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Honest and dishonest displays, motivational state and subsequent decisions in hermit crab shell fights

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Animal fights are typically preceded by displays and there is debate whether these are always honest. We investigated the prefight period in hermit crabs, *Pagurus bernhardus*, during which up to four types of display plus other activities that might provide information are performed. We determined how each display influences or predicts various fight decisions, and related these displays to the motivational state of the attacker, as determined by a startle response, and of the motivational state of the defender, as determined by the duration for which it resisted eviction from its shell. Two displays appeared to have consistent but different effects. Cheliped presentation, where the claws were held in a stationary position, often by both crabs but for longer by the larger, seemed to be honest, and allowed for mutual size assessment. This display enhanced the motivation and the success of the larger crab. In contrast, cheliped extension, involving the rapid thrust of the open chelae towards the opponent, did not seem to allow for mutual size assessment and may contain an element of bluff. It was performed more by the smaller crab and enhanced its success. The complexity of displays in this species appears to allow for both honesty and manipulation.

Contests in animals commonly involve the use of displays. These may be relatively low-intensity activities at the start of an encounter but may escalate as the contest progresses. In many species, both contestants use the same type of display, but may differ in the vigour or magnitude of performance. This variation may be used in settling the outcome of the contest without recourse to physical combat, presumably because it provides honest and reliable mutual evaluation of fighting ability or resource-holding potential (Parker 1974; Hughes 2000; Maynard Smith & Harper 2003; Hurd & Enquist 2005). Examples are found in the roaring contests of red deer, *Cervus elaphus* (Clutton-Brock & Albon 1979) and 'lateral displays' in cichlid fish, *Cichlasoma nigrofasciatum* (Keeley & Grant 1993). Other species have several distinct displays and those selected may vary between contestants and, within contestants, between encounters. The function of these displays is less clear but there seems to be scope for deception and manipulation of the opponent (Krebs & Dawkins 1984). Stomatopods, *Gonodactylus bredini*, for example, use various displays including the 'meral spread' (Adams & Caldwell 1990), which is typically shown by aggressive individuals and may cause the opponent to retreat. It may, however, be shown by newly moulted individuals, which have a low fighting ability, as a bluff. Also, the 'open chela display' of snapping shrimps, *Alpheus heterochaelis*, is used more often by those individuals that have larger chelae than predicted by body size and the display exaggerates their true fighting ability (Hughes 2000). In male fiddler crabs, *Uca annulipes*, recently regenerated major chelae are thinner and lighter and hence less energy is required when they are used in displays than in displays of original claws. Males with recently regenerated chelae can bluff fighting ability as it is impossible for the opponent to determine claw mass by means of visual assessment (Backwell et al. 2000). Theory suggested that deceptive displays by the weaker opponent should be rare and that on average displays should be honest (Johnstone 1998), although Backwell et al. (2000) suggested that cheating may be more common than was previously thought on the basis of the evidence from fiddler crabs.

In either situation, displays clearly have the potential to change the behaviour of the opponent (Rubenstein & Hazlett 1974; Hyatt & Salmon 1979). In the case of 'honest displays' the advantage to the sender is that the displays may settle the contest without costly combat, even if the sender loses the interaction (Hurd 1997; Deag & Scott

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1999). In the case of manipulation or deception, however, the advantage to the sender is that the displays could mask or exaggerate the true fighting ability of the sender and reduce the receiver's motivation to fight (Hurd & Ydenberg 1996). The receiver's motivation may easily be detected if the receiver immediately retreats from a weak opponent after that opponent has used a display typically given by an individual of high fighting ability (Hughes 2000).

Regardless of the honesty of the signal a fight might still occur. In this case the motivation of the opponent clearly has not been reduced sufficiently to induce retreat. However, causing a slight reduction in the opponent's motivation to fight, while not preventing a fight, might yet alter the probability of eventual victory. For instance, the time or energy the opponent is prepared to commit may be reduced. Even a slight increase in the probability of victory may make performing the display worthwhile. The benefit to a weak sender of a false signal may thus be great because it might avoid a fight that it would otherwise lose. If the signal does not deter the opponent then the sender is in the same position as if it had not sent the false signal. Thus, if the cost of sending the false signal is low and there is no specific retribution from the receiver then the use of false signals will be selected for (Adams & Mesterton-Gibbons 1995; Johnstone 1998).

We investigated the use of various prefight displays in hermit crabs, *Pagurus bernhardus*, contesting ownership of shells. These displays use the chelipeds and walking legs and also a high posture in which the shell is lifted high off the substrate (Hazlett 1968; Elwood & Neil 1992). However, other activities not normally described as displays may convey important information. These include mutual grappling, approaching the opponent and retreat from the opponent. The prefight phase may be followed by an escalated fight in which one crab, termed the 'attacker', initiates the shell fight by grabbing 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. The effect of the power, number of raps per bout, number of bouts and the duration of pauses between bouts on the physiology and resistance of the defender, and the interplay between the physiology and the performance of rapping of the attacker, have been the subject of recent investigation (Briffa & Elwood 2000, 2001a, 2002, 2003, 2005). This energetically demanding rapping is difficult to fake as only animals in good condition (with low lactate) are able to produce high-power vigorous rapping and only these crabs are guaranteed victory (Briffa & Elwood 2001a, 2002, 2005). In contrast, the relatively brief postures seen in prefight displays are unlikely to be energetically costly and thus the condition of the animal is thus less likely to limit their use.

Studies on hermit crab prefight displays have used models (e.g. Hazlett 1968) and information theory (Hazlett & Bossert 1965) in which the immediate effects of a display on the behaviour of the receiver were noted. Our aim in the present study, however, was to determine longer-term consequences of prefight displays. First, we asked whether prefight displays, and other activities, influence or predict which crab takes the role of attacker. This is an important decision as it is only the attacker that, if it evicts the defender, is able to choose which of the two shells to occupy. Second, we examined whether prefight activities influence or predict the winner of the contest. Third, we aimed to determine whether displays influence the motivation of the attackers (but not that of the defenders) by presenting a novel, startling stimulus and recording the duration of the attacker's startle response (Elwood et al. 1998), which is inversely related to the level of motivation. Attackers with a high potential gain in shell quality and low probable costs have short startle responses (Elwood et al. 1998) and highly motivated attackers are more likely to win (Briffa & Elwood 2001b). Finally, we examined how these prefight activities influence the duration for which the defender resists eviction. Again, this should elucidate relations between the prefight displays and motivation because the duration of resistance is a common measure of motivation in losers of fights (Hack et al. 1997; Bridge et al. 2000). Our key aim was thus to determine how various displays by one crab influence the behaviour or motivation of the receiver and if those displays provide honest information or a means of manipulation.

METHODS

Small (0.10–0.64 g) littoral specimens of the common European hermit crab were collected weekly from Ballywalter, Co. Down, Northern Ireland, U.K. between October 2004 and February 2005. They were held in groups of 40–50 in plastic tanks (60×30 cm) filled with aerated seawater at 12°C to a depth of 10 cm, and fed ad libitum on commercial fish food (catfish pellets). We removed the crabs from their shells by cracking the shells open in a bench vice. We used only males for staging encounters. We gave females new shells and returned them to the sea, thus avoiding sex differences in behaviour that have been noted in previous studies (Neil & Elwood 1985). Only male crabs that were free from obvious parasites, loss of appendages and recent moult were used. Use of the vice did not harm the crabs.

We allocated male crabs to pairs and pairs to one of three groups. Each crab was weighed and the relative weight difference (RWD) of the pair was calculated by RWD = 1 − (small crab weight/large crab weight). The relative weight difference ranged from 0.05 to 0.58 ($\overline{X} \pm SE = 0.22 \pm 0.008$) and there was no difference in RWD between the three groups. To determine the preferred weight of shell for the larger crab of each pair we used previously calculated regression lines that relate crab weight to preferred shell weight (Jackson 1988). In all cases the smaller crab received a *Littorina obtusata* shell that was 100% of the preferred weight for the larger crab. In group 1 (L50), the larger crab received an *L. obtusata* shell that was 50% of its preferred size. In group 2 (G50), the larger crab of each pair received a shell of *Gibbula cineraria* that was 50% of its preferred shell weight. This species is normally avoided by hermit crabs if given