Signal residuals and hermit crab displays: flaunt it if you have it!

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In animal contests selection should favour information gathering regarding the likely costs and benefits of continued conflict, and displays may provide a means for contestants to gain information about the fighting ability or aggressive intent of competitors. However, there is debate over the reliability of such displays and low levels of deception may occur within otherwise honest signalling systems. Hermit crabs use displays involving the chelipeds during agonistic encounters. We examined how variation in chelae size in relation to body size, a determinant of fighting ability, affects their use in displays and the process and outcome of contests over gastropod shells. In accordance with deceptive use of an otherwise honest signal, we found that contestants with large chelipeds for their body size spent more time performing the cheliped presentation display. Moreover, cheliped residuals and displays influenced the escalation level of encounters. There was a positive association between cheliped displays and the occurrence of ‘grappling’, but a negative association between displays and the occurrence of shell fights, suggesting that displays may signal aggressive intent and a reluctance to back off or accept the more passive defender role in a fight. Furthermore, the smaller of the two contestants in shell fights had larger cheliped residuals compared to those smaller contestants not involved in shell fights, which is consistent with disrupted opponent assessment. This study adds to mounting evidence that when acting as a signaler, individuals for whom the display exaggerates competitive ability attempt to manipulate opponents, using the display more often.

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Agonistic encounters may be costly, in terms of energy use, time, risk of injury and increased risk of predation (e.g. Glass & Huntingford 1988; Kelly & Godin 2001; Briffa & Elwood 2004) and selection should favour information gathering regarding the likely costs (Arnott & Elwood 2009) and benefits (Arnott & Elwood 2008) of continued conflict, to enable contestants to make economic tactical decisions (Parker 1974; Maynard Smith & Parker 1976; Parker & Rubenstein 1981). Competitors might gain information about fighting ability (Parker 1974; Parker & Rubenstein 1981; Enquist & Leimar 1983) or aggressive intent (van Rhijn & Vodegel 1980; Enquist 1985) from prefight displays.

Early game theory models (e.g. Maynard Smith & Parker 1976; Maynard Smith 1979) suggested that competitors should not convey accurate information about resource-holding potential (RHP) or aggressiveness (intent), and individuals were expected to try to manipulate opponents (Krebs & Dawkins 1984). However, models incorporating handicap theory (Zahavi 1975, 1977) showed that honest signalling was likely (e.g. Enquist 1985; Grafen 1990; Johnstone 1998). Furthermore, some signals were considered to be a nonfakeable index of an animal’s size or condition (RHP) and thus to be accurate (Maynard Smith & Harper 2003; Vanhooydonck et al. 2007). Yet other models, however, showed that honest and deceitful signals can coexist in a stable system (e.g. Adams & Mesterton-Gibbons 1995; Szamado 2000). In particular, it has been argued that honest signalling is vulnerable to cheating in the sense that low levels of deception may be evolutionarily stable within otherwise honest systems (Bond 1989; Gardner & Morris 1989; Dawkins & Guilford 1991; Adams & Mesterton-Gibbons 1995; Getty 1997; Hughes 2000).

Studies on crustaceans provide a number of examples of apparent dishonesty. For example, during agonistic encounters in the stomatopod Gonodactylus breddini the meral spread display is given by both newly moulted and intermoult individuals, even though the former are incapable of following through with aggressive behaviour, and thus are effectively bluffing. Deception is possible because newly moulted individuals are rare in the population (Steger & Caldwell 1983). Fiddler crabs, Uca annulipes, with a regenerated large claw, may also deceive opponents. This claw weighs less, is a less effective weapon, and costs less to use in signalling, than the original claw (Backwell et al. 2000; Laiiaux et al. 2009). Males with regenerated claws tend to lose fights against those with original claws; however, the latter do not preferentially initiate fights with the former, because regenerated
claws act as an effective visual bluff of fighting ability (Backwell et al. 2000). In these two examples we can clearly distinguish between honesty and bluff by the ability or inability to follow up the threat display. However, since cheaters are evolved to go unnoticed, it may be difficult to distinguish between a successful bluff and an honest signal in other signalling systems.

An honest signal of competitive ability implies a close relationship between variation in the structure or performance of the signal and variation in RHP. For example, in the big-clawed snapping shrimp, Alpheus heterochaelis, chela (claw) size is positively related to body size (RHP; Hughes 2000). Thus chela displays should provide receivers with a reliable estimate of competitive ability. However, variation in signal structure that is not explained by variation in competitive ability may occur and Hughes (2000) suggested that the presence of dishonesty, defined as benefiting from an exaggerated advertisement that results from producing an inaccurately high level of the signal (Briffa 2006), could be detected by residual analysis. Snapping shrimp with positive residuals had larger chelae than predicted by body size, effectively signalling an overestimate of competitive ability. Thus, signal residuals indicate which individuals have the opportunity to exaggerate their RHP, and it is possible to test for deceptive use of the signal by determining whether signal use is related to signal residuals (Hughes 2000).

Deceptive use was indicated because the smaller snapping shrimp of contesting pairs produced chela displays in relation to their chela residuals. Deceptive use may thus depend on context. When facing a larger superior opponent it may pay smaller individuals with positive residuals to attempt to bluff, whereas the larger individuals may not need to bluff or exaggerate their competitive ability. Furthermore, when the smaller individual exaggerates its RHP, the contestants may appear to each other to be more closely matched than they are, making assessment difficult, leading to a higher level of escalation or longer contests (Parker 1974; Maynard Smith & Parker 1976; Parker & Rubenstein 1981). In line with this prediction, contests involving shrimp with larger chela residuals were longer and more highly escalated, suggesting that chela residuals affect assessment of competitive ability (Hughes 2000).

European hermit crabs, Pagurus bernhardus, use two types of cheliped display. 'Cheliped presentation', where the claws are held in a stationary position perpendicular to the substrate, often by both crabs, but for longer by the larger of a pair, enables a clear view in a stationary position perpendicular to the substrate, often by the attacker and winning a shell fight (Elwood et al. 2006). By contrast, the ‘cheliped extension’ display, in which the claws are held horizontal to the substrate and thrust at an opponent, does not appear to allow for mutual size assessment (Elwood et al. 2006). Furthermore, this display has been associated with increased chances of the larger crab becoming the attacker and winning a shell fight (Elwood et al. 2006). By contrast, the ‘cheliped extension’ display, in which the claws are held horizontal to the substrate and thrust at an opponent, does not appear to allow for mutual size assessment, and may contain an element of bluff. This display is performed more by the smaller crab and it reduces the probability of the larger crab assuming the attacker role, and, if it does take that role, decreases the chances of the larger attacker winning the contest (Elwood et al. 2006), presumably by having an effect on attacker motivation.

Laidre (2009) also investigated cheliped displays, using a model hermit crab with an extended cheliped that was moved towards the subject, which could either display or not to the model. Subsequently, the response of subjects was examined after the model probed them to the point of imminent physical contact. This revealed that 10% of probed crabs behaved as ‘liars’, by initially threatening the model, only to flee, rather than attack or stand their ground, when probed (Laidre 2009). Intriguingly, once again it was the smaller individuals that blufffed, with ‘liars’ weighing significantly less than those giving honest displays of intent, and threateners weighed less than the model (Laidre & Elwood 2008; Laidre 2009). Such low-level dishonesty about future intentions is perhaps unsurprising, given that theory predicts signals of intent to be especially prone to dishonesty (Maynard Smith 1974, 1979, 1982), particularly since these signals typically involve few or no production costs.

Our overall aim in the present study was to elucidate how variation in the size of chelae in relation to body size affects their use in displays. We first examined whether hermit crabs with larger cheliped residuals perform more cheliped displays, consistent with deceptive use. Second, we investigated the influence of cheliped residuals and displays on the escalation level of contests. Two types of escalation were examined: shell fights and grappling. In a shell fight one crab, termed the ‘attacker’, approaches and grapples the shell of the defender, causing the defender to withdraw into its shell (Dowds & Elwood 1983). The attacker may then engage in repeated bouts of vigorous shell rapping in which the attacker hits its shell upon that of the defender, until either the defender is evicted from the shell, enabling the attacker to take that shell, or the attacker gives up. It is only by engaging in a shell fight that contestants have the prospect of switching shells. By contrast, grappling involves mutual wrestling with the chelipeds and walking legs rather than one crab withdrawing into its shell. We compared interactions with or without grappling, and with or without a shell fight, with regard to associations with cheliped residuals and cheliped displays. Finally, we examined whether having large cheliped residuals influences the outcome of the encounter.

METHODS

The data for the present study on signal residuals were collected as part of a previous study (Arnott & Elwood 2007), involving staged encounters between pairs of crabs.

Collection and Maintenance of Specimens

Small (0.10–0.36 g) littoral specimens of P. bernhardus were collected weekly from the shore at Ballywalter, Co. Down, Northern Ireland, between June and December 2006. Specimens were kept in groups of up to 75 in plastic tanks (60 × 30 cm) filled with aerated sea water to a depth of 10 cm, at 12 °C with a 12:12 h day:night regime, and fed ad libitum on commercial fish food ‘catfish pellets’. We removed crabs from their shells by cracking the shells open using a small bench vice in such a way that no crabs were harmed. Each crab was then sexed (based on the number, position and morphology of abdominal pleopods, Elwood & Neil 1992), and males only were used in the study. Females were supplied with new shells, and returned to the sea, thus avoiding sex differences in behaviour that have been noted in previous studies (Neil & Elwood 1985). We used only male crabs that were free from loss of appendages, obvious parasites and recent moult.

Encounters

Each male was weighed and placed ‘naked’ in an individual 765 ml plastic dish 12 cm in diameter containing 300 ml of aerated sea water. Crabs were then allocated to pairs so that the larger of the two was no more than 10% heavier than its opponent. The study by Arnott & Elwood (2007) involved the use of two treatment groups to investigate how private information about shell resource value affects hermit crab contests, namely, how the presence of sand, glued to the inner whorls of shells, affected aggressive behaviour. Thus, pairs of crabs were allocated randomly to one of two treatment groups based on the toss of a coin. In the ‘control’
group, the smaller crab was given a shell that contained glue only and in the ‘sandy’ group the smaller contestant of each pair was provided with a shell that had sand glued to the inner whorls (see Arnott & Elwood 2007). The preferred weight of shell for the larger crab of each pair was determined using previously calculated regression lines that relate crab weight to preferred shell weight, obtained during previous shell choice experiments (Jackson 1988).

In all cases, the smaller crab of each pair was provided with a L. obtusata shell that was matched to the preferred weight for the larger crab, while the larger crab of each pair was given a L. obtusata shell that was 50% of its preferred weight (N = 60 for each group). Supplying the larger crab of each pair with a suboptimal shell heightens motivation to engage in a contest, and the presence of the smaller opponent in an apparently optimal shell for the larger crab further increases the likelihood of a shell fight.

Each crab was isolated with its new shell in a 765 ml plastic dish 12 cm in diameter containing 300 ml of aerated sea water at 12 °C for 3 h prior to the contest being staged. Interactions were observed in a glass bowl 14 cm in diameter containing 350 ml of aerated sea water and a layer of aquarium gravel 3 cm deep. The crabs were separated in the contest arena by placing them inside two clear plastic cylinders (3.7 cm diameter and 5.5 cm height) positioned such that the cylinders were touching, enabling visual contact for 2 min before the cylinders were removed and the observation started. A camcorder was used to record the subsequent interactions and then analysed using a Psion Workabout hand-held computer configured as a time-event recorder using the Observer 3.0 software (Noldus Technology, Wageningen, Netherlands).

Interactions were allowed to continue until the attacker either evicted the defender or gave up without effecting an eviction or, if a shell fight was not initiated, after 30 min.

We recorded displays, including ‘cheliped presentation’ (the proximal part of the chelipeds is held forward, towards the opponent, with the distal part (claw) being approximately perpendicular to the substrate); ‘cheliped extension’ (the major, often with the minor, cheliped is moved forwards with the claw(s) approximately horizontal to the substrate and raised up at least to the level of the head of the displayer, typically with the chela(e) open); and ‘grapple’ (mutual wrestling with the chelipeds and walking legs). If a shell fight occurred, the pattern of shell rapping, duration and outcome were also recorded.

After the interaction, crabs were removed from their shells and shield length (a measure of body size), defined as the distance from the tip of the rostrum to the end of the hardened section of the carapace (Markham 1968) was recorded. Major cheliped length and width were also measured to calculate major cheliped surface area. Crabs were then provided with suitable shells and returned to the collection site. In total 120 agonistic interactions were staged (60 for each treatment group).

**Ethical Note**

No specific licence was required for this work. Each crab was only used once before being supplied with a new shell and returned unharmed to the collection site. Furthermore, on visual inspection, no crabs appeared to have been injured or adversely affected by the staged encounters.

**Statistical Methods**

Categorical data were investigated using chi-square tests, with Yates’ correction. Chela residuals, used in subsequent analyses, were calculated from the linear regression of cheliped surface area (major cheliped length mm × major cheliped width mm) on shield length (a measure of body size) with a data set comprising all 240 crabs used in the study.

Arnott & Elwood (2007) noted differences between the experimental groups by use of principal components analysis. Here, using individual displays in separate analyses there were no significant group effects in ANCOVA or ANOVA and this factor is excluded. However, inclusion of group as a factor had no effect on the findings presented here. We used simple regression analysis to investigate whether cheliped residuals had an effect on the display behaviour of individuals, with cheliped residuals of the smaller or larger crab as the independent variable and the display behaviour as the dependent variable. Since the duration of the prefight display phase varied between interactions, the proportion of time spent performing each display was calculated and used in all analyses.

Rather than being separate displays, cheliped extension and presentation may grade into each other and may represent a more general cheliped ‘threat’ display (Laidre 2009). Thus, to facilitate comparison with Laidre (2009), we conducted analyses combining these two displays (and termed cheliped ‘threat’ display), followed by separate examinations for cheliped extension and presentation. Two-way ANOVA was used to examine whether cheliped residuals differed between encounters that escalated to grappling or not, and encounters that escalated to a shell fight or not.

Furthermore, we examined the effect of cheliped residuals on the outcome of interactions for cases where the smaller crab was the attacker, using independent t tests. It was not possible to examine the effect of displays and residuals on the outcome of interactions for cases where the larger crab was the attacker, since there were only three cases where the larger attacker failed to cause eviction of the smaller defender. Data were log (n + 1) transformed as appropriate.

**RESULTS**

**Interactions**

We staged 120 encounters; however, of these, only 105 involved cheliped display (cheliped extension and/or cheliped presentation) by one or both contestants, and only 91 involved cheliped display (cheliped extension and/or presentation) by both contestants during the encounter. One hundred and two encounters involved cheliped extension by one or both contestants, and 71 involved cheliped presentation by one or both contestants. There was an association between cheliped extension by the larger and smaller crab ($\chi^2 = 28.034, P < 0.0001$; Table 1). The same pattern was observed for cheliped presentation, with it either being mutually performed or not at all ($\chi^2 = 53.319, P < 0.0001$; Table 2).

Of the 120 encounters, 68 escalated to grappling, whereas 61 escalated to a shell fight. Table 3 details chi-square tests for associations between grappling and shell fights, displays and shell fights, and displays and grapples. There was a negative association between cheliped displays and the occurrence of shell fights (Table 3). By contrast, there was a positive association between cheliped displays and grapples (Table 3).

| Table 1 Cheliped extension use by the smaller and larger crabs of a pair |
|-----------------------------|----------------|----------------|
| Cheliped extension use      | Large crab yes | Large crab no  |
| Small crab yes              | 80             | 14             |
| Small crab no               | 8              | 18             |

Cheliped Residuals and Displays

Cheliped surface area was significantly positively related to shield length ($F_{1,238} = 283.1, R^2 = 0.541, P < 0.0001; \text{Fig. 1}$).

Owing to the negative association between cheliped displays and the occurrence of shell fights, only those interactions that did not escalate to a shell fight were considered in the regression analysis, to examine whether cheliped residuals influence display duration. For the smaller individual of an interacting pair, there was no association between cheliped residuals and total cheliped 'threat' display ($F_{1,57} = 2.257, \beta = 0.022, R^2 = 0.021, P = 0.139$) or for cheliped extension ($F_{1,57} = 0.001, \beta = 0.00023, R^2 = 0.000015, P = 0.977$). However, there was a significant positive relation between cheliped residuals and the duration of cheliped presentation display by the smaller crab ($F_{1,57} = 4.037, \beta = 0.028, R^2 = 0.050, P = 0.049; \text{Fig. 2}$). For the larger crab of a pair, there was a significant positive relation between cheliped residuals and total cheliped threat display ($F_{1,57} = 5.893, \beta = 0.029, R^2 = 0.078, P = 0.018; \text{Fig. 3}$). Further analysis revealed a nonsignificant trend for larger individuals with large cheliped residuals to use more cheliped extension display ($F_{1,57} = 3.049, \beta = 0.015, R^2 = 0.034, P = 0.086$), and more cheliped presentation display ($F_{1,57} = 3.965, \beta = 0.023, R^2 = 0.049, P = 0.051; \text{Fig. 4}$).

Escalation Level of the Encounter

Cheliped residuals of the smaller crab did not differ between encounters that escalated to grappling, compared to those that did not ($F_{1,116} = 1.039, P = 0.310$). However, those encounters that escalated to a shell fight involved smaller individuals with significantly larger cheliped residuals ($F_{1,116} = 9.351, P = 0.003; \text{Fig. 5}$). There was no interaction effect ($F_{1,116} = 1.98, P = 0.162$). For the larger crab, cheliped residuals did not differ between encounters that escalated to grappling or not ($F_{1,116} = 2.615, P = 0.109$), or encounters that escalated to a shell fight or not ($F_{1,116} = 2.919, P = 0.09$), and there was no interaction effect ($F_{1,116} = 0.255, P = 0.615$).

Effect of Cheliped Residuals on Outcome of Interactions

There was no difference in cheliped residuals between cases where the smaller crab evicted its larger opponent, compared to those cases involving nonevictions by smaller attackers ($t_{35} = 0.455, P = 0.652$), and there was also no difference in the cheliped residuals of larger defenders that successfully resisted eviction, compared to those that were evicted ($t_{35} = 0.400, P = 0.692$).

DISCUSSION

Both smaller and larger contestants with large chelipeds for their body size spent more time performing the cheliped presentation display. This display, in which the chelipeds are clearly visible to an opponent, is thought to facilitate opponent assessment by acting as a honest signal of RHP (Elwood et al. 2006), even to the extent of acting as an index of body size (sensu Maynard Smith & Harper 2003). However, individuals with large residuals used their exaggerated signal of competitive ability by displaying more 'presentation', which is consistent with deceptive use of an otherwise honest signal (Hughes 2000). That is, they can effectively signal an overestimate of competitive ability. By contrast, the cheliped extension display, involving thrusting the open chelipeds towards an opponent, is thought to disrupt the assessment process, containing an element of dishonesty (Elwood et al. 2006). Therefore, since this display is of less value in terms of signalling ability, and may function more as a signal of aggressive intent (Laidre & Elwood 2008; Laidre 2009), it is perhaps unsurprising that individuals appeared less prone to use this display in a manner related to residuals.

We found support for both the smaller and larger contestants signalling in a manner related to cheliped residuals, whereas in the snapping shrimp (Hughes 2000) it was the smaller contestant that attempted to signal dishonestly, and Laidre (2009) found that, in

<table>
<thead>
<tr>
<th>Test for association</th>
<th>$\chi^2$</th>
<th>P</th>
<th>Encounters</th>
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<tr>
<td>No association between grappling and shell fights</td>
<td>2.101</td>
<td>0.147</td>
<td>Grapple and shell fight: 39/61</td>
</tr>
<tr>
<td>Negative association between displays and shell fights</td>
<td>17.3</td>
<td>&lt;0.0001</td>
<td>Shell fights when both display: 36/91</td>
</tr>
<tr>
<td>Negative association between cheliped extension use by smaller crab and shell fights</td>
<td>10.421</td>
<td>0.001</td>
<td>Shell fights with cheliped extension: 40/94</td>
</tr>
<tr>
<td>Negative association between cheliped presentation use by smaller crab and shell fights</td>
<td>17.669</td>
<td>&lt;0.0001</td>
<td>Shell fights with cheliped presentation: 19/61</td>
</tr>
<tr>
<td>Negative association between cheliped extension use by larger crab and shell fights</td>
<td>8.921</td>
<td>0.003</td>
<td>Shell fights with cheliped extension: 37/88</td>
</tr>
<tr>
<td>Negative association between cheliped presentation use by larger crab and shell fights</td>
<td>19.280</td>
<td>&lt;0.0001</td>
<td>Shell fights with cheliped presentation: 19/62</td>
</tr>
<tr>
<td>Positive association between displays and grapples</td>
<td>6.519</td>
<td>0.011</td>
<td>Grapples when both display: 58/91</td>
</tr>
<tr>
<td>Positive association between cheliped extension use by smaller crab and grappling</td>
<td>4.480</td>
<td>0.034</td>
<td>Grapples with cheliped extension: 58/94</td>
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<tr>
<td>Positive association between cheliped presentation use by smaller crab and grappling</td>
<td>8.546</td>
<td>0.004</td>
<td>Grapples with cheliped presentation: 43/61</td>
</tr>
<tr>
<td>No association between cheliped extension use by larger crab and grappling</td>
<td>1.203</td>
<td>0.273</td>
<td>Grapples with cheliped extension: 53/88</td>
</tr>
<tr>
<td>Positive association between cheliped presentation use by larger crab and grappling</td>
<td>3.914</td>
<td>0.048</td>
<td>Grapples with cheliped presentation: 41/62</td>
</tr>
</tbody>
</table>

Significant P values are shown in bold.
terms of signalling intent in hermit crabs, it was the smaller individuals that bluffed. Moreover, in green tree frogs, *Rana clamitans*, some small males exaggerate their quality by lowering their acoustic pitch to resemble that of larger males (Bee et al. 2000). Thus, it has been suggested that it may be particularly advantageous for the smaller, inferior individual to exaggerate its ability and signal dishonestly (Bond 1989; Adams & Mesterton-Gibbons 1995; Hughes 2000). However, while the larger contestant may gain less advantage by bluffing, it may still gain some benefit from displaying in a manner related to cheliped residuals, particularly if there is ambiguity regarding contestant sizes, as would be the case if the relative size difference between opponents was small, as in the present study. In contrast, the study by Hughes (2000) involved much greater size differences and, as a result, the larger contestant in that study did not need to bluff or attempt to exaggerate its competitive ability.

Cheliped display use in the current study tended to be mutual in nature, with both contestants either displaying their chelipeds or not (Tables 1, 2). Furthermore, when one contestant used a particular display there was a high probability of the other contestant using the same display, presumably indicating communication by exchanging similar types of information.

Three levels of escalation occur in hermit crab interactions. First, the encounter may consist only of a period of display. Second, the interaction may escalate to ‘grappling’ which may denote a reluctance of individuals to accept the defender role (Elwood et al. 2006). Third, the encounter may escalate to a shell fight involving
vigorous shell rapping by the attacker, until either the defender is evicted from the shell or the attacker gives up. In the current study, there was no association between grappling and the occurrence of shell fights.

We might have expected smaller contestants with large cheliped residuals to be more likely to grapple as a result of ambiguity over which is the larger animal, but there was no difference in the cheliped residuals of the smaller (or larger) crab between interactions where contestants grappled and those cases where they did not. However, cheliped displays by crabs were positively associated with the occurrence of grapples. For the smaller crab, both the extension and presentation displays were positively associated with grappling, while for the larger crab only the presentation display was associated with grappling. Cheliped extension is thought to disrupt size assessment (Elwood et al. 2006) and, when used extensively by the smaller crab, increases the likelihood of the smaller crab taking the advantageous attacker role (Elwood et al. 2006). Furthermore, if cheliped displays signal aggressive intent (Laidre & Elwood 2008; Laidre 2009), it is possible that they denote a reluctance either to back off or to accept the defender role in a fight. This may result in grappling because in a shell fight the attacker moves forwards and grabs the opponent’s shell and causes the defender to withdraw into its shell. However, if the opponent does not withdraw at this point a grapple is likely.

There was a negative association between the occurrence of presentation and extension displays and shell fights. This suggests that cheliped displays inhibit the opponent from engaging in a shell fight by signalling aggressive intent or an intention to resist (e.g. Laidre 2007, 2009; Laidre & Elwood 2008), and perhaps an unwillingness to submit to the more passive defender role. Moreover, it is possible that in some interactions individuals were contesting an alternative resource such as personal space (Laidre 2009) or dominance (Hazlett & Bossert 1965; Laidre 2007). As such, displays may provide an efficient way to facilitate assessment and settle those disputes that are not about shells (Parker 1974; van Rhijn & Vodgel 1980; Parker & Rubenstein 1981; Enquist & Leimar 1983; Enquist 1985). However, small crabs engaging in shell fights had larger residuals than those that did not fight (Fig. 5).

It has been suggested that when the smaller individual in a contest exaggerates its RHP, the contestants may initially appear to each other to be more closely matched than they are, making assessment difficult, and leading to a higher level of escalation or longer contests (Parker 1974; Maynard Smith & Parker 1976; Parker & Rubenstein 1981). The results of Hughes (2000) supported this, since contests involving shrimp with larger chela residuals were longer and more highly escalated. Thus, in the current study smaller individuals with large cheliped residuals might initially have appeared more similar in size to their larger opponent leading to more escalated contests and more costly fighting, as predicted when assessment of relative competitive ability is difficult (Maynard Smith & Parker 1976).

In the present study, when the smaller crab was the attacker, there was no evidence in support of cheliped residuals having an effect on whether the attacker could evict the opponent or not. However, the sample size for this analysis was small and should be viewed with caution, although it is also the case, as demonstrated by previous studies (e.g. Dugatkin & Olsien 1990; Arnott & Elwood 2007), that changes in fight behaviour may only result in small, hard to detect, changes in outcome. None the less, it remains to be shown that apparent deception, by individuals capable of exaggerating their competitive ability, meets with greater contest success (Searcy & Nowicki 2005).

A number of studies report positive relationships between investment in weapons and escalated fight behaviour (e.g. Eberhard 1982; Mozsik & Emlen 2000; Tomkins et al. 2005; Okada et al. 2007). For example, in the broad-horned flour beetle, Gnatocerus cornutus, males fight with their enlarged mandibles for access to females, and males artificially selected to have long mandibles fought for longer than either control males or those selected to have short mandibles (Okada & Miyatake 2009). This indicates that investment in a weapon and fight behaviour may be correlated because of either pleiotropic genetic effects or some form of self-assessment (Arnott & Elwood 2009). This may, at least in part, account for the finding that smaller contestants with large chelipeds are more likely to enter a shell fight.

In terms of using the signal residual approach advocated by Hughes (2000), the current study is, to our knowledge, the only other to show that individuals with exaggerated signals display more. Briffa (2006) also used the residual approach in hermit crabs to examine whether a costly signal involved in P. bernhardus shell fights, namely the duration of pauses between bouts of rapping, can be used deceptively. Perhaps unsurprisingly, given the costly nature of rapping signals (Zahavi 1975, 1977), there was no evidence for deception. However, those individuals that successfully evicted the defender had larger signal residuals than those that gave up without causing an eviction, indicating that the residuals themselves correlated with competitive ability (Briffa 2006). In the escalated shell fights of hermit crabs, repeated bouts of vigorous shell rapping by the attacker are energetically demanding, that is, costly, and the power of the signal is constrained by the physiological state of the sender, rendering shell rapping particularly insensitive to deception (Briffa & Elwood 2001, 2002, 2004, 2005; Elwood et al. 2006). By contrast, the chelae displays of hermit crabs involve relatively brief movements of the chelipeds, and may not incur significant energetic costs (Elwood et al. 2006), making them particularly susceptible to deceptive use, especially if any retribution is similar to that if the signal was not used (Adams & Mesterton-Gibbons 1995; Johnstone 1998).

Consistent with theoretical predictions (e.g. Adams & Mesterton-Gibbons 1995; Szamado 2000; Rowell et al. 2006), there is increasing evidence that animal signals are not always honest (e.g. Steger & Caldwell 1983; Popp 1987; Backwell et al. 2000; Bee et al. 2000; Elwood et al. 2006; Wilson et al. 2007; Laidre 2009). Moreover, deception has been observed in numerous primate species, with differences in deception rate between species correlating with neocortex size, suggesting that benefits of deception may have driven neocortex expansion (Byrne & Corp 2004). However, it is becoming increasingly apparent that viewing signals

Figure 5. Cheliped residuals (mean ± SE) for the smaller individual in interactions that differed in escalation level (fight or no fight and grappling or no grappling).
in terms of honesty and deception is too simplistic. When acting as receiver, animals have evolved to take advantage of a relationship between signal structure and RHP (or next aggressive act for signals of intent), but, when acting as a signaler, individuals for whom the display exaggerates competitive ability attempt to manipulate opponents, using the display more often. Thus, as also stated by Hughes (2000), the fixation with the terms honesty and deception may be hindering our progress in understanding the function of animal signals. Our study provides further supporting evidence that the signal residual approach is a useful tool to understand the subtleties of animal displays better. Herrmit crabs, as well as snapping shrimp, seem to flaut it if they have it!

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References


Backwell, P. R. Y., Christy, J. H., Telford, S. R., Jennions, M. D. & Passmore, N. I. 2002. Power of shell-rapping signals influences animal signals. Our study provides further supporting evidence that the signal residual approach is a useful tool to understand the subtleties of animal displays better. Herrmit crabs, as well as snapping shrimp, seem to flaut it if they have it!


