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Dishonest signalling of fighting ability and multiple performance traits in the fiddler crab *Uca mjoebergi*

Simon P. Lailvaux[1]*, Leeann T. Reaney[2] and Patricia R. Y. Backwell[2]

[1]*Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia; and* [2]*School of Botany and Zoology, The Australian National University, Canberra, Australia, 0200*

Abstract

1. Signals used during male combat are expected to be honest indicators of fighting ability. However, recent studies show that dishonesty in male signalling is more prevalent than previously believed.

2. Here we show that regenerated (leptochelous) claws in male *Uca mjoebergi* fiddler crabs are not only dishonest signals of two types of whole-organism performance capacities that are likely to be useful during fights (claw closing force and pull-resisting force), but they are also less effective as weapons in situations where males are unable to bluff.

3. Original (brachychelous) male claws are statistically significant predictors (independent of body size) of both closing force and the force required to pull a male out of a tunnel. By contrast, leptochelous claw size does not convey information on those performance capacities following control for body size.

4. Furthermore, claw size affects fighting ability such that leptochelous residents are at a significant competitive disadvantage to brachychelous residents, although claw type does not affect the ability of non-resident males to win fights.

5. This study is among the first to show that male armaments can dishonestly signal performance traits that are likely important for winning fights, and is the first to show evidence for dishonest signalling of multiple components of fighting ability.

Key-words: performance, signalling, weapons, dishonesty, fiddler crabs, sexual selection

Introduction

Males of many animal species possess exaggerated secondary sexual characters which are used to either attract females or to gain access to them through direct competition with male rivals (Andersson 1994; Berglund *et al.* 1996). In species where sexually selected male traits are used as weapons during combat (e.g. Otte & Stayman 1979; Bean & Cook 2001; Emlen *et al*. 2005), weapon size and the probability of victory are linked such that males with larger weapons typically win fights against males with smaller weapons (Panhuis & Wilkinson 1999; Pomfret & Knell 2006). An important principle underpinning the evolution of sexually selected weapons and armaments is that for such traits to be useful as signals during male combat, they should be 'honest' or reliable indicators of male fighting ability (Harper & Maynard Smith 2003), allowing individuals to evaluate differences in their relative competitive ability (Jennions & Backwell 1996). From a purely functional perspective, this means that morphological structures used as signals or weapons during male combat should be linked, either developmentally or mechanistically, with individual traits that are important for winning fights (Lailvaux & Irschick 2006). Importantly, such relationships are expected to be independent of potentially confounding scaling effects associated with body size (see Lailvaux *et al*. 2005; Vanhooydonck *et al*. 2005a; Vanhooydonck *et al*. 2005b; Lailvaux & Irschick 2006; Lailvaux & Irschick 2007 for examples and discussion). Recent work has shown that fight outcomes are often mediated by whole-organism performance capacities (i.e. the capacity of an organism to conduct a dynamic, ecologically relevant task; Irschick & Garland 2001) such as bite force or locomotor ability, and that such capacities are indeed typically positively related to male secondary sexual traits used during fights following control for body size (reviewed in Lailvaux & Irschick 2006). In *Euoniticellus intermedius* dung beetles, for example, fight outcomes can be predicted based on individual horn size alone (Pomfret & Knell 2006), and horn size is a significant predictor, independent of body size, of two types of whole-organism performance capacities used during male combat (i.e. locomotor endurance and pull-resisting force; Lailvaux *et al*. 2005). Rivals may therefore glean information on individual performance capacities that

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*Correspondence author. E-mail: s.lailvaux@unsw.edu.au

underlie fighting ability from the size or shape of male armaments, and hence avoid potentially costly escalated encounters (Sneddon *et al.* 2000; Lappin *et al.* 2006).

Although it is typically assumed that most traits signalling fighting ability are honest (Johnstone 1995), if weapon size and fighting ability become decoupled then the potential exists for dishonestly signalling 'cheater' males to appear within a population. Despite the general assumption that the costs of producing signals and weapons used during agonistic encounters preclude the evolution of cheaters (Zahavi 1975; Harper & Maynard Smith 2003), several recent studies have shown that dishonesty can arise within species (e.g. Backwell *et al.* 2000; Hughes 2000; Seebacher & Wilson 2006). In highly territorial *Cherax dispar* crayfish, for example, which routinely use their enlarged front claws during fights, males appear to invest energy in producing larger claws rather than high-quality claw muscle (Wilson *et al.* 2007). Claw size is therefore a dishonest signal of male claw strength in this species (but not in females; Bywater *et al.* 2008), because actual claw performance is poorer than would be expected based on claw size alone. Thus, male signals may bluff not only behavioural determinants of fight outcomes, but also components of fighting ability based on performance. However, given that fighting ability may comprise multiple performance capacities (e.g. bite force and locomotor endurance capacity in some lizards; Lailvaux & Irschick 2006; Meyers *et al.* 2006), an unresolved question is whether male weapons such as claws also dishonestly signal performance capacities other than those with which they share a direct mechanical relationship.

Fiddler crabs of the genus *Uca* are an ideal system for studying dishonesty in signalling (Backwell *et al.* 2000). Males possess a greatly enlarged major claw which is used both to attract females and in fights with rival males over access to burrows, and fight outcomes are determined in many cases by individual claw size, with winners possessing significantly larger claws relative to losers (Jennions & Backwell 1996; Morrell *et al.* 2005; Reaney *et al.* 2008). Assessment of rival claw size is also the first stage in male aggressive interactions, and an important factor determining the initiation, escalation and overall duration of fights in male fiddlers. As such, claw size is considered to be a primary signal of overall male fighting ability (Jennions & Backwell 1996; Backwell *et al.* 2000; Morrell *et al.* 2005; Reaney *et al.* 2008). However, previous studies have shown that following claw loss due to, for example, predation or male combat, males from several *Uca* species regenerate a new (leptochelous) claw, which is lighter, more slender, and less robust than the original (brachychelous) claw. The two claw types are nonetheless very similar in size (Yamaguchi 1973; Backwell *et al.* 2000; Reaney *et al.* 2008), and while regenerated claws can be identified based on the more slender dactyl and reduced number of tubercles relative to original claws (see Fig. 1), previous work has shown that male crabs are unable to distinguish between original and regenerated claws (Reaney *et al.* 2008). Although leptochelous claws are predicted to deliver a weaker closing force than brachychelous claws as a result of their different morphology and lower muscle mass, males with leptochelous claws are nonetheless able to deter brachychelous rivals from initiating combat (Backwell *et al.* 2000), despite being inferior fighters in escalated contests (Reaney *et al.* 2008). Leptochelous claws also do not change over time to become more brachychelous in form (Backwell *et al.* 2000) and are therefore both effective and permanent bluffs of fighting ability (Backwell *et al.* 2000; Reaney *et al.* 2008).

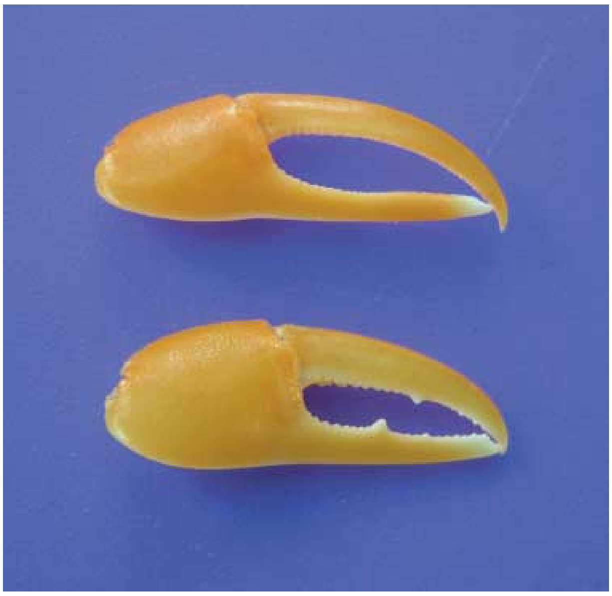

Fig. 1. Leptochelous (regenerated) (top) and brachychelous (original) (bottom) male *U. mjoebergi* claws.

Previous studies have examined the relative utility of original and regenerated claws for winning fights and attracting mates (Backwell *et al.* 2000; Reaney *et al.* 2008), but the functional mechanism by which males with regenerated claws are able to bluff rival males is not known. In particular, although regenerated claws would be expected to be significantly weaker based on biomechanical considerations (Levinton *et al.* 1995; Backwell *et al.* 2000), the performance of the two types of claws has never been compared directly. During escalated fights, rival males use their major claws to grapple with each other during male combat (Jennions & Backwell 1996), so claw strength is likely to be an important factor underlying the superior fighting ability of crabs with large major claws (Sneddon *et al.* 2000; Levinton & Allen 2005). Empirical demonstration of the performance of original and regenerated claws is therefore crucial to understanding how the two types of males are able to win fights. Given the overall importance of claw size to male combat during both assessment and escalated phases, the possibility also exists that claw size may signal components of fighting ability other than claw strength or similar traits directly related to claw morphology (e.g. Lailvaux *et al.* 2005; see also Meyers *et al.* 2006). Testing this idea requires measurement of performance components that are likely to be important for winning fights, and examination of the relationships between claw size and these performance measures for both original and regenerated claws independent of body size.

In this article, we examine the relationship between claw size and closing force in the major claws of male *Uca mjoebergi* crabs. In particular, we test the hypothesis that claw size is an honest signal of closing force in brachychelous claws (i.e. that claw size is a significant predictor of residual closing force following statistical control for body size; see Vanhooydonck *et al*. 2005a, Lailvaux & Irschick 2007 for similar examples), but not in leptochelous claws (hereafter original and regenerated males, respectively). We also address the possibility that claw size might signal other types of whole-organism performance relevant to male fighting ability. Given that male combat in fiddler crabs frequently occurs inside burrows, we test the hypothesis that claw size signals pull-resisting force (i.e. the capacity to prevent being pulled or pushed out of a tunnel) in original but not regenerated males. This capacity has previously been shown to be an important component of fighting ability in *E. intermedius* dung beetles, which also fight inside burrows (Lailvaux *et al*. 2005). Finally, we compare the fight success of original and regenerated males during naturally occurring fights, and assess the relative importance of claw size and residency on fight duration and outcomes in *U. mjoebergi*.

Methods

Uca mjoebergi is a small fiddler crab that lives in dense mixed-sex colonies. Resident males aggressively defend their burrows against burrowless (floater) males (Morrell *et al*. 2005). We studied a population of *U. mjoebergi* fiddler crabs at East Point reserve, Darwin, Australia between September and December 2006. Males used in performance trials were removed from their burrows and transported back to the laboratory. Claw length and carapace width were measured to the nearest 1 mm using dial callipers. For regenerated claw males, we only used individuals with fully regenerated claws for all components of this study.

CLAW CLOSING FORCE

We measured *in vivo* closing force of the major claw in all crabs using an isometric Kistler force transducer (type 9023, Kistler Inc., Winterthur, Switzerland) connected to a Kistler charge amplifier (type 5058a, Kistler Inc.) (see Herrel *et al*. 2001a; Herrel *et al*. 2001b for a detailed description) and using a protocol similar to that for measuring bite force in lizards (e.g. Lailvaux *et al*. 2004; Lailvaux & Irschick 2007) and claw strength in crayfish (Wilson *et al*. 2007). Briefly, we induced the crabs to pinch down forcefully on the free ends of the transducer by placing the plates between the open major claws. We measured closing force five times per individual, with a 20-min rest between measures. Of the five measures, the one with the greatest closing force in newtons (N) was retained for analysis (see Losos *et al*. 2002 for justification of the use of maximum values in performance trials). We obtained data on claw closing force for 48 original and 38 regenerated males.

PULLING FORCE

We measured the force required to pull a male crab out of an artificial burrow using methods similar to those of Lailvaux *et al*. (2005). The burrow was made from a plastic tube 13 mm in diameter (similar to the size of burrows found in the field; LTR, pers. obs.) and lined with a fine mesh for traction. A piece of cotton thread attached at one end to a force transducer was run over a smooth, horizontal, aluminium rod and attached to the posterior end of the carapace of a crab with cyanoacrylate adhesive (*sensu* Lailvaux *et al*. 2005). The crab was allowed to enter the tunnel until it was completely inside. We then measured the amount of force required to pull the crab out of the tunnel by pulling down on the opposite end of the force transducer at a slow and constant rate until the crab was pulled clear. (Note that, because of the friction of the thread passing over the rod, a small amount of force will be lost.) We measured pulling force three times for each individual with a 1 h rest between trials (Lailvaux *et al*. 2005). Room temperature averaged 30 °C for all trials. The trial that resulted in the largest pulling force was retained for statistical analysis (Losos *et al*. 2002). Crabs were monitored closely during all trials, and no individuals were eliminated for consistently sub-maximal performance. We ultimately obtained data on maximal pulling force for 49 original and 41 regenerated males.

MALE COMBAT

To document fighting behaviour, we caught and released resident regenerated and original claw males into the population, at least 1 m from their original burrow and within 1 min of capture. We followed each male until he had his first complete interaction with another original claw resident male. A fight was defined as any interaction where the two males touched claws. We recorded the duration of the fight (from first to last contact), and noted who won. Winners and losers are easily distinguished, as the loser will always leave the area, while the winner will remain and take residency of the burrow. The previous (i.e. unreleased) resident male was then caught and measured for carapace width and claw length (mm).

STATISTICAL ANALYSES

We compared claw-closing forces for males with original and regenerated claws using *t*-tests. To compare closing forces for those same males independent of claw size, we performed an ANCOVA with closing force as the dependent variable, claw type as a factor, and claw size as a covariate. To examine relationships between claw size and performance variables independent of body size, we included both a measure of body size (carapace width) and claw size as predictor variables in multiple regressions. The resulting partial regression coefficients express the correlation between claw size and performance with the effects of body size statistically removed (analogous to residual analyses but without losing a degree of freedom; Kachigan 1991; Darlington & Smulders 2001; Garcia-Berthou 2001; see also Lailvaux *et al*. 2005). Both signal size and functional capacities often scale positively with body size, and hence we need to examine the relationships among relative (i.e. size-free) rather than absolute values to determine if claw size honestly signals performance (see Vanhooydonck *et al*. 2005a; Lailvaux *et al*. 2005; Lailvaux & Irschick 2007 for examples). Tolerance was within acceptable levels in all cases, and collinearity was therefore never large enough to distort the results of multiple regressions (i.e. always greater than 0·1; Quinn & Keogh 2002). To examine effects of residency and claw type on fight outcome, we used G-tests to compare the proportions of original and regenerated males that won fights as both residents and floaters. Specifically, we compared 'homoclaw' fights between resident and floater males where both had original claws (OO) to 'heteroclaw' fights where either the resident or the floater male had a regenerated claw (RO, OR; first letter signifies the resident). Regenerated males were always compared with original males, because this is the context within which signal dishonesty is most likely to be apparent. To examine relationships between claw size and carapace size for original ($n = 394$) and regenerated males ($n = 157$), we pooled measurements for all individuals used in this study and conducted regressions with carapace size as the lone predictor variable and claw size as the dependent variable. Variables were $\log_{10}$ transformed to meet assumptions of normality and homoescedasticity as required. All statistical analyses were carried out using R 2·5·0 (http://cran.r-project.org/).

Results

CLAW ALLOMETRY AND HONEST SIGNALLING

Claw size and carapace size were closely related in original males, with carapace size accounting for over 95% of the variation in claw size ($r = 0·977$, $F_{1,388} = 8265·242$, $P < 0·001$). By contrast, carapace size accounts for less than 70% of the variation in claw size in regenerated males ($r = 0·835$, $F_{1,153} = 351·045$, $P < 0·001$). Thus, claw size is much more tightly linked to carapace size in males with original as opposed to regenerated claws. Indeed, the relationship between carapace size and regenerated claws exhibits a significantly lower slope than that between carapace size and original claws ($F_{1,547} = 4·6961$, $P < 0·03$).

For crabs with original claws, the regressions of absolute claw length versus both absolute closing force ($r = 0·646$, $F_{1,46} = 32·87$, $P < 0·001$) and absolute pulling force ($r = 0·574$, $F_{1,47} = 23·15$, $P < 0·001$) were significant (Fig. 2). Crabs with regenerated claws also exhibited significantly positive relationships between absolute claw length and both absolute closing force ($r = 0·546$, $F_{1,38} = 16·16$, $P < 0·001$) and absolute pulling force ($r = 0·626$, $F_{1,39} = 25·1$, $P < 0·001$) (Fig. 2).

Within original males, the regression for maximum closing force with carapace and claw size as predictor variables shows that claw size is a statistically significant predictor of closing force following control for carapace size (Table 1a; Fig. 3a). Similarly, pulling force is significantly predicted by claw size following control for carapace size (Table 1b; Fig. 3b). Within regenerated males, however, claw size did not significantly predict either closing force (Table 1c; Fig. 3c) or pulling force (Table 1d; Fig. 3d) after controlling for carapace size.

CLAW TYPE AND PERFORMANCE

Closing force for original claws is significantly higher than that of regenerated claws for both absolute ($t_{83} = 2·804$, $P = 0·006$; Fig. 4a) and claw size-corrected data ($F_{1,82} = 8·158$, $P = 0·005$; Fig. 4b). By contrast, original and regenerated males do not differ in either absolute ($t_{88} = 0·505$, $P < 0·615$) or claw size-corrected pull-resisting force ($F_{1,87} = 0·175$, $P < 0·677$).

CLAW TYPE AND MALE COMBAT

The proportions of original males that won fights differed significantly among OO, OR and RO fights ($G = 11·23$, d.f. = 2, $P < 0·004$). In fights between heteroclaw males, fight outcomes depended not only on claw type, but also on whether or not the original male was the resident or the floater. For example, the proportion of original residents that won OO fights (92/98) was not significantly different from the proportion of original residents that won OR fights (38/44; $G = 2·06$, d.f. = 1, $P = 0·124$), but was significantly greater than for RO fights (24/34; $G = 11·17$, d.f. = 1, $P < 0·001$). Thus, floater males with regenerated claws appeared to suffer no competitive disadvantage (OO vs. OR), whereas claw regeneration has a clear effect on the success of resident males (OO vs. RO).

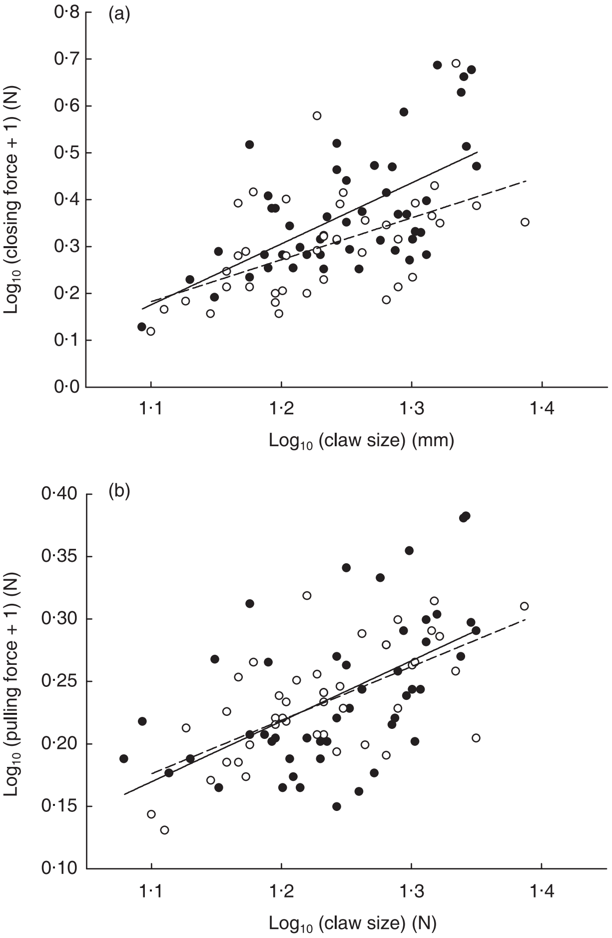

Fig. 2. Relationships between absolute claw length and (a) absolute claw closing force, and (b) absolute pull-resisting force for leptochelous (open circles) and brachychelous (closed circle) males. The slopes for leptochelous males are given by the dashed lines, whereas the solid lines are the slopes for brachychelous males.

To test whether fight durations differ depending on the claw type of residents, we pooled OO and OR fight durations and compared them with RO fights. The duration of RO fights tended to be lower than other fight types ($n = 154$, $F_{1,153} = 3·65$, $P = 0·058$). Residents with regenerated claws therefore not only lose more fights than original males, but there was also a trend for their fights to be briefer.

Discussion

Understanding the signalling of fighting ability by males and the maintenance of honest signals is a long-standing problem in evolutionary biology (Harper & Maynard Smith 2003).

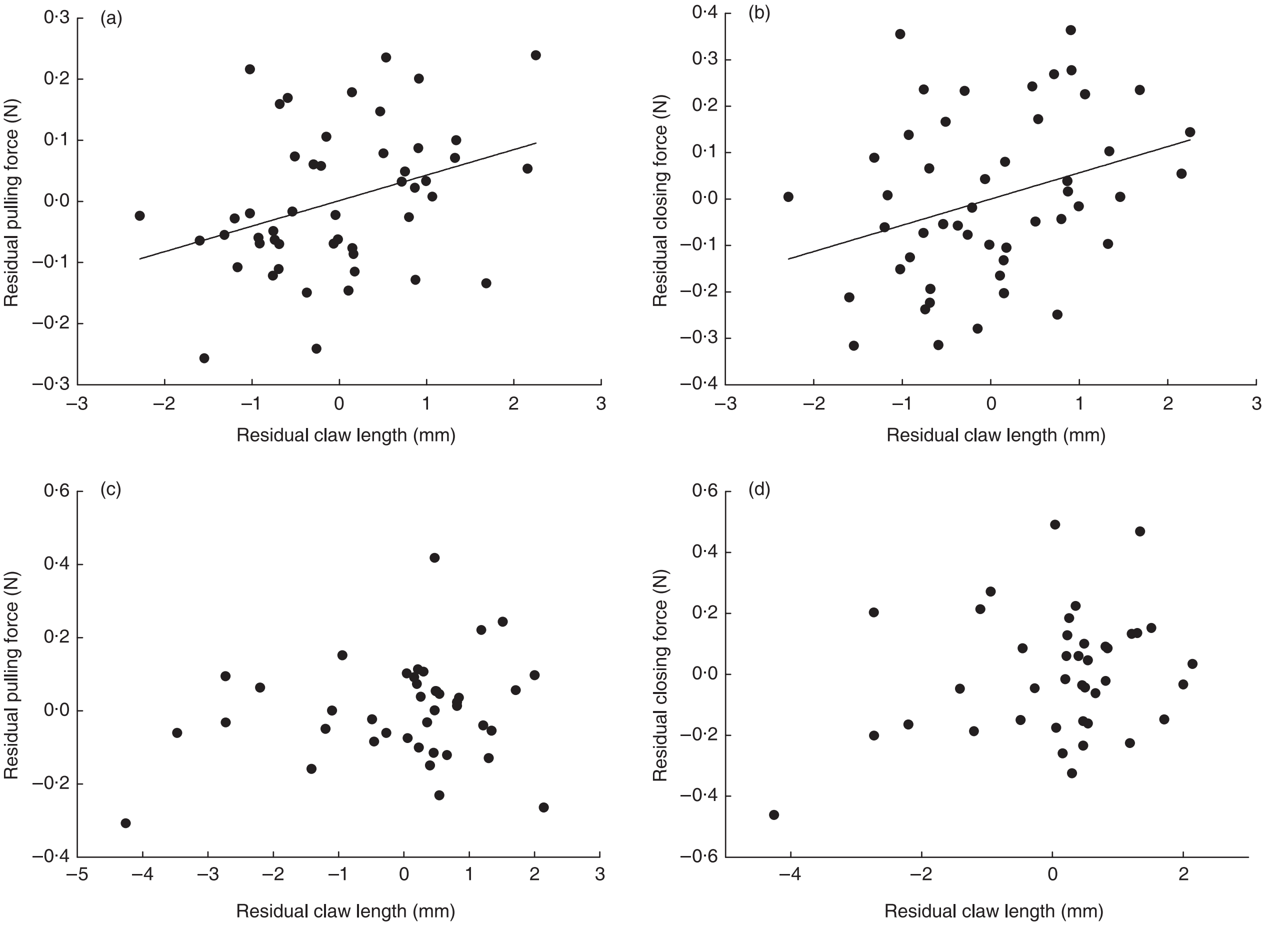

Fig. 3. Residual (i.e. size-free) relationships between original *U. mjoebergi* male claw length and (a) pull-resisting force, and (b) pinching force; and residual relationships between claw length and (c) pulling force and (d) pinching force for males with regenerated claws.

Table 1. (a) Results of a multiple regression with claw size and carapace size as predictors and the log of the maximum closing force as the dependent variable for brachychelous males. Adjusted r^2 is 0·392. (b) Results of a multiple regression with the same predictors and the log of the maximum force required to pull a crab out of a tunnel as dependent variable. Adjusted r^2 is 0·310. (c) Results of a multiple regression the same predictors and log maximum closing force as dependent variable for leptochelous males. Adjusted r^2 is 0·262. (d) Results of a multiple regression with the same predictors and maximum pulling force as dependent variable for leptochelous males. Adjusted r^2 is 0·403

Performance Measure	Variable	Coefficient	SE	*t*	*P*
Brachychelous claws					
(a) Log closing force (N)	Intercept	–0·854	0·384		
	Carapace size	–0·017	0·068	–0·246	0·806
	Claw size	0·064	0·026	2·441	0·019
(b) Log pulling force (N)	Intercept	–0·486	0·259		
	Carapace size	–0·036	0·045	–0·792	0·432
	Claw size	0·042	0·017	2·519	0·015
Leptochelous claws					
(c) Log closing force (N)	Intercept	–0·924	0·456		
	Carapace size	0·017	0·069	0·251	0·803
	Claw size	0·041	0·024	1·694	0·099
(d) Pulling force (N)	Intercept	–0·422	0·296		
	Carapace size	0·072	0·043	1·667	0·104
	Claw size	0·019	0·015	1·267	0·213

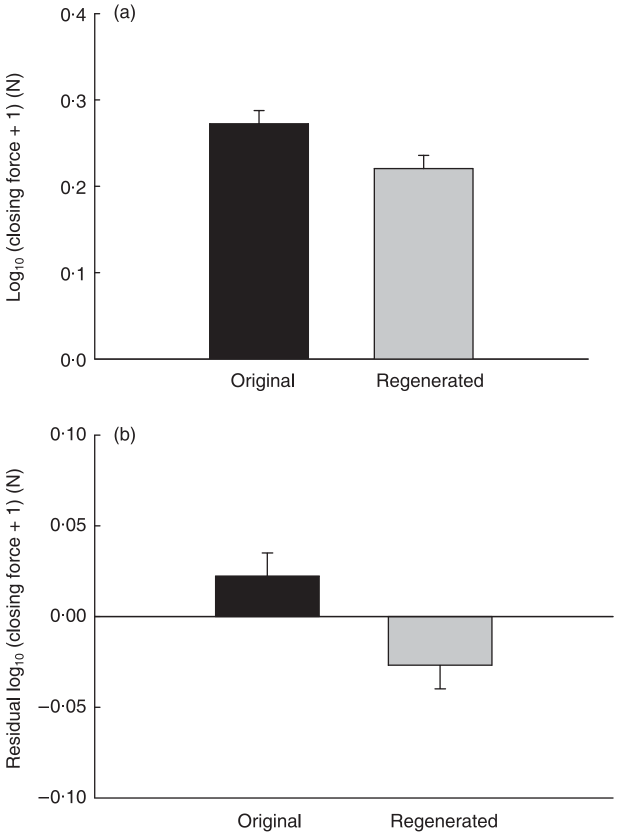

Fig. 4. Closing force of original vs. regenerated claws for (a) absolute and (b) size-corrected data.

Our study offers a functional perspective on this phenomenon by taking advantage of a model dishonest signalling system in fiddler crabs. Males replace autotomized major claws with lighter and less robust regenerated claws that are nevertheless superficially similar in overall shape and size to original claws (Fig. 1; Backwell *et al.* 2000; Reaney *et al.* 2008). The available evidence suggests that regenerated claws are dishonest signals of performance capacities underlying fighting ability. Regenerated claws provide inaccurate information on both relative claw closing force (because regenerated claws are weaker than would be expected based on claw size alone [Fig. 4]; see also Seebacher & Wilson 2006; Wilson *et al.* 2007), and relative male pull-resisting force (Fig. 3c), and hence males with regenerated claws are able to dissuade rival original-clawed males from engaging in combat (Reaney *et al.* 2008). In addition, males wielding weak regenerated claws are also able to win fights with conspecific males possessing stronger original claws in some specific contexts. Given both the previously demonstrated general importance of rival claw assessment to male combat in fiddler crabs (Backwell *et al.* 2000; Morrell *et al.* 2005; Reaney *et al.* 2008), and the fact that *U. mjoebergi* males cannot distinguish between original and regenerated claws (Reaney *et al.* 2008) these results suggest that males involved in visual assessment of rivals with regenerated claws will be unable to accurately assess any asymmetries in fighting ability. Importantly, our results for pull-resisting force build on previous findings by showing that a deterministic relationship between weapon size and performance capacities useful for fights (as in Wilson *et al.* 2007) is not required for weapon size to convey dishonest information on those capacities (see Lailvaux *et al.* 2005 for a similar example).

Recent studies have shown that success in male combat is related to whole-organism performance capacities in a range of animal taxa (reviewed in Lailvaux & Irschick 2006). Our data suggest that whole-organism performance also mediates male combat outcomes in *U. mjoebergi*. Original claws exhibit significantly higher absolute (Fig. 4a) and relative (Fig. 4b) closing forces than do regenerated claws, as expected based on the smaller available cross-sectional area for muscle attachment in regenerated claws (Backwell *et al.* 2000). Furthermore, original claw size is a statistically significant predictor of both claw closing force (Table 1a) and pull-resisting force (Table 1b), even after controlling for body size. Indeed, claw size is a better predictor than body size of both performance variables in original males, a finding that parallels that for horn size in male *E. intermedius* dung beetles (Lailvaux *et al.* 2005). Regenerated claws, however, do not significantly predict either closing force or pull-resisting force following control for body size. Thus, while male crabs may potentially assess relative performance capacities from the size of an original claw (as in *E. intermedius*), regenerated major claws do not convey such information. Most importantly *U. mjoebergi* males are unable to differentiate between similarly sized original and regenerated claws (and hence between the different fighting abilities of the bearers) despite clear visual assessment of rival male claw size before actual physical combat, and regenerated males are no more likely to be challenged than original males (Reaney *et al.* 2008). Given that males with regenerated claws constitute approximately 7·4% of this study population (Reaney *et al.* 2008), the dishonesty associated with regenerated claws goes largely unnoticed, and regenerated males are as successful as original males in obtaining burrows from residents despite likely significantly reduced claw-closing forces, and hence reduced fighting ability, compared to original clawed males (Fig. 4).

In addition to potential frequency-dependent constraints on bluffing in this species, and despite the effectiveness of regenerated claws as bluffs of male fighting ability, our data show that possession of a regenerated claw incurs an important cost in the context of burrow defence. Although all males exhibited similar fighting abilities regardless of claw type when searching for a territory, residents with regenerated claws won significantly fewer fights than those with original claws, and these fights also tended to end sooner. In general, there is a residency advantage when fighting in fiddler crabs (e.g. *Uca annulipes*; Jennions & Backwell 1996), so the inferior fighting ability of resident regenerated males requires some explanation. We argue that resident males with regenerated claws lose fights because floater males choose their opponents based primarily on claw size, whereas resident males cannot choose their opponents (see also Reaney *et al.* 2008). Claw size and carapace size are closely correlated in original males, such that original claw size not only signals closing force and pull-resisting force, but overall body size as well. By contrast, the relationship between claw size and body size is much weaker in regenerated males, with regenerated claws exhibiting a lower allometric slope than brachychelous claws. Fights in *U. mjoebergi* are typically size-assortative (Morrell *et al.* 2005); thus, if a regenerated floater male challenges an original clawed resident of a similar claw size then, based on claw size alone, the regenerated clawed male is likely to have a larger body size (and potentially a higher pull-resisting) force than his opponent. He will therefore be more liable to win an escalated fight, despite the relatively lower closing force of the regenerated claw (Fig. 4). By contrast, residents with regenerated claws cannot choose who they fight; they must defend themselves against all challengers regardless of claw size or else risk losing their burrow, and hence may find themselves facing males that they would otherwise avoid, thereby exposing their bluff (Reaney *et al.* 2008). This finding is similar to that for *C. dispar* crayfish, where dishonest signalling is only effective in the initial stages, and males risk having their bluff exposed should fights escalate (Wilson *et al.* 2007).

The idea that social context affects fight strategies intraspecifically is mirrored at the interspecific level by recent work suggesting that social context and type of social system modify both male fight strategies and how male signals are used during fights in several species of Caribbean *Anolis* lizards (Lailvaux & Irschick 2007). Future studies should consider both the relative dishonesty and the utility of regenerated claws for winning fights across *Uca* species that differ in key variables such as frequency of regenerated males, degree of territoriality, sexual size dimorphism, or operational sex ratio. Furthermore, we note that other performance or physiological traits in addition to closing and pulling force might also influence the outcomes of male fights; for example, a trade-off exists between closing force and closing speed in major fiddler crab claws (Levinton & Allen 2005). Comparisons of this relationship in original and regenerated claws might offer further insight into mechanics of male combat in fiddlers. The existence of relationships between original weapon size and functionally unrelated traits such as pull-resisting force suggests that these traits may be linked developmentally (see also Lailvaux *et al.* 2005). Studies attempting to manipulate or disrupt such relationships, perhaps using life-history approaches, would be valuable for understanding the evolution of both honest and dishonest signalling. As a final point, future studies might experimentally examine intra-individual changes in performance following claw loss and regeneration, as this may guide researchers towards a fuller understanding of the costs of regeneration.

In summary, our data show that the weaker regenerated claws of *U. mjoebergi* (relative to original claws) are dishonest signals of at least two unrelated whole-organism performance capacities that are likely to be important during male combat. In addition, regenerated claws are effective bluffs of male fighting ability in all social contexts examined, except when regenerated resident males are forced to defend their burrows against intruders. We suggest that because males cannot distinguish between original and regenerated claws, males with regenerated claws are consequently able to bluff original clawed males through size-assortative combatant selection based on own claw size, although resident males with regenerated claws who are forced into escalated fights risk having their bluff exposed. These findings have important implications for the evolution of male signalling, because they suggest that male signals may dishonestly signal not only behavioural aspects of fighting ability, but multiple components based on whole-organism performance as well.

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