

# Weapon size is a reliable indicator of strength and social dominance in female slender crayfish (*Cherax dispar*)

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## Summary

1. Weapons are specialized structures that are commonly used by animals to signal fighting ability and resource holding potential during agonistic encounters. Current theory predicts weapon size should reliably indicate weapon strength and unreliable signals should only occur at very low frequencies in nature. However, a recent study found weapon size was an unreliable signal of strength during agonistic interactions among males of the slender crayfish (*Cherax dispar*).

2. In this study, we investigated the relationship between morphology, performance and social dominance in females of *C. dispar*. Based on current theory, we predicted chela size would reliably indicate chela strength and would relate indirectly to dominance via its influence on strength.

3. We found females that possessed large chelae were more likely to possess stronger chelae, and those individuals with stronger chelae were more likely to win competitive bouts. The best predictive model of the relationships among morphology, performance and dominance indicated chela size indirectly affected social dominance via its influence on strength, thus demonstrating displays of weaponry are reliable signals of fighting ability.

4. Reliable signals of strength among females of *C. dispar* supports current theory predicting stable signalling systems should largely consist of honest displays of strength. However, this contrasts with previous work demonstrating that male *C. dispar* routinely uses unreliable signals of weapon strength during agonistic encounters.

**Key-words:** Honest signals, weapons, performance, signalling, dishonesty

## Introduction

Intra-specific displays are commonly used by organisms during courtship and aggression (Backwell *et al.* 2000; Searcy & Nowicki 2005; Lappin *et al.* 2006). Displays are employed to portray availability for mates, attractiveness and demonstrate strength during aggressive interactions. Specialized structures (weapons) are often used to signal fighting ability and resource holding potential (RHP) (Searcy & Nowicki 2005) and individuals can use these signals to assess the competitive ability of their opponents (Hughes 2000). Fighting can be costly for organisms because it can be energetically expensive to partake in a fight and there are increased risks of injury and death (Hack 1997; Hardling *et al.* 1999; Briffa & Sneddon 2007; Oufiero & Garland 2007). Displays of potential fighting ability can be used to minimize the costs associated with intra-specific aggression by deciding disputes without physical contact (Briffa & Sneddon 2007), thus avoiding injury or death. Although there are costs associated with

displays, these would presumably be less than the costs associated with fighting. Conflicts should only escalate when individuals are fairly evenly sized, possess similar perceived RHP and the perceived benefit of the resource is high (Maynard Smith 1979; Vorburger & Ribi 1999).

Current theory predicts weapon size should be a reliable signal of weapon strength and unreliable or dishonest signalling of strength should be rare or absent in nature (Dawkins & Guilford 1991; Searcy & Nowicki 2005; Vanhooydonck *et al.* 2007; see Maynard Smith & Harper 2003 for review). Honest or reliable signalling of strength appears to be the most common system employed in nature (e.g. Dawkins & Guilford 1991; Vye *et al.* 1997; Sneddon *et al.* 2000; Vanhooydonck *et al.* 2005, 2007), suggesting reliable signalling provides more benefits to both the sender and receiver of signals than an unreliable system would. The benefits and costs within a reliable system are related to the strength of the competitors and the value of the resource being fought over. Hence, a reliable system should be an evolutionary stable strategy (Searcy & Nowicki 2005). However, few studies have tested the reliability of weapon size as a signal by directly

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examining the relationships between the size and strength of the primary weapon and social dominance (Irschick *et al.* 2007; but see Lappin *et al.* 2006). Despite current theory predicting most signals of strength should be reliable, researchers have reported several cases of unreliable signalling of strength (e.g. Steger & Caldwell 1983; Backwell *et al.* 2000; Elwood *et al.* 2006; Wilson *et al.* 2007). For example, Steger & Caldwell (1983) found that newly moulted stomatopods had weakened exoskeletons and employed a 'bluff' strategy to mislead opponents of their immediate strength. In a recent study, Wilson *et al.* (2007) reported that males of the slender crayfish (*Cherax dispar*) also routinely use unreliable signals of strength during agonistic interactions.

Males and females of the slender crayfish use the size of their enlarged front chelae as signals of dominance during aggressive encounters (Wilson *et al.* 2007). Most disputes between competing individuals (> 80%) are resolved before they escalate into physical fights (Wilson *et al.* 2007). For encounters that do not escalate into a fight, relative size of the chelae is a better indicator of dominance than body size, thus chela size is used as a means of determining whether an individual engages in a fight or retreats. At least for males, only individuals closely matched for chela size engage in physical combat, and the winners of these disputes are those individuals with the strongest chelae (Wilson *et al.* 2007). Given individuals use relative chela size as a signal of potential strength (Maynard Smith & Harper 2003; McGregor 2005), then theory predicts that chela size should be associated with dominance via its effects on strength (reliable signal of strength). However, weapon size was not always a reliable indicator of weapon strength for males of *C. dispar* (dishonest signals of strength) and chela size was directly related to social dominance (Wilson *et al.* 2007).

In this study, we examined the relationship between morphology, performance and social dominance among females of the Australian slender crayfish (*C. dispar*). We investigated whether dishonest signals of strength were only restricted to the larger and more territorial males of this species or if they were routinely employed by both sexes. In a reliable signalling system, we predict chela size (weapon size) would determine social dominance via its influence on chela strength. In an unreliable system, chela size would directly affect social dominance but would not be a reliable indicator of chela strength. We evaluated five competing models relating morphological and physiological traits to dominance during agonistic encounters. Using path analysis and AIC, we distinguished among competing models that incorporated direct and indirect effects between weapon size, strength and social dominance. Thus, we directly tested the reliability of weapon size as a signal of weapon strength and social dominance.

## Methods

The Australian slender crayfish, *C. dispar*, is one of 17 species of freshwater crayfish found in Queensland (Riek 1951). *Cherax dispar* is found on the mainland from Brisbane to Maryborough (Riek

1969; Crandall *et al.* 1999) and on the sand islands off the coast of South-East Queensland (Riek 1951). All slender crayfish used in this study were collected from streams on North Stradbroke Island, Australia (27°30' S, 153°30' E). All animals were caught using baited traps and by dip netting.

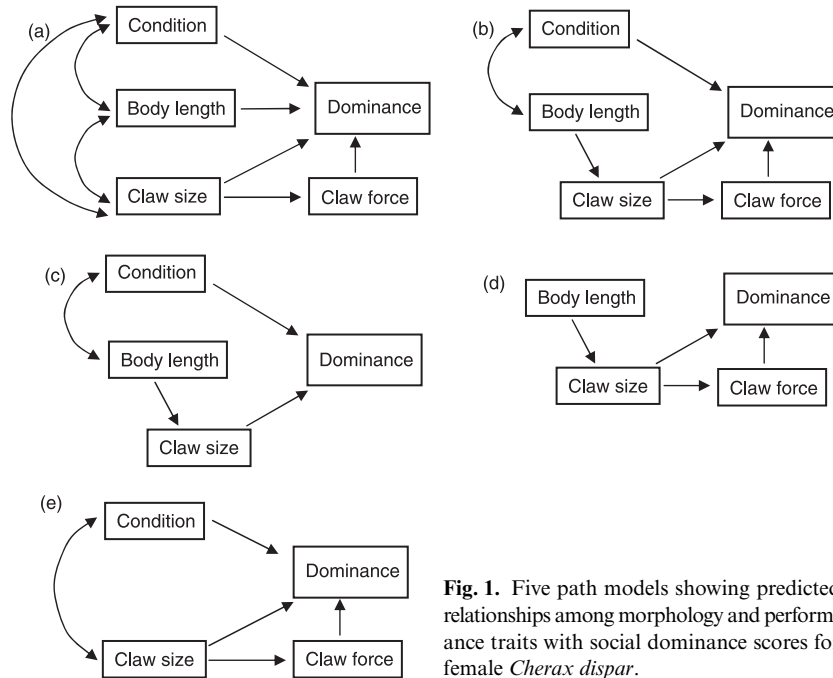
## STUDIES OF DOMINANCE

Forty-one females were collected from the field and immediately returned to Moreton Bay Research Station where they were individually housed in 5-L jars containing natural creek water (maintained at 20 °C), gravel substrate and shelter. For each individual crayfish, we recorded the size of each chela, the maximal chela strength for both chelae and social dominance.

For each crayfish, we recorded body mass, body length (distance from the tip of the rostrum to the end of the tail) and chela size. Body lengths were measured using digital callipers and mass with an electronic balance. Photographs were taken of the left and right chelae of each crayfish, using a Canon digital camera (Model: IXSUS50) and by holding chelae against graph paper for scale. Photographs were analysed using morphometric software (SIGMASCAN PRO 5); seven measurements for each chela were taken from the digital images to quantify its overall size. These measurements included the following: 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, principal components (PCs) analyses of all individuals combined were used to derive a single measure of size from the seven measurements recorded. Each chela was analysed separately and both analyses produced a first PC which accounted for more than 90% of the variation found among the seven variables. All seven measures of chela size were loaded in the same dimension and the first component of the PCA was a reflection of chela size. Mean score for the chela PCs (left and right chelae) was used as the measure for chela size in subsequent analyses.

Maximum strength of the left and right chelae was measured for each individual crayfish using a custom-built apparatus consisting of two flat pieces of metal (0.7 mm-thick) separated by a third (1.7 mm-thick), with strain gauges (RS Components, Australia) glued onto the outer side of each 0.7 mm-thick piece. When force was applied to each side of the apparatus, the 0.7 mm-thick metal pieces would bend at a rate proportional to the force applied. Each strain gauge could quantify the amount of bending in the metal plate and was connected to BridgePod amplifiers (AD Instruments, Australia) via a custom-made wheatstone bridge. The force applied to each side of the metal was recorded using a PowerLab (AD Instruments, Australia) system connected to a laptop. Data were recorded using Chart 5.0 and the chela strength apparatus was calibrated by hanging objects of known mass onto each of the metal pieces (with attached strain gauges). Force was recorded via the crayfish grabbing onto the metal pieces and the data were then converted to Newtons (N) for analysis. At least five chela grabs were recorded for each chela for each individual crayfish, and the greatest force measured for each chela was used as their maximum performance. Total chela force was calculated from the sum of both left and right chelae for each individual.

Competitive bouts were conducted between pairs of crayfish to quantify the social dominance capacity of each individual. Fights were conducted in a plastic observation tank (320 × 220 × 170 mm-deep)



**Fig. 1.** Five path models showing predicted relationships among morphology and performance traits with social dominance scores for female *Cherax dispar*.

that contained aerated natural creek water and a 2-cm layer of gravel. Two crayfish were placed in the observation tank and were observed for a 10-min period. During this time dominance activity was recorded based on two behaviours; 'chases' and 'fights'. Chases involved one crayfish retreating away from the other with minimal contact occurring. The remaining animal was scored as the winner. Fights were defined as aggressive interactions between the two crayfish. This was usually characterized by several actions including antennal and antennule contact (antennas touching or flicking), chela contact, grabbing with chelae and flipping. The winner was viewed as the crayfish remaining after one had retreated. The experimental design consisted of having a focal crayfish and a randomly assigned competitor that ensured that any winner- or loser-effects would be controlled (Seebacher & Wilson 2007). Each focal crayfish undertook three fights against opponents randomly chosen from the other 40 individuals. For each bout, points were awarded for winning a fight (two points) and chasing an opponent away (one point). At the end of each bout, three additional points were given to the winner; one point was awarded to each crayfish for a draw. Thus, a score of social dominance was calculated for each individual using the following equation;

$$\text{Dominance score} = \frac{[(W \times 3) + (D)] + [(F - A)]}{F_N}$$

where  $W$  is the number of wins,  $D$  is the number of draws,  $F$  is the total number of points accumulated during the bouts,  $A$  is the total number of points against and  $F_N$  is the total number of fights for that individual (Fig. 1).

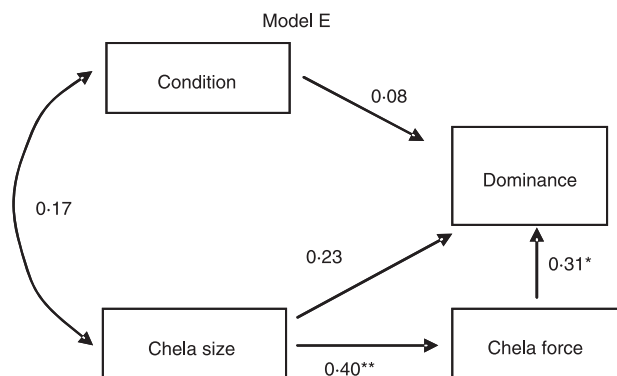
To describe the relationship between morphology and performance with social dominance ability, we compared the fits of five path models using an information-theoretic approach (Fig. 2). Each model was fit to the data using AMOS 5.0 (SPSS Inc., Chicago, IL). For the purpose of dominance analyses, body condition was used as a measure of body size. We used the residuals of body mass regressed onto body length as an index of body condition. Models were then ranked in order of likelihood by calculating the second-order AIC<sub>c</sub>;

$$\text{AIC}_c = \chi^2 + 2K + \frac{2K(K+1)}{n-K-1}$$

where  $\chi^2$  is the goodness-of-fit,  $K$  is the number of estimated parameters and  $n$  is the sample size (Burnham & Anderson 2002). Akaike weights were used to assess which model was the best descriptor of the data from the set of models.

#### REPEATABILITY OF CHELA STRENGTH

Repeatability of chela strength was determined for both male and female *C. dispar*. The maximum chela strengths of 30 males and 23 females were assessed each day for 2 days. Whilst in captivity, crayfish were individually housed in 5-L jars containing creek water, gravel and a shelter. Chela strength was assessed at 20 °C on 2 days separated by 24 h. Our methods were identical to those described above.



**Fig. 2.** The best path model explaining morphological and performance relationships with social dominance. Dominance is largely determined by chela force ( $P < 0.05$ ). Significant correlations were detected at the level of \* $P < 0.05$  and \*\* $P < 0.01$ .

**Table 1.** A comparison of path analysis models describing the relationships among morphological and performance traits with social dominance scores

Model	$\chi^2$	d.f.	$K$	AIC <sub>C</sub>	$\Delta_i$	$w_i$
Condition, chela size and force (Fig. 1e)	0.522	1	13	46.74	0	0.9530
Chela size, force and indirect effect of length (Fig. 1d)	13.415	2	12	53.84	7.09183	0.0275
Condition, chela size and indirect effect of length (Fig. 1c)	14.097	2	12	54.52	7.77383	0.0195
Condition, chela size, force and indirect effect of length (Fig. 1b)	17.456	4	16	85.72	38.97844	0.0000
Condition, length, chela size and force (Fig. 1a)	6.361	2	18	94.98	48.23216	0.0000

Where  $\chi^2$  is the goodness-of-fit; d.f. is the degrees of freedom;  $K$  is the number of parameters; AIC<sub>C</sub> is the Akaike information criterion;  $\Delta_i$  is the differential of AIC<sub>C</sub>; and  $w_i$  is the Akaike weight. The Akaike weight of each model is the likelihood that a particular model best describes the data. Model D was more than 95% likely to be the best predictor of the relationship among morphology, performance and social dominance.

All statistical analyses were run using SIGMASTAT 3.0 and STATISTICA 6.0. Repeatability of strength was determined by Pearson product-moment correlations between forces generated on days 1 and 2. Statistical significance was taken at the level of  $P < 0.05$  and data are presented as means  $\pm$  SE.

## Results

Of the five models that we evaluated, a model relating body condition and chela size to strength and dominance (Model E) was more than 95% likely to provide the best description of the data (Table 1; Fig. 2). Based on this model, larger chelae were capable of generating more force ( $P < 0.01$ ; Fig. 2). Furthermore, chela strength was significantly related to social dominance, suggesting displays of weaponry were reliable signals of potential strength during agonistic encounters ( $P < 0.05$ ; Fig. 2). Since body condition and chelae size were uncorrelated ( $r^2 = 0.03$ ,  $P = 0.32$ ), our interpretation of this model was unaffected by multicollinearity (see Petraitis *et al.* 1996). Given our results, chelae size reliably predicts RHP in females, even though it does not do so in males (Wilson *et al.* 2007).

This discrepancy between our results and those previously obtained for males were not caused by poor repeatability of performance. Measures of maximal chela force for both males and females of *C. dispar* were significantly repeatable over consecutive days (Fig. 3). Both male ( $r = 0.92$ ,  $P < 0.001$ ) and female ( $r = 0.85$ ,  $P < 0.001$ ) performed similarly between days, suggesting chela force accurately reflects an individual's physical capacity in both sexes.

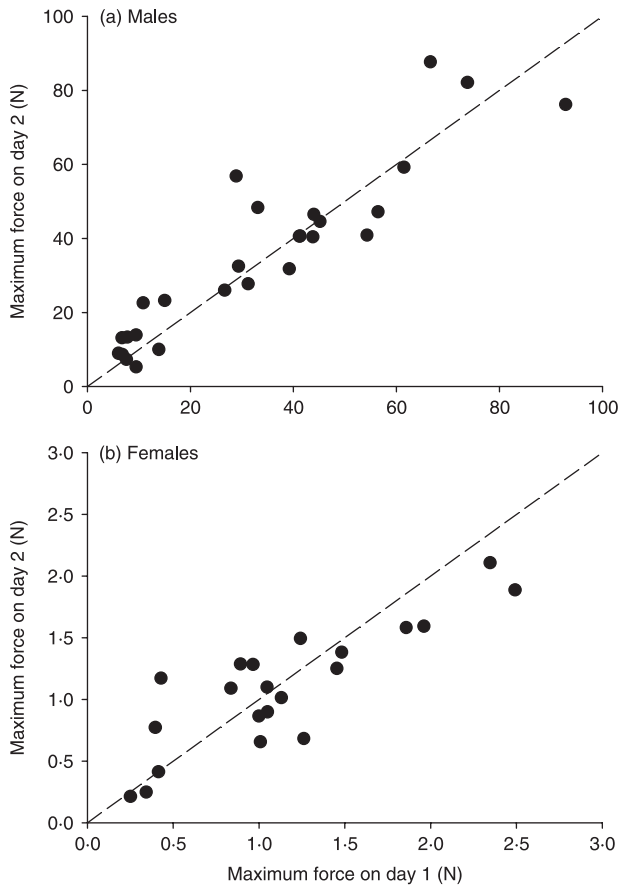
## Discussion

Most aggressive interactions among animals, and the slender crayfish (*C. dispar*) in particular, are resolved before direct fighting occurs (Hughes 1996; Vye *et al.* 1997; Wilson *et al.* 2007). Weaponry are used as signals of RHP and determine whether interactions advance to physical aggression (Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Briffa & Sneddon 2007). Similarly, we found that the majority of all disputes between female *C. dispar* were resolved before they escalated into physical combat. Thus, the relative size of the chelae was being assessed by each female and used a signal

of potential strength during combat. Current theory of signalling during agonistic encounters predicts weapon size should be a reliable indicator of weapon strength and weapon size should influence social dominance via its effect on strength. The signal of potential physical strength in crayfish is chela size, and most studies have found a close association between chela size and social dominance (e.g. Elwood *et al.* 2006). However, few studies have examined the effects of weapon size on social dominance via its influence on strength. We directly tested this prediction using females of *C. dispar* by comparing alternative models that explained the relationship between morphology, performance and social dominance. We found the best predictive model of our data demonstrated that weapon size was an important predictor of social dominance via its effects on weapon strength. Thus, weapon size was a reliable signal of strength for female *C. dispar*, and was also associated with their RHP.

In contrast with the reliable signalling of weaponry among females of *C. dispar*, Wilson *et al.* (2007) found social dominance among males of *C. dispar* depended on chela size alone and did not act via its influence on strength. This observation suggests chela size is an unreliable signal of strength among males of *C. dispar* (Wilson *et al.* 2007). Recently, Elwood *et al.* (2006) found small hermit crabs employed a dishonest signal by altering the type of displays produced during agonistic interactions according to the size and strength of their weapons: crabs were more likely to extend their chelipeds out of their shell if they were smaller than their opponent, impairing their opponent's ability to assess the size and strength of the cheliped. In contrast, Lappin *et al.* (2006) found honest signalling occurred in male collared lizards that displayed their jaw size (weapon) during gaping displays. Displays of their jaw muscles were clear and honest signals of their potential ability to inflict injury through biting (Lappin *et al.* 2006).

Assessment of whether signalling of potential strength is reliable or unreliable assumes we obtained accurate measurements of physical capabilities. By quantifying the repeatability of chela strength for both males and females, we assessed the validity of this assumption. The repeatability of an individual's performance measures illustrates the stability of the trait within an individual (Chappell *et al.* 1995; Elnitsky & Claussen 2006), the degree to which differences in



**Fig. 3.** Relationship between maximal chela force recorded on days 1 and 2 for males and females of the slender crayfish, *Cherax dispar*. Significant correlations were detected between days 1 and 2 for males ( $r = 0.92$ ,  $P < 0.001$ ) and females ( $r = 0.85$ ,  $P < 0.001$ ). The dotted lines represent a reference line with a slope of 1 that passes through the origin.

the trait vary over time (Austin & Shaffer 1992) and the upper limits for the heritability of a trait (Snyman & Olivier 1999). We found that measures of chela strength were highly repeatable for both males and females of *C. dispar*. Thus, differences in signalling systems between male and female *C. dispar*, and the conclusion that weapon displays are routinely unreliable among males, were unlikely an artefact of our measurements. Given males appear to routinely use unreliable displays of weaponry (Wilson *et al.* 2007), further investigations should focus on the underlying physiological determinants of chela strength for both males and females.

The ability to maintain territories and secure access to vital resources is believed to be an important determinant of fitness. Weapon size, weapon strength and body size are believed to be indicators of RHP and important factors associated with social dominance (Sneddon *et al.* 2000; Briffa & Sneddon 2007). Understanding the relationship between measures of whole-animal performance and social dominance enables one to infer the ecological consequences of performance. Although dominance has been previously linked to locomotor performance in lizards (Lailvaux *et al.* 2004), biting force appears to be more important for social dominance in staged

contests (Lailvaux *et al.* 2004; Huyghe *et al.* 2005; Husak *et al.* 2006; Lappin *et al.* 2006) and reproductive success in the field (Lappin & Husak 2005). As the bite apparatus appears to be the key weapon in agonistic encounters, this demonstrates a positive relationship between weapon performance and dominance in lizard populations. Dominance and fighting is important to the structure of crayfish populations (Bovbjerg 1953, 1956) and can determine an individual's RHP (Holdich 2002). The winner of a fight could control the resource for which it is fighting, whether it be territory, food or mates (Sneddon *et al.* 2000; Holdich 2002). Variability in chela strength has previously been found to influence the fighting success of shore crabs, but did not influence whether fights actually occurred (Sneddon *et al.* 2000). Although weapon strength was also a good predictor of social dominance among female *C. dispar*, this is not the case for males of this species (Wilson *et al.* 2007).

In summary, we found that the social dominance of females of *C. dispar* was enhanced by chela strength directly and chela size indirectly. Females that possessed large weaponry (chela) were more likely to possess stronger weaponry, which made them more likely to win competitive bouts. Thus, females used reliable signals of weaponry during competitive bouts, whereas males of *C. dispar* use unreliable ones (Wilson *et al.* 2007). Current models of signalling systems cannot account for the prevalence of dishonesty among male *C. dispar* (Maynard Smith & Harper 2003) and the theory underlying these predictions should be revisited.

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