

Costs and benefits of increased weapon size differ between sexes of the slender crayfish, *Cherax dispar*

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SUMMARY

Unreliable signals of weapon strength are considered to be problematic for signalling theory and reliable signals are predicted to be the dominant form of signalling among conspecifics in nature. Previous studies have shown that males of the Australian freshwater crayfish (*Cherax dispar*) routinely use unreliable signals of strength whereas females use reliable signals of weapon strength. In this study, we examined the performance benefits of increased weapon (chela) size for both males and females of *C. dispar*. In addition, we investigated the possibility of functional trade-offs in weapon size by assessing the relationship between chela size and maximum escape swimming performance. We found males possessed larger and stronger chelae than females and the variance in chela force was greater for males than females. By contrast, females possessed greater absolute and body length-specific escape swimming speeds than males. Swimming speed was also negatively correlated with chela size for males but not females, suggesting that a functional trade-off exists for males only. Decreases in swimming speed with increases in weapon size suggest there could be important fitness costs associated with larger chelae. Larger weaponry of males may then act as a handicap ensuring large chelae are reliable signals of quality.

Key words: dishonest signals, physical performance, signals of strength, weapon size.

INTRODUCTION

A mechanism explaining the elaborate colours, ornaments and displays commonly exhibited by males of many sexually dimorphic species was first explained by Darwin (Darwin, 1871). He suggested such traits could evolve by increasing a male's access to mates, either *via* male competition or female choice. Theory predicts that these elaborate signals are reliable indicators of a male's quality and/or resource holding potential (RHP) (Maynard Smith and Harper, 2003). The reliability of these sexual signals is believed to be ensured *via* two main pathways (indices and handicaps) (Andersson, 1994), although other mechanisms have been suggested (Searcy and Nowicki, 2005). 'Indices' are signals that are reliable because they cannot be faked (Maynard Smith and Harper, 1995; Hughes, 2000) and their intensity is causally related to the quality being signalled [performance-based signal (Enquist, 1985)]. 'Handicaps' are reliable because they are costly to produce and/or have costly consequences such as increased predation (Zahavi, 1975; Adams and Mesterton-Gibbons, 1995).

Males of many species possess specialised weapons that are often displayed to resolve territorial disputes without direct physical contact. For most organisms, signals of weapon size appear to be accurate or reliable predictors of strength or fighting ability (e.g. Dawkins and Guilford, 1991; Vye et al., 1997; Sneddon et al., 2000; Malo et al., 2005; Vanhooydonck et al., 2005), although not all studies have directly measured weapon performance (see also Sneddon et al., 2000; Huyghe et al., 2005; Lappin et al., 2006). However, there are a few reported cases of unreliable (or dishonest) signals of both fighting ability and mate choice signals (Steger and Caldwell, 1983; Backwell et al., 2000;

Wilson et al., 2007). Unreliable signals of potential fighting ability are considered to be problematic for signalling theory as it is not clear how these signals are maintained as a stable strategy within a population (Maynard Smith and Harper, 2003). Current theory predicts unreliable signalling of weapon strength should be rare or absent in nature (Maynard Smith and Harper, 1988; Gardner and Morris, 1989; Dawkins and Guilford, 1991; Adams and Mesterton-Gibbons, 1995). However, Számadó provides a model that predicts some level of dishonesty during symmetrical aggressive signalling can be maintained as a stable strategy within a population (Számadó, 2000).

Signals of weapon strength should be expected to be physiologically linked to competitive ability so that animals of low competitive ability cannot produce the signal of an animal with high competitive ability (Wiley, 1983; Maynard Smith and Harper, 1988) [i.e. indices of RHP (Maynard Smith and Harper, 2003)]. In contrast with theoretical predictions, males of the Australian slender crayfish (*Cherax dispar*) routinely use unreliable signals of weapon strength during agonistic interactions (Wilson et al., 2007) whereas females use reliable signals of strength (Bywater et al., 2008). Both males and females of the slender crayfish use the size of their enlarged front claws (chelae) as signals of dominance during aggressive encounters (Wilson et al., 2007). Most disputes between competing individuals are resolved before they escalate into physical fights (Wilson et al., 2007) and the relative size of the chelae is usually 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) [see also Seebacher and Wilson for *Cherax destructor* (Seebacher and Wilson, 2006)].

In this study, we examined both the functional benefits and costs of possessing larger chelae (weapons) for males and females of the Australian slender crayfish (*Cherax dispar* Riek 1951). Firstly, we examined the benefits of possessing larger weaponry for chela strength. Given that chela size is an unreliable signal of strength for males (Wilson et al., 2007) and a reliable signal for females (Bywater et al., 2008), we expected that males would display greater variation in chela strength for a given chela size than females. We also provided a detailed investigation of the *in vitro* contractile performance of chela muscle for both males and females. Finally, we investigated the possibility of functional trade-offs in weapon size (handicap) by assessing the relationship between chela size and maximum escape swimming performance for both males and females. We predicted that the larger chelae of males would lead to slower escape performance than females and males with larger chelae would display relatively slower swimming speeds.

MATERIALS AND METHODS

We collected adult slender crayfish from the western creeks of North Stradbroke Island (south east Queensland; 27 deg.29'S, 153 deg.24'E) and transported them to the Moreton Bay Research Station (University of Queensland, Australia) for experiments. Slender crayfish inhabit clear and tannin-stained freshwater streams and swamps on the sand islands off the south east Queensland coast. Slender crayfish routinely engage in disputes with conspecifics during both the day and night and visual signals are an important part of the aggressive behaviour of this particular *Cherax* species (Wilson et al., 2007). All experimental protocols were in accordance with the UQ Animal Ethics Committee and Queensland National Parks and Wildlife Service guidelines. All crayfish used in experiments were more than three days outside the pre- or post-moult stage. For analyses of the benefits of large chelae, we measured chela size and maximum chela closing force for 97 male and 60 female crayfish [male body length, 53.2±0.7 mm; female body length, 51.1±0.6 mm ($t=-2.23$; $P=0.027$)]. In addition, we compared the *in vitro* performance of chela muscle from males ($N=7$) and females ($N=7$) of *C. dispar*. Finally, we assessed the relationships between chela size and strength and escape swimming speed for 41 males and 28 females. All performance and behavioural tests were performed at 25°C. All individual crayfish were housed in individual 5-litre plastic containers filled with natural creek water and a 2 cm base layer of gravel. Crayfish were fed daily on pellets and maintained in the laboratory for 72 h before use in experiments.

Chela size and strength

Chela size was determined from images of the left and right chela recorded with a digital camera and analysed with morphometric software (SigmaScan 5.0, San Jose, CA, USA). For each chela, seven measures were taken to quantify size: total chela length, wrist depth, maximum chela depth, dactylus length, dactylus depth, propodus depth and propodus length (see Wilson et al., 2007). Because these variables were highly correlated, we used principal components analyses (PCA) to derive a single measure of mean chela size for our analysis. A separate analysis was conducted for each chela. Both analyses yielded a principal component that described over 90% of the variation in the seven variables. As both chelae are approximately symmetrical and equally used during agonistic encounters, we used mean PCA scores for both chelae of an individual for subsequent analyses.

Maximum strength of the left and right chela 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 piece of metal (1.7 mm thick), with one strain gauge (RS Components, Smithfield, NSW, Australia) glued onto the outer side of each of the 0.7 mm-thick pieces. 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 bridge amplifiers (BridgePod, AD Instruments, Sydney, Australia) *via* a custom-made Wheatstone bridge. The force applied to each side of the metal was recorded using a PowerLab (AD Instruments) system connected to a laptop and force measurements from each strain gauge were added together. 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.

In vitro chela muscle performance

We built upon earlier analyses of the *in vitro* performance of *C. dispar* chela muscle (Wilson et al., 2007) using more detailed analyses of *in vitro* muscle performance from seven males and seven females. Crayfish were euthanased prior to dissection. The propodal process was removed to free the dactyl from the rest of the propodus, whilst leaving the chela closer muscle intact. Dissection was performed at 25°C in an aerated saline solution with the following composition (in mmol l⁻¹): NaCl, 205; KCl, 5.4; MgCl₂ 2.7; glucose 10; HEPES 10.0; CaCl₂, 13.5; pH 7.4 at 20°C. The dactyl was clamped in a crocodile clip attached to a force transducer (Dynamometer UF1, Pioden Controls Ltd, Newport, Isle of Wight, UK) and the propodus was clamped in a crocodile clip attached to a servomotor (V201, Ling Dynamic Systems, Royston, Herts, UK). The muscle preparation was placed inside a temperature-controlled perspex bath with circulating saline solution saturated with air and maintained at 20±0.5°C.

A series of twitches was used to determine the stimulation amplitude and muscle length that generated the greatest isometric twitch force. Stimuli of 1.5 ms in duration were delivered *via* two parallel platinum wire electrodes placed on either side of the muscle. A 200 ms train of stimuli was then delivered to the muscle to elicit a tetanic contraction and the frequency of stimulation was adjusted to maximise the height of the tetanus (90–100 Hz). A resting period of 5 min was provided between each tetanic response. The experimental apparatus was controlled and data were collected using the Testpoint software package (CEC, Boston, MA, USA). Data were then exported and analysed in Microsoft Excel (Redmond, WA, USA). The maximal force produced by each muscle was corrected for propodus size, enabling us to compare muscle quality/stress between genders.

Trade-offs between chela size and maximum swimming performance

We determined the maximum burst swimming speed of 41 males (body lengths, 55.93±1.05 mm) and 28 females (body lengths, 51.90±0.78 mm) (body length; $t=-4.95$; $P<0.05$) by filming five startle responses for each individual with a high-speed digital camera recording at 250 Hz. We elicited swimming responses by placing crayfish into the centre of a swimming arena (glass aquarium 0.3×0.2×0.1 m deep) and gently touching the end of their chelae. Only responses from a stationary position that led to a powerful backwards swimming stroke with limited vertical movement (as

observed during filming) were analysed. We used a pair of metallic tongs to always touch the front chelae of each crayfish by approaching them from a frontal direction. Individuals were given five minutes rest between each recorded stimulus response and they displayed no signs of fatigue across the trials. Three types of escape tailflicks have been described in crayfish and lobsters: the medial giant tailflick (MG), the lateral giant tailflick (LG) and the non-giant tailflick (NonG) (Wine and Krasne, 1972; Edwards et al., 1999; Finley and MacMillan, 2002; Herberholz et al., 2004). Distinguishing among these three different types of escape responses can be difficult when observing freely moving crayfish (Jackson and MacMillan, 2000). Both the MG and NonG usually result in linear backwards swimming responses whereas the LG tailflick results in the crayfish pitching forwards and upwards away from the stimuli. The MG tailflicks are initiated by the receptive field at the anterior end of the animal and are activated by visual or tactile stimuli. Given we elicited responses that resulted in linear backwards swimming with one powerful backwards stroke and crayfish were stimulated by touching their chelae, we expect most of our observed responses were the more powerful MG type tailflicks. Although we cannot be certain an MG response was recorded in each case (rather than a NonG response), we only used the fastest recorded swim speed for each individual as a measure of their maximum performance.

We filmed swimming sequences by recording the image captured off a mirror angled at 45 deg. to the bottom of the glass-bottomed aquarium with a high-speed digital camera (Redlake Imaging Corporation, Tallahassee, FL, USA). The accompanying Redlake software package was used for analysis of the startle responses. We replayed sequences frame-by-frame and the centre rostrum region of the head (i.e. between the eyes) was digitised. We determined the distance moved by individual crayfish between each successive frame for each startle response sequence. We then calculated instantaneous measures of velocity by differentiating distance data that had been subjected to a three-point moving average filter (Walker, 1998; Wilson and Franklin, 1999). Smoothing filters are commonly utilised to minimise and control for measurement error during frame-by-frame analyses of high-speed video recordings when calculating instantaneous measures of speed (see Walker, 1998). The three-point moving average filter is one of the simplest algorithms that controls for this potential measurement error. From each startle response, we calculated maximum burst velocity and the total distance moved throughout the initial 120 ms response period. We used the fastest of the swimming sequences analysed for each individual as a measure of its maximum burst swimming performance (see Oufiero and Garland, 2007).

Statistical analyses

Chela shape was described by the residuals of the linear regressions of all original seven morphological variables on the estimate of 'chela size' (first component of PCA). These regressions were significant ($R^2 > 0.8$) and homogeneity of slopes allowed statistical analyses on these residual values. Thus, analyses comparing the shape of chela morphology between males and females were performed on residuals (relative differences) to remove the overall effects of chela size from individual traits. The relationship between body length/chela size and maximum chela force was compared between sexes using a general linear model with one continuous (body length/chela size) and one categorical factor (sex). Correlations between measures of swimming performance, chela force and chela size were performed on body length- or chela size (first component of PCA of chela size) residuals using the

Pearson's product moment correlation. Negative correlations between measures of performance and morphological traits indicate a functional (i.e. performance) trade-off. Some authors suggest that utilising residuals to examine relationships among continuous variables whilst holding a third factor constant may result in the loss of degrees of freedom (d.f.) (see Garcia-Berthou, 2001). Alternative methodologies utilise partial regression coefficients to express the correlation between two variables whilst maintaining other variables constant (Kachigan, 1991). In our study, both methodologies produced similar results and only those results using residual analyses are reported for continuity and graphical representation of the data. However, to demonstrate the rigour of the negative relationship between chela size and swimming speed for males, both analyses are reported. All results are presented as means \pm s.e.m. Significance was taken at the level of $P < 0.05$.

RESULTS

Chela size and strength

Males and females of *C. dispar* did not significantly differ in their relationship between body length and mean chela size ($F_{1,65}=1.65$; $P=0.203$). However, males possessed significantly larger mean chelae (0.21 ± 0.11) than females (-0.62 ± 0.07); $F_{1,65}=30.31$; $P < 0.001$). In addition, variance in mean chela size was greater for males than females (F -ratio=12.5; $P < 0.001$). There was a significant relationship between body length (*BL*) and chela force (F_{\max}) for

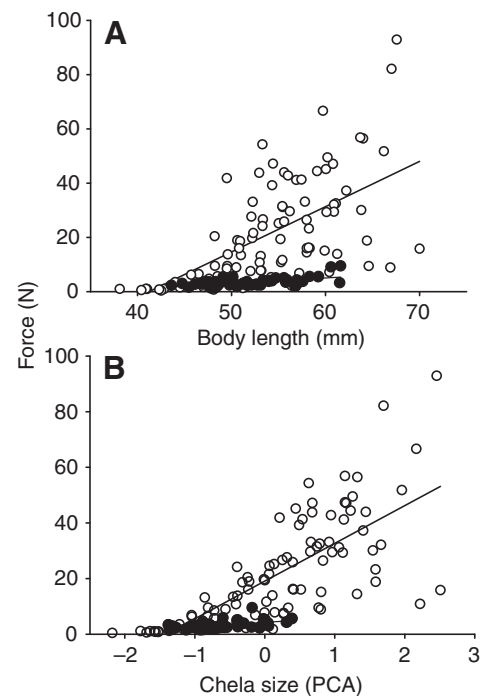


Fig. 1. The relationship between (A) body length and (B) chela size (first component derived from a PCA on the seven morphological variables) with maximum chela closing force for males ($N=97$) and females ($N=60$) of the Australian slender crayfish (*Cherax dispar*). Data points for the males are denoted by the open circle symbols and females by the closed circle symbols. A significant relationship between body length (*BL*) and chela force (F_{\max}) was detected for both males ($F_{\max}=1.67-63.8 BL$) ($R^2=0.38$; $P < 0.0001$) and females ($F_{\max}=0.42-7.56 BL$) ($R^2=0.45$; $P < 0.0001$). In addition, we also detected a significant relationship between chela size (*CS*) and chela force (F_{\max}) for both males ($F_{\max}=13.5+19.1 CS$) ($R^2=0.54$; $P < 0.0002$) and females ($F_{\max}=1.59+3.91 CS$) ($R^2=0.42$; $P < 0.0001$).

Table 1. Univariate analysis of variance (ANOVA) results testing the effect of sex on several morphological traits of chela size for *Cherax dispar*

Variable	Sex $F_{1,66}$	P
Wrist depth	7.80	0.007*
Maximum depth	7.96	0.006*
Chela length	6.45	0.013
Propodus depth	4.69	0.034
Dactylus depth	5.11	0.027
Propodus length	8.52	0.0048*
Dactylus length	7.73	0.007*

Analyses were performed on the relative size of morphological traits to chela size that was calculated as the first component derived from a principal component analysis (PCA) on the seven morphological variables (see Materials and methods for details). *Significant difference among groups taken after Bonferroni adjustment across the seven tests.

both males ($F_{\max}=1.67-63.8BL$) ($R^2=0.38$; $P<0.0001$) and females ($F_{\max}=0.42-7.56BL$) ($R^2=0.45$; $P<0.0001$). Additionally, males and females differed in the relationship between body length and chela force ($F_{1,158}=34.5$; $P<0.0001$) (Fig. 1A). Males produced significantly greater chela closing forces ($18.2\pm 1.6N$) for a given body length than females ($3.20\pm 0.18N$; $F_{1,158}=22.1$; $P<0.0001$) and the variance in chela force was greater for males than females (F -ratio=112.5; $P<0.0001$). There was also a significant relationship between chela size (CS) and chela force for both males ($F_{\max}=13.5+19.1CS$) ($R^2=0.54$; $P<0.0002$) and females ($F_{\max}=1.59+3.91BL$) ($R^2=0.42$; $P<0.0001$) (Fig. 1B). Male and female *C. dispar* also differed in the relationship between chela size and chela force ($F_{1,136}=10.3$; $P=0.002$) (Fig. 1B). Thus, for a given chela size, variation in chela force was greater for males than females.

Post-hoc tests revealed that the relative size of several chela dimensions (based on residual scores against chela size) differed significantly between sexes (Table 1). Males possessed greater wrist depths ($F_{1,66}=7.80$; $P=0.007$) and maximum chela depths ($F_{1,66}=7.96$; $P=0.006$) than females whereas females had greater propodus ($F_{1,66}=7.80$; $P=0.0048$) and dactylus ($F_{1,66}=7.80$; $P=0.007$) lengths than males (Fig. 2). Females with greater wrist depths ($N=37$, $r_p=0.40$; $P=0.01$) and maximum chela depths ($N=37$, $r_p=0.46$; $P=0.004$) possessed relatively stronger chela forces whereas females with greater propodus ($N=37$, $r_p=-0.42$; $P=0.01$) lengths possessed weaker chela forces. Females with greater dactylus lengths also had a tendency to possess weaker chela forces but this was not statistically significant ($N=37$, $r_p=-0.32$; $P=0.06$). Males with greater wrist depths did not have stronger chela forces ($N=25$, $r_p=0.20$; $P=0.33$) but those with greater maximum chela depths possessed stronger chelae ($N=25$, $r_p=0.58$; $P=0.003$). Males with greater propodus ($N=25$, $r_p=-0.48$; $P=0.01$) and dactylus ($N=25$, $r_p=-0.52$; $P=0.008$) lengths also possessed weaker chela forces.

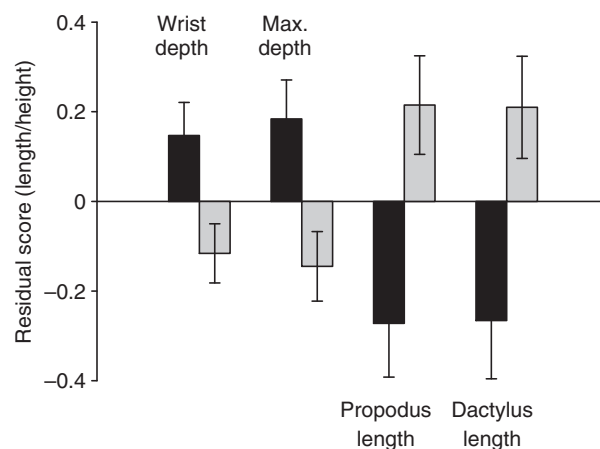


Fig. 2. Relative wrist depth, maximum chela depth, propodus length and dactylus length for males (black bars) and females (grey bars) of the Australian slender crayfish (*Cherax dispar*). Effects of overall chela size were removed from the analysis by taking the residuals of morphological measurements from a regression with 'chela size' (first axis of PCA). Significant differences were detected between sexes for all four morphological measurements. Data show means \pm s.e.m.

In vitro chela muscle performance

Maximum absolute tetanic force of male chela muscle was significantly greater than females ($P<0.001$) (Table 2). Twitch activation and relaxation times were significantly faster in females than males, being 41% faster to peak twitch force (Table 2) ($P<0.05$). Tetanus activation and relaxation times tended to be faster in females than in males, being 34% faster in time to half peak tetanus and 25% faster in time from last stimulus to half tetanus relaxation (Table 2) ($P<0.05$).

Trade-offs between chela size and maximum swimming speed

Females possessed greater absolute ($t=-5.67$, d.f.=67; $P<0.001$) and body length-specific ($t=-6.04$, d.f.=55; $P<0.001$) escape swimming speeds than males of *C. dispar*. The burst swimming speed of females was $142\pm 4.1\text{ cm s}^{-1}$ ($27.5\pm 0.94BL\text{ s}^{-1}$) whereas males only reached a peak speed of $107\pm 4.2\text{ cm s}^{-1}$ ($19.1\pm 1.0BL\text{ s}^{-1}$). In addition, swimming speed was negatively correlated with chela size in males of *C. dispar* ($N=41$, $r_p=-0.57$; $P<0.01$) (partial correlation coefficient=-0.45; $P=0.003$) (Fig. 3A). By contrast, swimming speed and chela size for females of *C. dispar* were not significantly correlated (Fig. 3B) ($N=28$, $r_p=-0.26$; $P=0.18$). Swimming speed and chela force were not significantly correlated in either males ($N=15$, $r_p=-0.29$; $P=0.30$) or females ($N=29$, $r_p=0.057$; $P=0.77$).

DISCUSSION

We found that male slender crayfish possess larger and stronger chelae than females and variation in chela force for a given chela size is greater for males than females. Thus, the greater variation

Table 2. Sexual dimorphism of chela muscle mechanics in Australian slender crayfish (*Cherax dispar*)

	Maximum tetanic force (N)	Time to peak twitch force (ms)	Time to half peak tetanus (ms)	Time from last stimulus to half tetanus relaxation (ms)
Male	1.3 \pm 0.04	43.6 \pm 5.6	42.4 \pm 8.5	168 \pm 20.8
Female	0.69 \pm 0.04	25.9 \pm 0.3	28.1 \pm 3.4	126 \pm 9.5
P	<0.001	0.019	0.14	0.10

Data represent means \pm s.e.m. $N=7$ in each case.

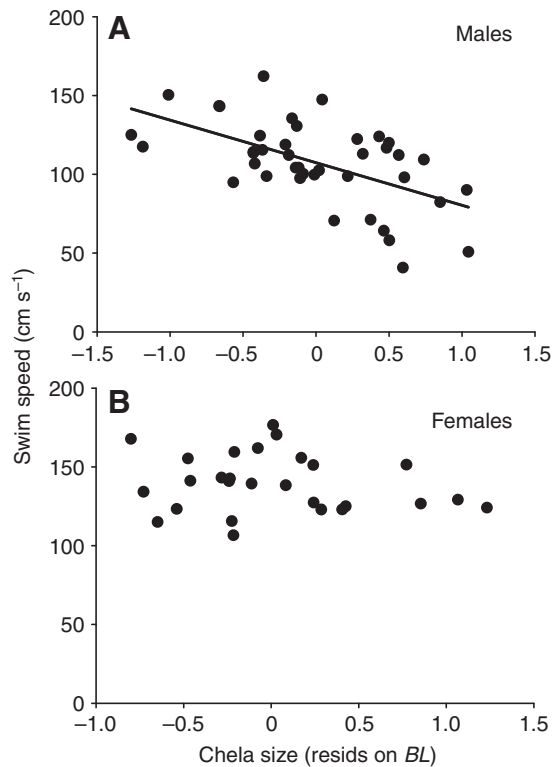


Fig. 3. The relationship between chela size and burst escape swim speed for (A) males and (B) females of the Australian slender crayfish (*Cherax dispar*). Males displayed a negative correlation between chela size and swim speed ($N=41$, $r_p=-0.57$; $P<0.01$) but there was no significant correlation for females ($N=28$, $r_p=-0.26$; $P=0.18$). Chela size was determined separately for males and females and was taken as first component derived from a PCA on the seven morphological variables.

in weapon strength makes the prediction of strength based on chela size alone more difficult. This would directly support the increased propensity for unreliable signals of strength among males of *C. dispar* (Wilson et al., 2007; Bywater et al., 2008). Females of *C. dispar* displayed less variation in strength for a given chela size, which supports the suggestion that displays of chela for females during agonistic encounters are reliable signals of strength (Bywater et al., 2008).

The effects of variation in chela morphology on force generation during chela closing have been studied in a variety of crab species (Schenk and Wainwright, 2001; Levinton and Allen, 2005). Essentially, the force generated is dependent on mechanical advantage of the chela, the mean angle of pennation, physiological cross-sectional area and maximal stress of the chela closer muscle. The mechanical advantage of the chela can be increased by reducing the length of the dactyl or increasing the distance from the dactyl pivot point to the point of chela closer muscle attachment. In our study, the combined effects of relatively greater chela depth and shorter dactyl length of males could support their greater chela force than females. Similarly, our analysis of individual variation in chela morphology with strength demonstrated that a decrease in dactyl and propodus length and an increase in chela depth all improved strength.

Most studies of weapon displays suggest they are commonly reliable signals of RHP (Maynard Smith and Harper, 2003). For example, the gaping displays of adult male collared lizards

(*Crotaphytus collaris*) provide a good example of an honest and accurate index of weapon (bite) performance. Male collared lizards expose the major jaw-adductor muscle complex to rivals (Lappin et al., 2006), which is correlated with the biting force of individual male collared lizards and is a good predictor of the number of females within their home range and mating success (Lappin and Husak, 2005). However, a few theoretical models (Adams and Mesterton-Gibbons, 1995; Számadó, 2000) and empirical analyses (Steger and Caldwell, 1983; Backwell et al., 2000; Wilson et al., 2007) indicate that some degree of dishonesty can be supported within natural populations. Newly moulted individuals of the stomatopod *Gonodactylus bredini* continue to give threat displays to opponents, despite their soft cuticle that impairs their fighting capacity (Steger and Caldwell, 1983; Adams and Caldwell, 1990). Interestingly, some of the most convincing examples of unreliable signals of strength are from studies of weapons among crustaceans (Steger and Caldwell, 1983; Backwell et al., 2000; Wilson et al., 2007). Although displays of chelae during agonistic encounters by crustaceans are obvious examples of signals of weaponry, their exoskeleton does not allow a direct visual assessment of the total muscle held, and thus strength, within the chelae. This provides an ideal prerequisite for the development of unreliable signals of strength and a possible mechanism for why crustaceans may have a greater predisposition for unreliable signals of weaponry.

The larger chelae of males were associated with decreased escape swimming performance. These costs for possessing larger chelae for males were not associated with chela strength and appeared to be directly related to the size of the chela rather than the size of the internal muscle. This negative correlation between swim speed and chela size does not necessarily mean a causative link. It is also possible that other variables may contribute to this pattern if they also covary with residual measures of chela size. However, further evidence suggesting larger chela directly reduced escape swim speed was the faster swim speeds of females than males, even though females possessed slightly smaller overall body lengths. Across the size range displayed by females, swim speed was unaffected by chela size. For crayfish with small chelae for their given body size, there appeared to be no difference in maximum swim speed between males and females. However, given male swim speed decreased with increasing chela size, there was a large disparity between the swim speeds of large chela males with all females. Decreases in swimming speed that are associated with increased weapon size in male *C. dispar* but unrelated to weapon strength suggest there may be important fitness costs for growing larger chelae. The mechanisms underlying this reduction in swim speed with larger chelae may be due to increased drag coefficients during swimming or resource-based costs caused by the diversion of energy away from the production of tail muscle to the chelae. The fitness costs are presumably associated with a decreased capacity to escape predators and an increase in overall energetic expenditure and can operate as a reliable handicap signal of possessing larger chelae. However, this does not take into consideration any possible compensatory changes in anti-predator behaviour that may minimise any potential fitness costs. For example, juveniles of the american lobster (*Homarus americanus*) possess chelae that are a smaller proportion of the body mass than their large abdominal muscles and they primarily rely on escape tailflicks when attacked by a predator (Lang et al., 1977). By contrast, adult *H. americanus* possess chelae that are a larger proportion of their body mass than the abdominal muscles and they utilise a raised claw threat display when confronted by predators (Lang et al., 1977).

Although weapons are usually considered indices of RHP (Maynard Smith and Harper, 2003), we found that weapon size of male *C. dispar* was not always a good predictor of chela strength and is thus not an incorruptible signal of performance. Furthermore, there were substantial locomotor costs associated with the development of large chelae for male *C. dispar*, suggesting the reliability of large chela size as a signal of quality may be ensured via a handicap. We suggest signals in intraspecific communication need not be exclusively classified as either indices or handicaps. Instead, some weapons may function as a combination of both types of signals that jointly ensure the reliability of indicators of individual quality (Maynard Smith and Harper, 2003). Thus, increases in weapon size for *C. dispar* may not only indicate an increased probability of greater weapon strength ('index'), which may be corruptible to some degree but may also have negative fitness consequences via a handicap. Combined signals of indices and handicaps (and other alternatives) (see Searcy and Nowicki, 2005), may ensure the reliability of the quality of individual males producing the signal during mate choice. We suggest the enlarged chelae of slender crayfish may act as both indices and handicaps, which may also explain the greater propensity for unreliable signals of strength among males of this species.

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