximate modification by a variety of biotic and abiotic factors (reviewed in Lailvaux & Husak 2014).

Several factors besides performance can determine male combat outcomes, and prime among these are aggressive motivation and recent combat experience. In some animal species, experience in past aggressive interactions modulates the expression of aggressive behaviour in subsequent conflicts, which can affect the odds of winning or losing (Rutte, Taborsky & Brinkhof 2006). In male *Anolis carolinensis* lizards, for example, losers of staged, size-matched contests exhibit decreased aggression in future bouts (which they are also more likely to lose than contest winners), whereas winners exhibit enhanced aggression to subsequent novel challengers and are equally likely to win or lose against future size-matched opponents (Garcia *et al.* 2012, 2014). Loser effects appear to be especially prevalent in invertebrates (e.g. Alcock & Bailey 1997), where they

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are modulated by the invertebrate analogue of noradrenaline, octopamine, with 'loser' individuals experiencing depletion of octopamine or its precursors, thereby suppressing aggressive behaviour (Hoyer *et al.* 2008).

Although aggressive behaviour, and thus the chances of victory in male combat, is affected by experience, the effect of combat experience on the expression of whole-organism performance traits that underlie escalated physical combat has received little attention. In most male combat studies that consider performance, it is the maximum performance abilities of which an individual is capable, quantified through repeated measure of a specific performance ability (Losos, Creer & Schulte 2002; Adolph & Pickering 2008), that are typically used to predict combat outcomes (Lailvaux & Irschick 2006). This is distinct from the potentially (but not necessarily) submaximal *preferred* or *ecological performance* actually expressed during an interaction, which is much harder to measure. Indeed, in nature, animals do vary their level of performance effort in different ecological contexts, such that they seldom operate at constant maximum capacity all the time (Irschick *et al.* 2005; Husak 2006b; Husak & Fox 2006). But while behavioural modulation is the most likely factor explaining the discrepancy between ecological and maximal performances, the maximal upper level of performance that it is possible for an individual to attain represents the output of a complex and integrated functional system involving morphology and physiology as well as behaviour (Arnold 1983; Garland & Losos 1994; Lailvaux & Husak 2014). As such those maximum capacities should remain constant in the face of short-term experiential effects alone, regardless of the extent to which the animal is motivated to use them. Nonetheless, previous studies have indeed implicated motivation in affecting an individual's likelihood of expressing its maximum performance capacity (e.g. Anderson, Mcbrayer & Herrel 2008). As such, a change in short-term aggressive motivation that is associated with male combat outcomes could temporarily affect the *realized* upper limit of a given expressed performance trait, especially if that trait is one that is utilized during aggressive conflicts.

Male house crickets (*Acheta domesticus*) engage in stereotyped and highly aggressive contests that frequently escalate to physical attacks on opponents with their mandibles (Hack 1997), suggesting that bite force is a potential determinant of male combat outcomes in this species, as has been shown previously to be the case in male *Teleogryllus commodus* crickets (Hall *et al.* 2010). Hack (1997) also reported experience effects on male combat outcomes in *A. domesticus*, with losers of a given combat bout being more likely to lose subsequent contests. House crickets are, therefore, an ideal system for addressing questions relating to experience effects, whole-organism performance and male combat. We measured maximum bite force of male *A. domesticus* crickets both before and after a series of staged conflicts to test: 1) whether bite force affects fight outcomes in house crickets and 2) whether contest outcomes alter maximum bite performance capacity. Specifically, we tested the hypothesis that losing a bout of fighting will decrease individual maximum bite force capacity measured using standard methods in a noncombat context.

Materials and methods

We obtained 166 *Acheta domesticus* nymphs from a commercial supplier (Flukers) and raised them separately to adulthood on a diet of cat food (Frisky's Go-Cat Senior, Nestlé) and carrots. We measured bite force on adult male crickets using the same methods as in previous studies (Hall *et al.* 2010; Lailvaux *et al.* 2011; Kelly 2014). Briefly, we placed a Tekscan FlexiForce wireless ELF system force circuit between the mandibles of each cricket, invariably coercing them to bite down on the circuit vigorously. Consistent with standard maximal performance methodology, we measured bite force of each individual five times (c.a. Hall *et al.* 2010) and retained the largest of an individual's five trials for analysis (Losos, Creer & Schulte 2002; Adolph & Pickering, 2008).

Immediately following bite force measurements, we staged the first round of fights between size-matched opponents by placing pairs of male crickets (matched by pronotum width to within 2 mm) within clear 5 × 5 × 5 cm plastic containers. We randomly marked one male of each pair with a small spot of nontoxic correction fluid for identification purposes, as has been done in other studies of cricket combat outcomes (Brown *et al.* 2006; Brown, Chimenti & Siebert 2007; Hall *et al.* 2010). Males interacted until a clear resolution was reached, and we determined fight outcomes based on observed fight behaviour, with the individual who continually retreated being judged the loser (c.a. Hall *et al.* 2010; Reaney, Drayton & Jennions 2011; Brown *et al.* 2006). Between 2 and 4 h later, we then pitted the winners of the first round of combat against the winners, and losers against other losers, and determined fight outcomes as before. All second-round fights were size-matched as well. We therefore grouped individuals based on their combat outcomes into 4 total fight combinations for analysis: loss–loss, loss–win, win–win and win–loss.

Following the two rounds of conflict, we remeasured bite force in all conflict individuals ($n = 134$) as before, giving us two measures of maximum bite force per individual. We also measured maximum bite force twice over the same time period as the conflicts in a separate group of male crickets ($n = 32$) that did not experience any male combat. All males were 10–15 days old post-eclosion at the time of bite force measurement and combat trials (c.a. Reaney, Drayton & Jennions 2011), and thus similarly aged.

RESPONSE SURFACE ANALYSIS

We applied response surface analysis (Draper & John 1988) to the pooled first-round combatants only [following Hall *et al.* (2010)] to determine the influence of differences in bite force and body size on male combat outcomes. We calculated the standardized differences in bite force and weight between winners and losers (Lande & Arnold 1983) and used these as predictor variables in a generalized linear model with fight outcome as a binomial response variable using R 3.1.0 (R Development Core Team 2013, http://www.R-project.org). We first estimated a saturated model containing linear ($\boldsymbol{\beta}$), cross-product (γ_{ij}) and quadratic (γ_{ii}) terms, and used log-likelihood ratio deletion tests based on AIC criteria (Akaike 1983; Burnham & Anderson 2002) to determine the minimum adequate model. We visualized the relationships between the model terms and fight outcomes using generalized additive models (GAMs) as implemented in the mgcv package for R (Wood 2011).

CHANGES IN BITE FORCE

We used an ANOVA with change in bite force following two rounds of conflict as the response variable and combat outcome as a factor to test for an effect of fight outcome on bite performance. We coded the levels of the combat outcome factor as follows: (A) individuals lost the first round (i.e. pooling loss–loss and loss–win individuals); (AB) individuals were those that won the first round but lost the second (i.e. win–loss); and B individuals never experienced a fight loss (i.e. pooling win–win and control individuals).

Results

The best-fitting minimum adequate model for fight outcome retained both linear (**β**) and quadratic (γ_{ii}) terms for bite force as predictor variables (AIC = 91·44, no. parameters = 2; Table 1). Thus, there is a significant nonlinear relationship between bite force difference and fight outcomes, such that individuals with high bite forces relative to their opponents become more likely to win a fight as the difference in bite force between combatants increases (Fig. 1). Initial conflict losers showed a significant reduction in bite force relative to individuals that either won the first round or never experienced a loss ($F_{2,153} = 7{\cdot}28$, $P < 0{\cdot}001$, Tukey HSD $P < 0{\cdot}001$ comparing A to AB/B; Fig. 2). However, there was no significant reduction in bite force in individuals who won only the first conflict compared to those who either won both of their fights or did not fight at all (Tukey HSD $P < 0{\cdot}35$ comparing AB to B).

Table 1. Standardized parameter estimates for the best-fitting multiple regression model (based log-likelihood ratio deletion tests) describing how both linear and quadratic differences between males in bite force predict the outcomes of initial fight bouts

Trait	Estimate	SE
Intercept	−0·57	0·326
Bite force	0·166	0·178
Bite force^2	0·173	0·09

Discussion

Whole-organism performance traits are important intermediaries between the organism and the environment, with deterministic effects on fitness components ranging from survival to male combat. However, the maximal capacities of those traits are increasingly understood to be plastic, and thus subject to a variety of modifying factors (reviewed in Lailvaux & Husak 2014). Here, we show not only that bite force affects the outcome of male combat in *A. domesticus* (Fig. 1; Table 1), but that the maximum level of bite force expression is itself affected by those combat outcomes, being reduced in individuals that lost the first of two rounds of staged, size-matched conflicts. Furthermore, our results show that bite forces of individuals that won the first round but lost the second were not significantly different from those that either never lost a fight or never fought at all (Fig. 2). Thus, our hypothesis is partially supported, as losing specifically the first bout of combat (as opposed to winning the first and losing the second) diminishes the maximum bite capacity of fighting house crickets, and this 'loser effect' on performance appears to persist over the time period examined here (2–4 h). Our results for bite force mirror those for aggression and motivation reported by other studies of experience effects in insects, suggesting that performance motivation could potentially be subject to the same factors that influence aggression.

Previous studies of *A. domesticus* male combat have found that victors tend to be larger or heavier than their opponents (Hack 1997; Brown *et al.* 2006). We size-matched similarly aged combatants to reveal asymmetries in fighting ability independent of body size and found that the difference in bite force between size-matched combatants exhibits a nonlinear relationship with combat outcomes such that individuals with large bite forces relative to their size-matched opponents are most likely to win fights (Fig. 1). Furthermore, differences in mass are not retained in the best-fit model containing bite force asymmetries (Table 1). Thus, measured maximum biting capacity does

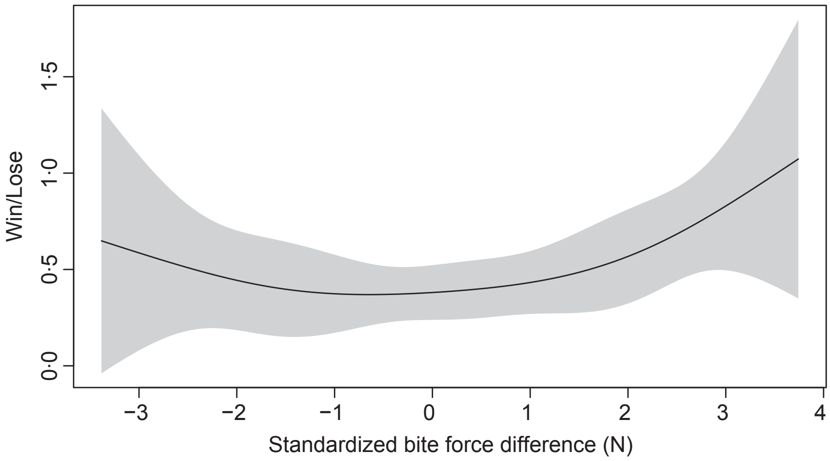

Fig. 1. Generalized additive model illustrating how differences in bite force predict male combat outcomes in the pooled first round of *A. domesticus* fights. Shaded areas represent 95% confidence intervals.

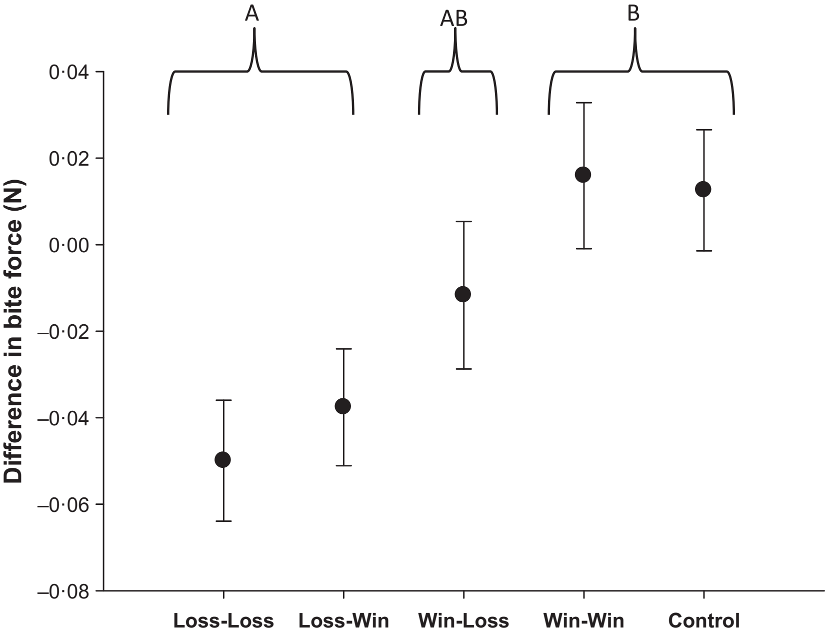

Fig. 2. Effects of individual combat history on difference in bite force in newtons (N) between pre-combat and post-combat bite measurements. Letters indicate pooling of outcomes for analyses: A = first round loss; AB = first round win, second round loss; B = never experienced a loss. Error bars represent mean change in bite force ± SE.

indeed predict male combat outcomes in *A. domesticus*. This finding is compatible with those of the many other studies that have investigated the influence of bite force on combat outcomes in other animal species (e.g. Lailvaux *et al.* 2004; Huyghe *et al.* 2005; Husak *et al.* 2006; Lailvaux & Irschick 2007), including crickets (Hall *et al.* 2010) and lend support to previous suggestions of bite force as being a key determinant of fight outcomes in other orthopteran species as well (Rillich, Schildberger & Stevenson 2007; Judge & Bonanno 2008; Umbers *et al.* 2012).

Maximum bite force is a proximate function of head and jaw morphology in orthopterans (Kelly 2014). Size and shape of morphological elements are fixed in adult crickets following eclosion, and as such, the major mechanical determinants of bite force are highly unlikely to have changed among the combat outcome groups, especially given the very short time frame of our study. We also observed no injuries or damage to mandibles in first-round losers that might affect bite ability between rounds, and indeed injuries during combat are rare in house crickets (Hack 1997). This reduction in measured bite force in individuals who lost the first round of combat is therefore most likely driven by changes in the factors affecting individual motivational state. Serotonin and octopamine both affect aggression in insect species (Hoyer *et al.* 2008; Bubak *et al.* 2014), and octopamine depletion reduces but does not entirely abolish aggressive behaviour intensity in crickets (Stevenson *et al.* 2000). The submissive effect of losing an aggressive bout can also be eliminated by octopamine replenishment, either experimentally or through flight (Stevenson *et al.* 2005), suggesting that it regulates experience-dependent modulation of aggression. The reduced aggressive motivation accompanying octopamine depletion might therefore reduce performance motivation in *A. domesticus* as well. Indeed, we consider it telling that losing a fight reduces bite force in a separate context unrelated to fighting (bite force measurement), suggesting that these effects are the result of a more general phenomenon, rather than a behavioural effect that is limited specifically to the competitive environment. In this regard, our finding that bite force reduction occurs in individuals that lost the first round of fighting but is not apparent in those that won the first round but lost the second (Fig. 2) is curious; in that one might predict that the loser effect would be ameliorated or abolished following victory in a second consecutive round of combat if that victory prompted octopamine replenishment. Future studies might address this issue by specifically considering the neurochemical underpinnings of fight behaviour with regard to maximum whole-organism performance expression in multiple rounds of male combat.

In conclusion, we have shown that relative maximum bite force predicts male combat outcomes in *A. domesticus*, and that losing specifically the initial round of combat decreases realized maximum bite performance in this same species. Changes in aggression after loss therefore translate to reduced physical ability to win via a reduction in a key performance predictor of fight outcomes, and these changes are not ‘rescued’ in the short-term by victory in a second, consecutive round of combat following an initial loss. These results illustrate that while the upper maximum limits of performance capacities are likely capped by morphology and physiology, the ability of organisms to express those maximum capacities is subject to behavioural and, possibly, neurochemical constraints as well.

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Data accessibility

Data deposited in the Dryad Digital Repository: doi:10.5061/dryad.n4m62 (Condon & Lailvaux 2016).

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