



Motor pattern during fights in the hermit crab *Pagurus bernhardus*: evidence for the role of skill in animal contests



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Fighting involves the repeated performance of demanding agonistic behaviours and winners usually fight more vigorously than losers. While 'vigour' describes the rate and duration of a behaviour, 'skill' refers to well-coordinated motor movements. We investigated the role of skill in animal contests for the first time, focusing on the shell-rapping behaviour of hermit crabs during contests over the ownership of gastropod shells. We quantified vigour by recording the total number of raps and the mean number of raps per bout, and we quantified skill by measuring the distances that attackers displaced their shell during each rap. Winners displaced their shells through shorter distances than losers, indicating that motor pattern, as well as vigour, differed between contest outcomes. Both vigour and skill improved as fights progressed for eventual winners, but worsened for losers. We suggest that in a contest, skilful motor movements allow vigorous fighting, and both aspects deteriorate with fatigue. Skill may be important in the wide range of contests where outcomes are driven by energetic constraints. Understanding the links between skill, vigour and energy could provide new insights into strategic decision making during animal contests.

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A key determinant of victory in a contest is the difference in fighting ability, or resource-holding potential (RHP), between opponents (Humphries, Hebblethwaite, Batchelor, & Hardy, 2006) and the importance of RHP variation has been clearly demonstrated among arthropods in particular (Vieira & Peixoto, 2013). Therefore, efforts have been made to uncover the traits that might influence RHP. Intuitively, larger individuals should be better at fighting and overall body size is commonly used as a proxy for RHP (Briffa et al., 2013). In contests where weapons are used, for example, larger individuals should have larger and potentially more powerful weapons (Sneddon, Huntingford, & Taylor, 1997). Even in non-injurious contests weapons may be used in static displays (e.g. Huntingford, Taylor, Smith, & Thorpe, 1995; Sneddon et al., 1997) or dynamic displays (e.g. Bridge, Elwood, & Dick, 2000; Morrell, Backwell, & Metcalfe, 2005) that advertise RHP through costly repetition (Payne, 1998; Payne & Pagel, 1997). The rate and duration of repetitive displays is usually described as the 'vigour' of the display (Briffa & Elwood, 2004; Byers, Hebets, & Podos, 2010). In contests, winners tend to display more vigorously than losers, and in some cases winners escalate in vigour as the fight progresses

(Briffa & Elwood, 2000a; Briffa, Elwood, & Dick, 1998; Jennings, Gammell, Payne, & Hayden, 2005). In addition to variation in the ability to perform vigorously, fighting animals might vary in their ability to perform these movements in a coordinated and precise way, an attribute described as 'skill'. Thus, vigour is the ability to perform energetically expensive motor acts repeatedly while skill is defined as the ability to perform these challenging actions 'well' (Byers et al., 2010). A challenging action is one that requires precise activation and coordination of motor units, exceeding the requirements of routine activities (Byers et al., 2010; Manica, Macedo, Graves, & Podos, 2017). While both skill and vigour can be constrained by energetic demands, skill is also subject to constraints that may arise from biomechanics, muscle architecture and the development of a capacity for coordinated movement (Manica et al., 2017), which is assumed to be related to neurological development (Byers et al., 2010).

In these distinctions between vigour and skill, it seems that there is some overlap between the two concepts as both may be constrained by physiological systems and by energy demands, and both are linked to temporal variation in behaviour. However, skill, thus defined, also encompasses an element that is absent in respect of vigour. This is variation in the spatial component of expressed behaviour, that is, in the patterns of the movements performed. Therefore, analyses that seek to determine whether skill is

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functionally significant should focus on analysis of variation in movement patterns. Typically, these movement patterns can be compared between individuals that achieve an outcome and those that fail to achieve an outcome that is dependent upon the behaviour in question.

It has already been suggested that the spatial component of motor coordination can yield information on individual quality in contexts where one individual attempts to convince another to make a decision in its favour. During courtship, females can be attracted to males that display skilfully as well as vigorously (Byers et al., 2010). For instance, in dancing displays, an element of human courtship behaviour, males that perform specific dance moves in a coordinated way are more successful at attracting females than clumsier dancers (Neave et al., 2011). In the leap displays of blue-black grassquits, *Volatinia jacarina*, the male birds perform an elaborate combination of jumps and vocalizations. Success is determined not only by the number of jumps (vigour) but also by the height of jumping (Manica et al., 2017). Although it is difficult to determine what traits constrain jump height, Manica et al. (2017) suggested that the ability to perform well-coordinated motor movements should contribute to jump height, such that it might represent a correlate of skill. Interestingly, leap rate is negatively correlated with leap height. This correlation is unlikely to be driven by the fact that higher jumps take longer to perform because the birds do not jump continuously, leaving pauses between consecutive jumps that are of greater duration than the time spent aloft. Therefore, this negative correlation represents a potential trade-off between these two components of the display (Manica et al., 2017).

Although contests are not necessarily a result of sexual selection (Briffa & Hardy, 2013; Briffa & Sneddon, 2007, 2010), agonistic behaviours show clear parallels with sexually selected displays, as both involve decisions (Mowles & Ord, 2012) based on challenging activities (Briffa & Sneddon, 2007). Thus, if skill is an important feature of courtship displays there is also the potential for skill to differ between the winners and losers of contests. In fact, current contest theory implies that skill could be important for two reasons. First, fights might be settled by a process of 'mutual assessment' whereby each opponent provides its rival with information on its RHP (Arnott & Elwood, 2009; Briffa & Elwood, 2009; Taylor & Elwood, 2003). Here, the loser only decides to give up when it has determined that it is the weaker individual by assessing its opponent's behaviour, and the performance of challenging motor patterns could yield information on individual quality (Byers et al., 2010). Second, fights might be settled through 'self-assessment' (Arnott & Elwood, 2009; Briffa & Elwood, 2009; Taylor & Elwood, 2003) where giving-up decisions are not dependent on information about the opponent's RHP. Rather, the loser is the first individual to reach a cost threshold, the maximum limit of costs that an individual is either willing or able to bear. Thus, repeated signals demonstrate stamina and the contest is won by the individual with greater endurance (although in the case of injurious fights, injuries may also contribute to the accumulation of costs, see Briffa & Elwood, 2009; Payne, 1998). In this case, skill could be important because performing the behaviour efficiently could delay the onset of fatigue.

We do not yet know whether skill contributes to the outcome of animal contests in either of these two ways. In contrast, well-coordinated motor patterns are known to influence outcomes in the analogous situation of combat sports in humans. During boxing, for example, competitors that land their punches on their opponent more accurately are more likely to win (Ashker, 2011). Repeated striking of the opponent also takes place in fights between European hermit crabs, *Pagurus bernhardus*, over the ownership of empty gastropod shells. These serve as 'portable burrows' protecting the crabs from predators and buffering them against

variation in the external environment. The opponents take on distinct roles characterized by different behaviours. The smaller of the two crabs usually adopts the role of 'defender', spending most of the fight tightly withdrawn into its shell, resisting the attempts of the larger crab, the 'attacker', to evict it by pulling it out of its shell through the aperture. To secure an eviction, attackers must perform vigorous bouts of shell rapping. Attackers grasp the shell of the defender using their walking legs. Then they use their abdominal musculature to repeatedly move their shell towards and away from the shell of the defender, so that the defender's shell is struck by a rapid succession of raps. Successful attackers perform more raps per bout of rapping, hit harder and often leave shorter pauses between bouts of rapping than those that give up without evicting the defender. They also show greater escalation in the rate of rapping than attackers that are unsuccessful, and the differences in the vigour of rapping between the two outcomes become more marked towards the end of the fight (Briffa et al., 1998). Analysis of postfight metabolites indicates that vigorous shell rapping is a challenging behaviour that exceeds the energetic requirements of routine activity (Briffa & Elwood, 2004). Previous analyses have focused on the vigour of shell rapping (Briffa & Elwood, 2000a, 2000b; Briffa et al., 1998; Briffa, Elwood, & Russ, 2003) but none have addressed the spatial component of the movements used in shell rapping. A simple measure of the spatial component of shell rapping is the distance that the attacker moves its shell away from the defender's shell prior to each strike, which we refer to as 'displacement distance'. Given that shell rapping involves repeated strikes of the attacker's shell against the defender's we predicted that there should be an optimal displacement distance. Displacement distances that are too short might reduce the impact of individual raps but distances that are too long could make rapping inefficient, effectively wasting effort.

If skill contributes to RHP in hermit crabs, there should be variation among attackers in displacement distance, corrected for crab size. If displacement distance influences the decision of defenders to give up, this measure should differ between fight outcomes (evictions and nonevictions). Since shell rapping is a demanding activity (Briffa & Elwood, 2004; Mowles, Cotton, & Briffa, 2009, 2010) we should see covariation between displacement distance and vigour, either because the two components are traded off or because efficient movements delay the onset of fatigue. Furthermore, if displacement distance is constrained by energetic state, it should be subject to temporal change as the fight progresses, and winners should be better than losers at maintaining optimal displacement. These relations between displacement distance, vigour and outcomes would indicate that the spatial component of skill influences fight outcomes and hence access to a critical resource.

METHODS

Collecting Crabs and Staging Fights

Hermit crabs were collected from Hannafore Point in Looe, Cornwall, U.K. between February and May 2014. The crabs were kept in groups of 70–100 individuals in 80-litre tanks of aerated sea water at 15 °C in a 12:12 h light:dark cycle. They were fed ad libitum on white fish. Crabs were removed from their gastropod shells by carefully cracking the shell in a bench vice. We only used male crabs that had not recently moulted and that were free of missing appendages and obvious parasites. All other individuals were provided with a new shell and returned to the sea.

Each crab was weighed and then allocated to a pair consisting of a larger (potential attacker) and smaller (potential defender) crab. We gave the larger crab of each pair a shell that was 50% of its

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