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Interactions among performance capacities predict male combat outcomes in the field cricket

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Summary

1. There is a growing appreciation that male fighting ability is influenced by multiple traits. In particular, studies of male combat have identified a variety of performance capacities that predict victory in conflicts between conspecifics in several animal species. However, while multiple aspects of male fighting ability are often examined with a single study, the interactions among traits are rarely considered.

2. We conducted fight trials between size-matched males in the black field cricket, *Teleogryllus commodus*, with the aim of testing how two whole-organism performance traits, jumping ability and bite force, together with weight at eclosion, interact to determine combat outcomes. We then examined the relationships between these traits and the outcome of a fight using: a univariate framework, where we examined the difference between winners and losers for each trait separately; and, a multivariate framework known as response surface analysis, where we examined how the interactions among traits predict the outcome of a fight.

3. We show that males that won fights tended to exert significantly more force when biting, but were neither better jumpers nor heavier at eclosion than their rivals. However, when we examined the effects of these three traits while statistically controlling for one another in a multiple regression, we showed that overall fighting ability depends not only on contributions of individual traits to contest resolution but also on the interactions among traits and their relationship to the capabilities of rival males. We found that the probability of winning was highest for a male with the greatest positive difference from his rival in the combination of bite force, jump power and weight at eclosion.

4. These findings highlight how studying multiple performance capabilities in isolation from each other may obscure the importance of some variables. Our multivariate analyses revealed that the interactions between multiple dimensions of performance are important in male combat. We discuss the broader implications of these findings, including the potential role of whole-organism performance in determining male quality.

Key-words: performance, locomotion, male combat, response surface, multivariate, *Teleogryllus commodus*

Introduction

Males from many taxa often compete vigorously with each other, either directly over access to females, or indirectly over resources that females require (Andersson 1994). A general trend across numerous animal species is that body size has a strong effect on male combat outcomes, with the likelihood of victory in fights being positively associated with larger size (e.g. Clutton-Brock, Albon & Guiness 1988; Reece, Innocent & West 2007; Triefenbach & Zakon 2008). However, there is mounting evidence to suggest that body size is only one among a suite of morphological, behavioural and physiological traits that contribute to overall fighting ability (reviewed in Lailvaux & Irschick 2006).

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Whole-organism performance capacities such as biting or locomotor ability (Irschick & Garland 2001) for example have increasingly been shown to influence both the outcomes of male contests (Perry *et al.* 2004; Huyghe *et al.* 2005; Husak *et al.* 2006; Lailvaux & Irschick 2007), as well as the expression of male weapons and secondary sexual characters that are used during fights with rivals (Lailvaux *et al.* 2005; Meyers *et al.* 2006; Lailvaux, Reaney & Backwell 2009; see also Bywater, Angilletta & Wilson 2008). Importantly, these relationships have been found to hold true even after controlling for potential scaling effects associated with body size.

Although controlling for variables such as size is important for understanding the contributions of individual traits to contest resolution, the multivariate nature of overall fighting ability allows for potential interactions among the individual components that fighting ability comprises. Previous studies have tested how multiple aspects of fighting ability may co-vary or contribute to the probability of victory in an additive fashion (e.g. Huyghe *et al.* 2005); however, whereas simple directional asymmetries in aspects of fighting ability are clearly important for predicting victory in fights between males, the potential for complex interactions (both linear and nonlinear) among prospective predictors has seldom been considered (Husak & Fox 2008; but see Pomfret & Knell 2006 for a recent example). Testing for such interactions is important, both because they reveal a more complete picture of overall fighting ability, and because they may guide us towards alternative male combat strategies based on different combinations of various aspects of fighting ability. Staged bouts between size-matched pairs of male *Anolis carolinensis* lizards, for example (Lailvaux *et al.* 2004), showed that the utility of two different whole-organism performance capacities (jumping ability and bite force) for predicting fight outcomes depended on body size, with larger lizards relying on biting to win fights, and smaller males relying on locomotor quickness. These results suggest an alternative strategy based on size or age, despite the size-matched nature of the male contests (Irschick & Lailvaux 2006); however, the exact nature of the multivariate interactions among predictor variables in this system was not considered.

Here, we take an integrative approach to understanding how the interactions among indicators of performance capacities influence male fight outcomes in the Australian field cricket, *Teleogryllus commodus*. In general, male combat plays an important role for Gryllid crickets in the wild as males vigorously defend against rivals the burrows from which they call to attract potential mates (Alexander 1961; Evans 1983, 1988). Accordingly, these crickets are ideal for studies of fighting ability, as fights can be easily staged and observed in the laboratory, and the outcome of male interactions clearly discerned (Alexander 1961; Evans 1983, 1988). However, while body size has previously been shown to be a key predictor of victory in fights between males in this and several other species of Gryllid cricket (Savage *et al.* 2005; Shackleton, Jennions & Hunt 2005; e.g. Judge & Bonanno 2008), performance has never been measured within the context of cricket male combat. Nevertheless, the potential for whole-organism performance to influence male combat in this species is clear, as males will lock mandibles and may bite each other in escalated fights (Alexander 1961), suggesting that bite force may be an important determinant of male combat outcomes in this species. Given that locomotor performance is correlated with success in male contests in several animal species (Garland, Hankins & Huey 1990; Robson & Miles 2000; Lawler, Richard & Riley 2005; but see Kemp 2002), it is also possible that locomotion might affect contest outcomes in *T. commodus* as well. The underlying performance basis of male combat in Gryllid crickets, however, remains unknown.

Following Lailvaux *et al.* (2004) we measured both jumping ability and bite performance and staged interactions between size-matched adult male *T. commodus* crickets to examine the relevance of these performance capacities to male combat outcomes. In addition, we also included body weight at adult eclosion as a predictor variable in our analyses as males not only vary considerably for a given size in their weight at eclosion, but weight at eclosion is also used commonly as an indicator of the ability of an individual to acquire resources during development (Hunt *et al.* 2004; Hunt, Brooks & Jennions 2005). We then used multivariate response surface analysis (Draper & John 1988) to test the prediction that jumping ability, bite force and weight at eclosion all influence fight outcomes in *T. commodus*, and that the interactions among these traits are important determinants of overall fighting ability. In particular, we compare the utility of univariate vs. multivariate analyses for discerning the contributions of individual traits to fighting ability in size-matched bouts.

Materials and methods

Animals used in this experiment originated from a large well-mixed laboratory stock of *T. commodus* collected in 2006 and 2007 from Smith's Lake (32°22′S, 152°30′E), New South Wales, Australia. From this stock we obtained 100 late instar males for use in the current experiment. The nymphs were isolated in individual plastic containers (7 × 7 × 5 cm) provided with cat food (Friskies Go-Cat Senior, Nestlé Australia, Sydney, Australia), vials of water stoppered with cotton wool and a piece of egg carton for shelter. We replaced the food and water weekly and kept the crickets in a constant temperature room (28 °C, 14 : 10 h light : dark regime) throughout. Every 2 days we checked for eclosions, weighed new adults and measured their pronotum width. The males were maintained in the individual containers for a further 10 days prior to the fight bouts to ensure they were sexually mature.

COMBAT TRIALS

Male field crickets follow a stereotypical sequence of events, involving escalation from antennal contact and aggressive calling to wrestling with interlocked mandibles and culminating in the retreat of one of the combatants (see references in Savage *et al.* 2005; Shackleton, Jennions & Hunt 2005). Fight outcomes can therefore be readily determined. We staged fights between 38 pairs of *T. commodus* males matched by pronotum width to within 2 mm. One male was randomly selected from each pair and marked with a small spot of non-toxic white paint to facilitate identification during fights. Male pairs were placed within clear plastic containers (5 × 5 × 5 cm) and allowed to interact until a resolution was observed.

PERFORMANCE MEASURES

We measured jumping performance and bite force in male *T. commodus* using standard methods. Bite force was measured using a Tekscan FlexiForce wireless ELF system (Tekscan Inc., Boston, MA, USA), which has previously been used to measure bite force in other animal taxa (Freeman & Lemen 2008). This system is better suited to small insects such as crickets than conventional force measurement systems because of the crickets' small gape size. Males were induced to bite down on the force circuit by placing the circuit between the cricket's mandibles, which invariably caused the animal to bite aggressively. Bite force was measured five times per individual (Adolph & Pickering 2008), and the highest bite value for each individual was considered to be the maximum bite force for that animal and was retained for analysis, consistent with previous performance studies (for justification of the use of maximal values in performance studies, see Losos, Creer & Schulte 2002).

Jump performance was measured using a Fastec high-speed camera (Fastec Imaging, San Diego, CA, USA) with a frame rate of 500 fps. A mirror placed at a 45° angle above the jump platform allowed us to film both dorsal and lateral views simultaneously. We later merged the two 2-dimensional jump trajectories into a single three-dimensional view of each jump using Pythagoras's rule. We used a 1 cm × 1 cm grid taped behind the jump platform for scale. We digitized each video using ProAnalyst v. 1.5.1.9 (Xcitex Inc., Cambridge, MA, USA). Given that there was little or no rotation of the trunk in most jumps, we digitized the movement of the head during each jump (Marsh & John-Alder 1994). We began digitizing 20 frames before the first movement, and stopped when the cricket either hit a wall or left the frame. We used a zero phase-shift Butterworth filter (Winter 2005) to smooth the x, y and z co-ordinates thus obtained, and calculated instantaneous velocity and acceleration from the smoothed displacements. Mass-specific power was obtained by multiplying the instantaneous velocity and acceleration profiles (following Toro *et al.* 2003; Toro, Herrel & Irschick 2004; Bergmann & Irschick 2006; Vanhooydonck *et al.* 2006). We tested the jumping ability of each individual five times, with the best jump (based on overall jump dynamics) retained for analysis. We used only one measure of jump performance (maximum mass-specific power output, hereafter referred to as jump power) in all analyses to avoid problems with collinearity; however, we note that substituting power for other jump descriptors such as velocity or acceleration does not alter our findings.

RESPONSE SURFACE ANALYSIS

To characterize how the differences between two rival males in jump power, bite force and weight at eclosion predict the outcome of male combat, we used a series of multiple regression models known as response surface analysis (Draper & John 1988). We first calculated the differences between the focal (marked) and non-focal male in jump power, bite force and weight, and then standardized the resulting traits to a mean of zero and a standard deviation of 1, as recommended by Lande & Arnold (1983). From the resulting data, we then estimated a series of multiple regression models (Chenoweth & Blows 2005) using a generalized linear model with fight outcome as a binomial response, as implemented in R (version 2.8.0, R Development Core Team, http://www.R-project.org). Specifically, we estimated a model containing only linear terms, a model containing both linear ($\boldsymbol{\beta}$) and cross-product terms (γ_{ij}) and finally, the full response surface as estimated by a second-order polynomial regression which includes linear ($\boldsymbol{\beta}$), cross-product (γ_{ij}) and quadratic (γ_{ii}) terms.

To examine whether the magnitude of the differences in our performance measures predicted the outcome of a fight in a linear fashion, we used a goodness-of-fit test (chi-squared) to assess whether the addition of the three linear terms improved the fit of the model containing only an intercept. Likewise, to test whether the interactions between bite force, jump power and weight at eclosion were also important, we assessed whether the addition of the three cross-product terms significantly improved the fit of the linear-only model. Finally, we assessed the potential for quadratic curvature in each trait by testing whether the addition of the quadratic terms improved the fit of the model containing both linear and cross-product terms. We also conducted a complementary analysis using model selection theory (Akaike 1983; Burnham & Anderson 2002), whereby we estimated Akaike Information Criteria (AIC) for each of the regression models estimated above. The calculated AIC values indicate how well the various models describe the data (Akaike 1983), with smaller values representing a better fit. Finally, we visualized the relationships between the outcome of a fight and jump power, bite force and weight at eclosion using thin-plate splines as estimated by the Tsp function of the *fields* package in R and then plotted the surfaces as contour plots.

Results

In size-matched combat trials the winning males, on average, were significantly stronger biters than losing males but were neither necessarily better at jumping, nor heavier at eclosion than their rivals (Table 1). Using a series of multiple regressions we characterized how the differences between two males in jump power, bite force and weight at eclosion predicted the outcome of a fight. We found that both the magnitude of the differences between males in bite force, jump power and weight at eclosion (linear terms, $\chi^2 = 8{\cdot}426$, d.f. = 3, $P = 0{\cdot}038$) and the interactions among these three traits (cross-product terms, $\chi^2 = 14{\cdot}278$, d.f. = 3, $P = 0{\cdot}003$) were important in predicting the overall outcome of a fight. However, we found no evidence for the importance of quadratic curvature in our performance measures, as the addition of the quadratic terms did not improve the fit of the model containing the linear and cross-product terms ($\chi^2 = 0{\cdot}538$, d.f. = 3, $P = 0{\cdot}911$). The results of the analysis using information criteria indicated that the model which best described

Table 1. Descriptive statistics (mean ± SE) for jump power, bite force and weight at eclosion for winners and losers of a single fight bout. Statistical differences in means between the two groups were assessed using a paired *t*-test

Trait	Winners	Losers	*t*-ratio	d.f.	*P*-value
Jump power (W kg^{-1})	4·430 ± 0·372	3·694 ± 0·351	1·666	37	0·104
Bite force (N)	1·683 ± 0·122	1·398 ± 0·087	2·403	37	0·021
Weight (g)	0·736 ± 0·019	0·724 ± 0·017	1·198	37	0·238

Table 2. The standardized parameter estimates for the best-fitting multiple regression describing how the differences between two males in jump power, bite force and weight at eclosion predict the outcome of a fight bout

Traits	Estimate	SE	Deviance	d.f.	*P*-value
Jump power	1·287	0·846	3·250	1	0·071
Bite force	2·420	1·002	11·704	1	< 0·001
Weight	−0·489	0·764	0·436	1	0·509
Jump power × bite force	−2·215	1·195	6·542	1	0·011
Jump power × weight	2·157	0·967	10·393	1	0·001
Bite force × weight	2·095	1·419	2·820	1	0·093

how performance traits predicts the outcome of male combat was the model containing both linear and cross-product terms (AIC = 43·553, no. parameters = 6), followed by the full response surface which included linear, cross-product and quadratic terms (AIC = 49·016, no. parameters = 9), and finally the model containing only linear terms (AIC = 51·832, no. parameters = 3).

The parameter estimates for the best fitting regression model (Table 2) indicate that the linear differences in bite force (*P* < 0·001) were again significant predictors of fight outcomes, with jump power being marginally nonsignificant (*P* = 0·071). Moreover, the interactions between our three measured traits were also important in male combat, as the cross-product terms for jump power and bite force (*P* = 0·011), and jump power and weight (*P* = 0·001) both significantly predicted fight outcomes. Visualising the nonparametric contour plots revealed that the probability of winning a fight was highest for males who have the greatest positive difference from their rivals in both jump power and bite force (Fig. 1) and jump power and weight at eclosion (Fig. 2).

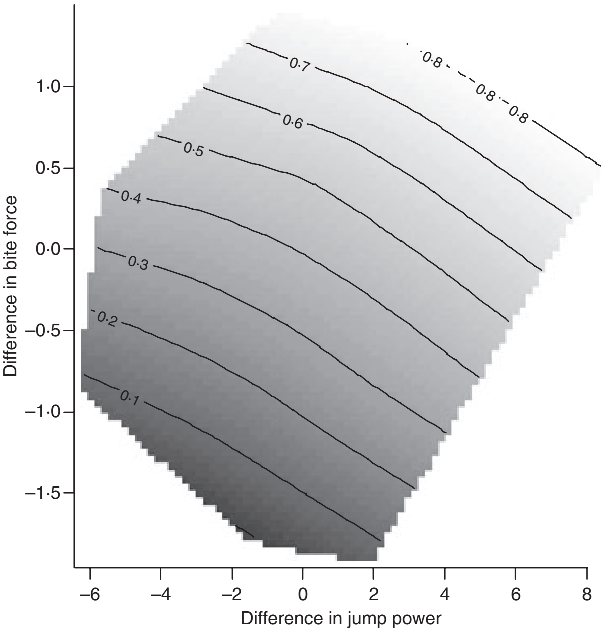

Fig. 1. The nonparametric reponse surface describing how the differences in jump power (W kg^{-1}) and bite force (N) predict the outcome of a single fight bout for two size-matched males, after controlling for weight at eclosion (g).

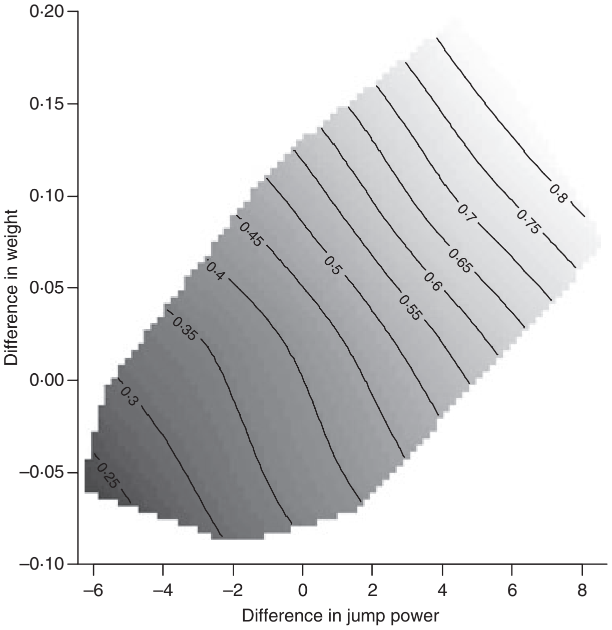

Fig. 2. The nonparametric reponse surface describing how the differences in jump power (W kg^{-1}) and weight at eclosion (g) predict the outcome of a single fight bout for two size-matched males, after controlling for bite force (N).

Discussion

We have shown that male performance capabilities play a significant role in determining the outcome of a fight between two size-matched *T. commodus* males. Our univariate results indicate that males that won fights tended to exert significantly more force when biting, but suggest they were neither necessarily better at jumping nor heavier at eclosion than their rivals. For a given male, however, overall fighting ability depends not only on contributions of individual traits to contest resolution but also on the overall effect of the combination of trait values, including multi-trait interactions. Particularly in field cricket species, where males have been shown to use a cumulative assessment strategy to establish dominance (Rillich, Schildberger & Stevenson 2007), multiple dimensions of male performance are likely to be important in determining male fight outcomes.

Using multiple regression techniques similar to those used in evolutionary selection analysis (Lande & Arnold 1983; Draper & John 1988; Chenoweth & Blows 2005), we examined how the differences in jump power, bite force and weight at eclosion between two rival males predict male combat outcomes. We found evidence for the importance of both the directional differences (e.g. significant linear terms) and interactions (e.g. significant cross-product terms) among these three measures, but no evidence for quadratic curvature in the effects of individual trait differences (e.g. non-significant quadratic terms). Our findings indicate that the outcome of a fight depends on the magnitude of the difference between males in multiple performance capabilities, with the probability of winning highest for the male with the greatest positive difference from his rival not only in bite force but also in jump power and weight at eclosion (see Figs 1 and 2). In contrast to when we examined the influence of individual traits, viewing performance capabilities within a multivariate framework revealed that the interactions between multiple dimensions of performance are important in male combat in *T. commodus*. Our findings highlight how univariate tests may underestimate the importance of individual performance traits by ignoring the multivariate nature of a male's fighting ability. For example, using only the univariate comparisons as a guide, we may have excluded jump power from the multivariate interaction model, and consequently missed the important interaction between jump power and the other traits of interest (Table 2). We suggest that future studies, particularly those using size-matching of contestants, test for similar interactions even if no directional differences in key trait are found.

Our finding that multiple performance capacities are important determinants of fight outcomes in *T. commodus* is consistent with findings in other taxa, including lizards and crabs (Sneddon *et al.* 2000; reviewed in Lailvaux & Irschick 2006). In addition to the intuitive influence of bite force on combat outcomes, this paper also adds to the growing list of studies demonstrating a relationship between locomotor performance and male dominance and/or fighting ability (Husak & Fox 2008). As in many of these studies, the advantage superior locomotor performance affords to victorious males is not readily apparent. One potential explanation that has been put forward is that locomotor capacities do not influence combat outcomes directly, but rather they are a general indicator of male vigour or 'quality' (e.g. Lailvaux *et al.* 2004; see also McElroy *et al.* 2007). Whole-organism performance traits represent the output of a number of integrated and complex physiological systems, and as such are likely to be related to overall physiological condition of an organism, including factors such as energy reserves, metabolic rates, fat stores or hormone levels (Garland 1984; Bennett & Huey 1990; Perry *et al.* 2004). However, as an understanding of male performance has only recently begun to be integrated with the sexual selection due to female choice (Lailvaux & Irschick 2006; Husak & Fox 2008), the extent that performance capabilities indicate overall male quality (as estimated by lifetime reproductive success) remains unclear.

In *T. commodus*, studies have commonly examined male quality in terms of the ability of a male to attract a mate, either via the amount that a male invests each night in the long-distance mate attraction call (Hunt *et al.* 2004; Bentsen *et al.* 2006; Zajitschek *et al.* 2007; Maklakov *et al.* 2008), or by characterising pre- and post-copulatory male attractiveness through behavioural trials (Loher & Rence 1978; Shackleton, Jennions & Hunt 2005; Bussière *et al.* 2006; Hall *et al.* 2008). However, unlike other species of field cricket in which fighting ability has been shown to covary positively with male attractiveness (Savage *et al.* 2005), in *T. commodus* it has previously been shown that females do not prefer to mate with males who win fights (Shackleton, Jennions & Hunt 2005). Together, these results suggest that in *T. commodus* whole-organism performance and sexual attractiveness may capture different aspects of male quality, yet without understanding the genetic relationships between these aspects of quality (and without understanding how male whole-organism performance affects female choice, if at all) this suggestion is difficult to assess (Wong & Candolin 2005; Lailvaux & Irschick 2006). In future, the incorporation of both whole-organism performance and sexual attractiveness with a common quantitative genetic framework will contribute to our understanding of how male quality is determined.

In conclusion, our results suggest that fight outcomes in *T. commodus* crickets are the result of multiple interactions among various performance variables which together constitute overall fighting ability. Given the nature of fighting ability in many animal taxa, we suggest that the potential for such multivariate interactions in other animal taxa will be larger than currently appreciated. Moreover, while our study has demonstrated that the linear trends and interactions amongst multiple traits are important in predicting the outcome of a fight, the potential for nonlinear, quadratic relationships should also be considered. Particularly in species where alternate fighting strategies might occur, a quadratic relationship between the probability of winning a fight and the expression of a trait would indicate that males are using alternate combat strategy, for example, based on size or age (e.g. Irschick & Lailvaux 2006). Using the multivariate framework provided by response surface analysis, researchers working on male combat might consider testing for potential linear and nonlinear interactions among determinants of fight outcomes (cf. Pomfret & Knell 2006) in other taxa as well.

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