

RESEARCH ARTICLE

Social control of unreliable signals of strength in male but not female crayfish, *Cherax destructor*

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Accepted 16 July 2011

SUMMARY

The maintenance of unreliable signals within animal populations remains a highly controversial subject in studies of animal communication. Crustaceans are an ideal group for studying unreliable signals of strength because their chela muscles are cryptically concealed beneath an exoskeleton, making it difficult for competitors to visually assess an opponent's strength. In this study, we examined the importance of social avenues for mediating the possible advantages gained by unreliable signals of strength in crustaceans. To do this, we investigated the factors that determine social dominance and the relative importance of signalling and fighting during aggressive encounters in male and female freshwater crayfish, *Cherax destructor*. Like other species of crayfish, we expected substantial variation in weapon force for a given weapon size, making the assessment of actual fighting ability of an opponent difficult from signalling alone. In addition, we expected fighting would be used to ensure that individuals that are weak for their signal (i.e. chela) size would not achieve higher than expected dominance. For both male and female *C. destructor*, we found large variation in the actual force of their chela for any given weapon size, indicating that it is difficult for competitors to accurately assess an opponent's force on signal size alone. For males, these unreliable signals of strength were controlled socially through increased levels of fighting and a decreased reliance on signalling, thus directly limiting the benefits accrued to individuals employing high-quality signals (large chelae) with only low resource holding potential. However, in contrast to our predictions, we found that females primarily relied on signalling to settle disputes, resulting in unreliable signals of strength being routinely used to establish dominance. The reliance by females on unreliable signals to determine dominance highlights our poor current understanding of the prevalence and distribution of dishonesty in animal communication.

Key words: biting, performance, sexual selection.

INTRODUCTION

Dominance hierarchies for many species are determined through a combination of both signalling and fighting. When the costs of fighting are high, it is mutually advantageous for opponents to passively establish dominance using signals of potential fighting ability (Maynard Smith, 1974; Sneddon et al., 1997; Martín et al., 2007). Agonistic interactions over resources should then be decided through an asymmetry of the signal, which represents an individual's resource holding potential (RHP) (Parker, 1974; Maynard Smith and Parker, 1976).

As a receiver's response determines the evolution of a signal, it is expected that most agonistic signals should be honest indicators of an individual's quality (Dawkins, 1976; Dawkins and Guilford, 1991; Maynard Smith and Harper, 2003). Signal honesty (or reliability) should then be maintained by two non-mutually exclusive mechanisms (Searcy and Nowicki, 2005): (1) performance-based signals, and/or (2) signal costs. Performance-based signals are those that cannot be maintained by low-condition individuals as they are mechanistically linked to the inherent quality being advertised [e.g. stotting in gazelles (FitzGibbon and Fanshawe, 1988)] (see also Rohwer and Ewald, 1981; Enquist, 1985; Lappin et al., 2006). Signal costs – the costs of producing or maintaining signals – can ensure only high-quality individuals can afford to pay the extra investment, and thus they

reliably convey accurate information about an individual's quality (Maynard Smith and Harper, 2003).

Dishonest (or unreliable) signalling occurs when the signals used to establish dominance become disassociated from an individual's actual quality or fighting ability. Although unreliable signalling is theoretically expected, it should only occur at low frequencies in natural populations (Gardner and Morris, 1989; Johnston and Grafen, 1991; Számadó, 2000; Searcy and Nowicki, 2005). Despite such theoretical expectations, there are many reported cases of unreliable signals of both fighting ability and mate choice across a range of species, including fiddler crabs (Backwell et al., 2000; Lailvaux et al., 2009), hermit crabs (Elwood et al., 2006), snapping shrimp (Hughes, 2000), stomatopods (Steger and Caldwell, 1983; Adams and Caldwell, 1990) and freshwater crayfish (Seebacher and Wilson, 2006; Wilson et al., 2007). Moreover, recent studies of male slender crayfish, *Cherax dispar*, revealed dishonest signals are routinely used during agonistic interactions and are far more common than previously predicted (Wilson et al., 2007; Bywater et al., 2008). In this system, male slender crayfish use relative chela size to determine dominance (Seebacher and Wilson, 2007), but chela size is a poor predictor of chela strength (a measure of fighting ability), and strength is unrelated to social dominance (Wilson et al., 2007). It is important to note that when fights do occur between males of the slender crayfish it is the individuals with the stronger

chela that win the disputes (Wilson et al., 2007). For female *C. dispar*, in contrast, there is a strong correlation between chela size and strength, suggesting that a female's chela provide a reliable signal of potential fighting ability (Bywater et al., 2008).

When both the ability for accurate signal assessment is constrained and there are substantial costs associated with ignoring the signals, theory predicts that the frequency of unreliable signallers should then increase within a population (Gardner and Morris, 1989; Johnston and Grafen, 1991; Számádó, 2000; Rowell et al., 2006). Although there is limited empirical support for these predictions, the high incidence of unreliable signalling among many crustaceans may partly support these theoretical assertions. The chela muscles of crustaceans (the basis of fighting capacity) are cryptically concealed beneath an exoskeleton, and their chelae are used as both weapons and signals (Steger and Caldwell, 1983; Berglund et al., 1996; Hughes, 2000; Wilson et al., 2007). Thus, it is impossible for competitors to accurately assess the strength of their opponents without physical contact, which means assessing an opponent's strength is inherently risky and potentially very costly. The simplest means that animals use to detect unreliable signals of strength, and to restrict their use, is social mechanisms. Without the social mediation of unreliable signalling, opponents might base dominance decisions on a signal disassociated from an individual's condition, leading to low-condition animals gaining dominance. Fighting represents the social control of dominance signals and ensures only individuals with high RHP can maintain high dominance status (Møller, 1987; Tibbetts and Dale, 2004). Thus, high levels of fighting or probing can be used to ensure that individuals that are producing signals of strength greater than their actual underlying strength will not be able to gain resources under false pretence. Despite the logical basis for this mechanism ensuring signal reliability, there are few convincing examples of these social mechanisms (Searcy and Nowicki, 2005) (but see Møller, 1987; Tibbetts and Dale, 2004; Tibbetts and Izzo, 2010).

In this study, we examined the importance of social mechanisms in mediating the potential advantages gained by unreliable signals of strength in freshwater crayfish. We quantified the relative importance of signalling and fighting during the establishment of dominance in male and female crayfish, *Cherax destructor* Clark 1936. The large chela size of both male and female *C. destructor* implies that there are substantial social costs associated with engaging in physical combat for unreliable signallers. Like other species of crayfish, we expected substantial variation in weapon strength for a given weapon size, making the assessment of actual fighting ability of an opponent difficult from signalling alone. Such variation between signal and actual performance provides the opportunity for unreliable signals of strength to be used to gain dominance. However, we expected there would be social mechanisms that ensure individuals that are weak for their signal size will not achieve higher than expected dominance.

MATERIALS AND METHODS

Study animals

C. destructor are highly aggressive freshwater crayfish native to Australia. We collected from a natural population of *C. destructor* in the water bodies at Idalia National Park, which is 1000 km north-west of Brisbane (latitude 24° 53' S, longitude 144° 46' E). For laboratory experiments, we sourced adults from a commercial aquaculture facility (Midwest Yabbies & Fish Traders Pty Ltd, Swan Bay, NSW, Australia). All crayfish were housed individually in aerated 12 litre containers with a 2 cm gravel base and polyvinyl chloride pipe for shelter. Crayfish were fed orca sinking pellets daily.

All experimental protocols used in this study were in accordance with the UQ Animal Ethics and Welfare Committee guidelines and Environmental Protection Agency permit number WITK05090908.

Signalling and fighting during competitive bouts

Competitive bouts were conducted between pairs of same-sexed crayfish to quantify the use of signalling and fighting during the establishment of dominance for males ($N=210$ bouts) and females ($N=195$ bouts). Animals used in this experiment were sourced from the aquaculture supplier. Fights were conducted in a 20 litre plastic observation tank that contained aerated water and a 2 cm layer of gravel. Two crayfish were placed in the observation tank and were observed for a 10 min period. Each bout continued until one of the individuals established dominance. For each bout we noted whether dominance was established after only signalling (rubbing and tapping of chelae) or after contact escalated into a fight (grappling and flipping). Dominance was established when one individual backed down and moved away from their competitor. We discarded data from bouts where no clear winner emerged.

Signal size and force in a natural population of *C. destructor*

We collected 56 adult male and 46 adult female *C. destructor* from natural populations at Idalia National Park during March 2008. For each individual, we measured maximum chela force and chelae size to assess their natural variation in signal size and force for this species. Chela force was measured using a custom-built force gauge consisting of two stainless steel plates bolted to either side of a 5 mm piece of acrylic that acted as a pivot (Seebacher and Wilson, 2006). Crayfish were encouraged to grab the two metal plates, which bent

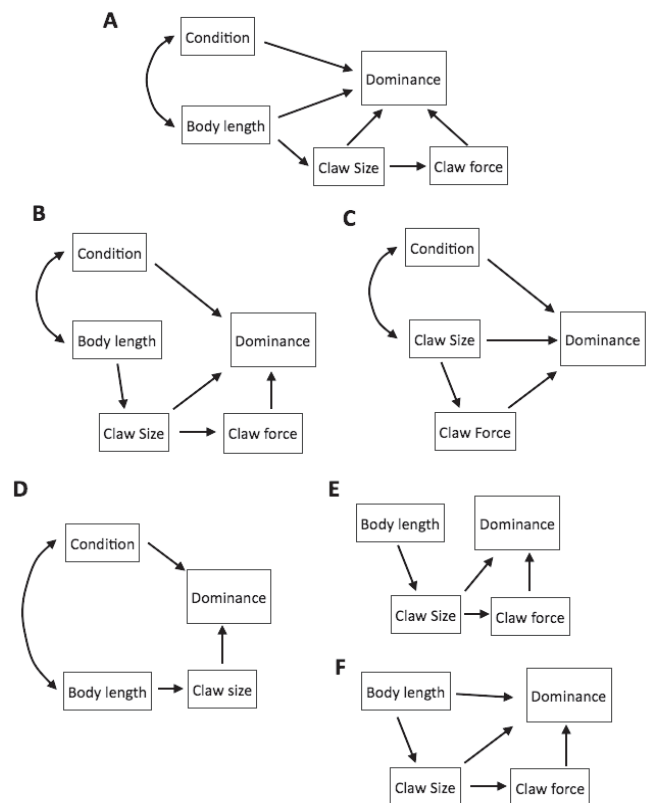


Fig. 1. Six path models (A–F) relating morphological and physiological characteristics of male and female common yabbies (*Cherax destructor*) to their dominance during competitive bouts.

proportionally to the force applied. A strain gauge was attached to the metal plate at the pivotal point to measure changes in resistance as the plates bent. The force gauge was calibrated using a series of known weights. Crayfish were induced to grab the plates five times and the strongest measurement was used as their maximum chela closing force. Both chelae of each crayfish were measured and the mean of the maximum force of each chela was used as a measure of chela force for each individual. Data were recorded in millivolts using Chart 5.0 for Windows *via* a Powerlab (ADInstruments, Sydney, NSW, Australia), which was connected to the transducer by BridgePod amplifiers (ADInstruments) and a custom-made wheatstone bridge. Repeatability of chela force measurements was tested in a sub-set of the crayfish by recording force (males $N=6$; females $N=11$) over two consecutive days. Correlation analysis indicated that our measures of maximum force were highly repeatable over consecutive days ($R_p=0.97$, $P<0.0001$).

Chela size was measured from digital images of the chelae using ImageJ software (www.rsweb.nih.gov/ij/). Seven measurements were taken of the left and right chela of each individual: the width of the propodus at the joint of the carpus, the width of propodus at the dactyl joint, the length of the propodus from the carpus joint to the dactyl joint, the width of the propodus at the dactyl joint, the width of the dactyl, the length of the propodus from the tip to the dactyl joint and the length of the dactyl. For each chela, a principal component analysis (PCA) of all individuals combined was used to condense the seven measurements into a single measure of overall chela size. For both chelae (in males and females) the first component of the PCA (PC1) accounted for more than 90% of the variation found among the seven variables. Because all morphological dimensions loaded strongly and positively onto this axis, PC1 was considered to be an accurate reflection of overall chela size. Chela size for each individual was then taken as the average of the first PCA component of the left and right chelae.

Determinants of social dominance in *C. destructor*

We used a total of 43 males and 36 females to assess the determinants of social dominance for *C. destructor*. Animals used in this experiment were sourced from the aquaculture supplier. Maximum chela force and size for each individual were measured as described above. Body length was measured from rostrum to telson using digital calipers (males, 109.87 ± 6.8 mm; females, 112.21 ± 5.9 mm) and body mass using digital scales (males, 43.74 ± 9.9 g; females, 43.30 ± 6.6 g). Social dominance was determined in staged competitive bouts between two individuals of the same sex.

In each trial, a focal individual was competed against a randomly selected opponent taken from a pool of separate crayfish with a

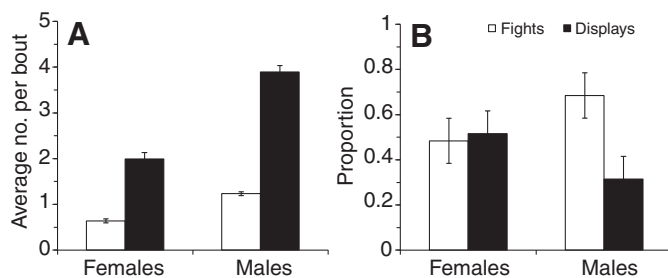


Fig. 2. The average number of fights (open bars) and signal displays (filled bars) per competitive bout (A) and the proportion of bouts in which signalling or fighting determined dominance (B) for male and female common yabbies (*Cherax destructor*). Values are means \pm s.e.m.

similar range of body sizes. Each focal individual was used in four separate trials, with four different opponents. Fights were staged in a 20 litre aquarium containing gravel and aged tap water maintained at 25°C. The focal crayfish and opponent were placed at either end of the tank separated by an opaque divider. At the end of a 2 min settling period the divider was removed allowing the crayfish to interact freely for 10 min. An overall measure of dominance was quantified by assigning scores to each focal crayfish. The average score across all bouts for each individual was taken as their total dominance score. Focal animals were awarded points according to their performances in the bouts. The two most prevalent and easily recognized interactions between crayfish were direct physical combat (fights) or signalling (displays). Fights were defined as two animals facing each other with each attempting to grasp and unbalance the other, with one backing down and retreating. In a bout using signalling alone, one of the animals would turn and retreat without engaging in a fight. At the conclusion of the interaction period, a dominance score was calculated for the focal crayfish using the following equation: dominance score = [(number of fights won – number of fights lost) $\times 2$] + (number of displays won – number of displays lost).

Data analyses

The level of interactions among competing crayfish and the mode of determining dominance during bouts were compared between the males and females of both species. The average number of fights and displays per bout was analysed using a generalised linear model (GLM) with a Poisson distribution. Where dominance was gained, the proportion of fights *versus* the proportion of displays, for each sex, was analysed using a χ^2 contingency table.

To describe the relationship between morphology and performance with social dominance for both males and females we used path analysis to construct six different models (Fig. 1). We compared how these different models fit our data using an information-theoretic approach using Amos 5.0 (SPSS Inc., Chicago, IL, USA). Morphological and physiological variables, included body condition (residuals of body mass on length), body length, chela size and chela

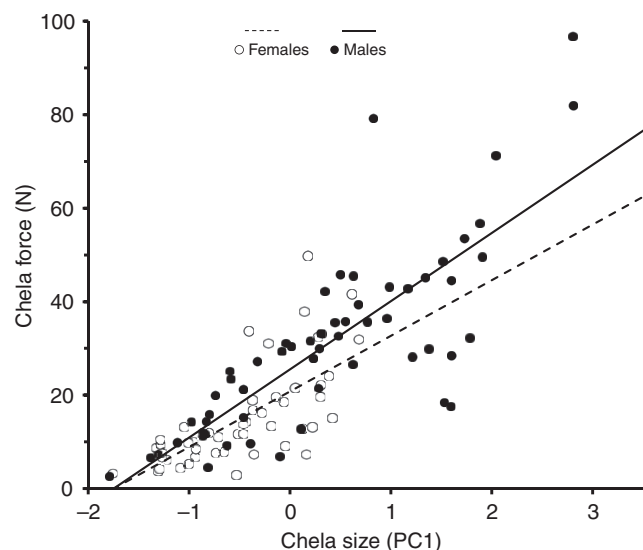


Fig. 3. The relationship between chela size (PC1) and force for male and female *C. destructor* from a natural population in Idalia National Park. Significant correlations between chela size and chela force were detected for both males ($F_{1,56}=98.0$, $P<0.0001$) and females ($F_{1,46}=40.8$, $P<0.0001$).

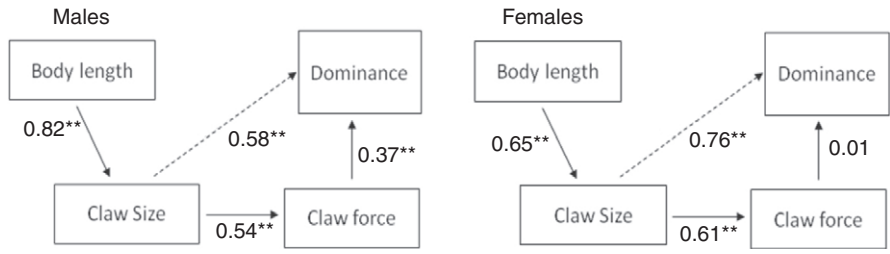


Fig. 4. The best path model relating morphological and physiological traits to dominance for male (A) and female (B) *C. destructor*. For males, dominance is determined by both chela size and force, whereas for females, dominance is determined by chela size alone. ** $P < 0.001$.

force. Models were then ranked in order of their likelihood based on their Akaike information criteria (AIC) using the equation:

$$AIC_c = \chi^2 + 2K + [2K(K + 1)] / (N - K - 1). \quad (1)$$

where K is the number of parameters estimated, N is the sample size and χ^2 is the chi-squared goodness of fit (Wilson et al., 2007). This equation ranks models by punishing for complexity and rewarding models that have a greater χ^2 goodness of fit.

Finally, we also assessed the relationship between chela force and dominance status among both males and females using residual analyses that corrected for overall chela size. These relationships were analysed using a Pearson's product moment correlation. All results are presented as means \pm s.e.m. and significance was taken at the level of $P < 0.05$.

RESULTS

We found that male *C. destructor* signalled more often ($F=1240.66$, d.f.=285, $P < 0.0001$) and engaged in more fights than females ($F=520.9$, d.f.=285, $P < 0.0001$; Fig. 2A). In addition, male *C. destructor* relied more on fights than displays when determining dominance ($F=32.285$, d.f.=144, $P < 0.0001$). In contrast, female *C. destructor* used an equal number of fights and displays to determine dominance ($F=40.703$, d.f.=138, $P=0.35$; Fig. 2B).

We found *C. destructor* collected from the natural population in Idalia National park exhibited substantial variation in chela force for any given size of chela (Fig. 3). For this natural population the coefficients of variation (CV) for chela force for both males and females was greater than 40% (males, CV=44.2%; females,

CV=45.6%; Fig. 3). When compared with individuals sourced from the commercial aquaculture facility, the natural population showed approximately 10% greater variation in chela force (aquaculture: male, CV=33.6%; female, CV=35.3%).

Of the six models evaluated, a model relating body length, chela size and force with dominance (model E) was the most likely to be the best descriptor of the data for males and females (Fig. 4; Table 1). However, the predictors of social dominance differed between the sexes. For males, both weapon size and force were significantly related to social dominance. However, for females, only chela size was significantly related to social dominance and there was no relationship between chela force and dominance (Table 1), suggesting dominance is often based on highly inaccurate signals alone (unreliable signals).

We also found that males with high force residuals (high force for their chela size) were more likely to have greater social dominance ($r_p=0.35$, $F_{1,36}=19.571$, $P < 0.0001$; Fig. 5A). In contrast, greater or weaker force for a given chela size did not affect the overall social dominance of the females ($r_p=9e^{-05}$, $F_{1,33}=0.003$, $P=0.957$; Fig. 5B), further indicating that unreliable signalling is routinely used by female *C. destructor*.

DISCUSSION

Variation in weapon force for a given weapon size creates a scenario whereby the actual fighting potential of an opponent is difficult to assess through signalling alone. In our study, we found substantial natural variation in weapon force for a given chela size for both male (CV=44%) and female (CV=46%) *C. destructor*, which is

Table 1. Comparison of path models describing the relationships among morphological traits, physiological performance and total score of dominance for both male and female *Cherax destructor*

Path	Model	χ^2	d.f.	K	AIC _c	Δ_i	Likelihood	w _i	Rank
Females									
A	Condition, direct effect of body length, claw size, claw force	45.2	3	17	113.20	66.73	0.00	0.00	6
B	Condition, indirect effect of body length, claw size, claw force	45.8	4	16	106.43	59.97	0.00	0.00	5
C	Condition, claw size, claw force	7.0	1	13	49.55	3.08	0.21	0.16	2
D	Condition, indirect effect of body length, claw size	36.3	2	12	73.87	27.40	0.00	0.00	4
E	Indirect effect of body length, claw size, claw force	8.9	2	12	46.47	0.00	1.00	0.75	1
F	Direct effect of body length, claw size, claw force	8.2	1	13	50.75	4.28	0.12	0.09	3
Males									
A	Condition, direct effect of body length, claw size, claw force	51.4	3	17	114.54	68.08	0.00	0.00	6
B	Condition, indirect effect of body length, claw size, claw force	52.6	4	16	109.33	62.86	0.00	0.00	5
C	Condition, claw size, claw force	2.8	1	13	43.36	-3.11	4.72	0.05	3
D	Condition, indirect effect of body length, claw size	49.8	2	12	85.80	39.33	0.00	0.00	4
E	Indirect effect of body length, claw size, claw force	1.6	2	12	37.60	-8.87	84.15	0.82	1
F	Direct effect of body length, claw size, claw force	0.7	1	13	41.26	-5.21	13.50	0.13	2

AIC_c, Akaike information criterion; d.f., degrees of freedom; K, number of parameters; Rank, ranking of models; w_i, the Akaike weight; Δ_i , differential AIC_c; χ^2 , χ^2 goodness of fit.

Model E was chosen as the best predictor of the data for both males and females as it was deemed to be >75% likely to be the best predictor for dominance using the morphological and physiological variables.

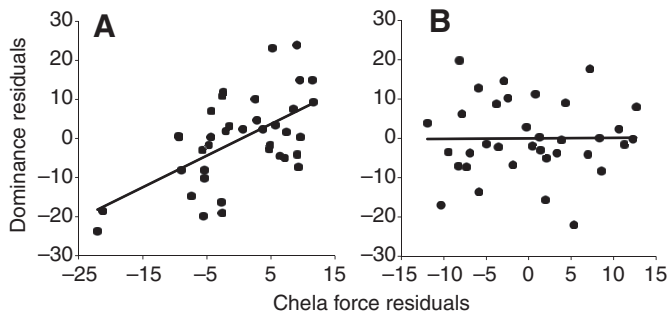


Fig. 5. The relationship between chela force (residuals on chela size) and dominance scores (residuals on chela size) for male (A) and female (B) *C. destructor*. There was a positive correlation ($r_p=0.35$, $F_{1,36}=19.571$, $P=8.6e^{-05}$) for males, but no significant correlation ($r_p=9e^{-05}$, $F_{1,33}=0.003$, $P=0.957$) for females.

similar to that previously reported for *C. dispar* (males, $CV=75\%$; females, $CV=31\%$) (Wilson et al., 2007; Bywater et al., 2008). It is this variation between signal and an individual's actual performance (or potential to inflict a cost on an opponent) that forms the basis or opportunity for unreliable signals of strength to be used to determine dominance. The concealment of muscle within the exoskeleton of crustacean claws may be the primary reason why unreliable signalling has often been observed in this group (Steger and Caldwell, 1983; Berglund et al., 1996; Hughes, 2000; Wilson et al., 2007). This seems particularly important for crustaceans, given that theory predicts that the likelihood of deception in natural populations should be governed by the potential costs associated with testing opponents and the difficulties with accurately assessing signal quality (Gardner and Morris, 1989; Johnston and Grafen, 1991; Számádó, 2000).

The simplest strategy for animals to detect unreliable signals of strength, and to restrict their use in gaining access to resources, is to use the social mechanisms of testing an opponent's strength. Without the social mediation of unreliable signalling, opponents may base dominance decisions on a signal disassociated from an individual's condition, leading to low-condition animals commonly gaining dominance (Searcy and Nowicki, 2005). However, the costs of engaging in combat and testing the actual strength of an opponent can make the reliance upon signalling based on these variable and inaccurate signals of strength a preferable strategy. This reliance on unreliable signals of strength has been previously reported for males of the slender crayfish *Cherax dispar* (Wilson et al., 2007). For male *C. dispar*, most disputes are decided at the signalling stage before any physical combat occurs, but the size of the weapon is often a poor indicator of an individual's strength. Thus, weaker *C. dispar* males often gain dominance over stronger rivals because signalling alone is used to determine the outcomes. In contrast, we found *C. destructor* males commonly engaged in physical fights to settle disputes, thus socially mediating their unreliable signals by directly limiting the benefits accrued to individuals employing high-quality signals with only low RHP. However, we found that female *C. destructor*, which also produce unreliable signals of strength, primarily rely on signalling to settle disputes and often make poor judgements on the relative chances of beating an opponent in a fight. Thus, we found male *C. destructor* were more aggressive, more likely to escalate encounters to physical fights and usually spent a greater amount of time signalling to opponents than females. As a result of these differences in fighting behaviour between male and female *C. destructor*, dominance among males was strongly

correlated with both chela size and chela force, whereas dominance among females was associated with chela size.

Recent theoretical advances in our understanding of the evolution of signal reliability (Getty, 2006; Számádó, 2011), which have also been mirrored with more directed empirical studies (Murai et al., 2009), offer us a clearer framework for investigating the prevalence and distribution of unreliable signalling in animal communication. One central issue requiring empirical attention is determining how individual quality affects the association between the benefits of increasing signal magnitude against the associated viability costs of possessing such signals. For the most part our empirical understanding of the viability costs associated with increasing signal magnitude is patchy: only a few studies have shown potential viability costs (via social punishment) when signal size is experimentally manipulated (e.g. Barbosa and Moller, 1999; Tibbetts and Dale, 2004; Tibbetts and Izzo, 2010). However, one recent study provides a neat and powerful test of the role of signal quality on a potential viability–fecundity trade-off in males of the fiddler crab *Uca perplexa* (Murai et al., 2009). The maximum claw height achieved by male fiddler crabs during a courtship display (signal magnitude) is a strong predictor of the likelihood a female will visit a male's burrow (benefit). Murai et al. manipulated individual claw mass to determine if there was a trade-off between claw mass and wave height, and whether this trade-off was dependent on individual quality (Murai et al., 2009). They found that individuals with greater initial unmanipulated wave height experienced a smaller decrease in wave height after weight was added to their claw. In this case, the functional manipulation of a performance trait provided good support for the reduced marginal costs of signalling in higher-quality males. However, despite this recent work, the field of animal signalling lacks crucial data on how signal reliability affects the survival, growth, metabolism and behaviour of individuals. For most crustaceans, signal honesty is governed by the strength of their weapons, and as such they offer a neat experimental system for manipulating signal reliability and quantifying the various associated consequences.

ACKNOWLEDGEMENTS

We thank everyone in the Integrative Ecology Lab (www.insideourlab.blogspot.com) for assistance in both the field and lab. Our research was financially supported by an ARC project awarded to R.S.W.

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