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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.

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 the 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 preferred shell weight and the smaller crab a shell that was 100% of the larger crab's preferred shell weight. Preferred shell weights were obtained from regression equations derived from a previous shell selection experiment (Briffa & Elwood, 2007). Following provision of the new shell each crab was placed into a plastic dish, 12 cm in diameter, containing sea water as above, and allowed to acclimate to the new shell for 15–20 h. Following this period, fights were staged in an identical plastic container, which was placed behind the one-way mirror of an observation chamber, such that the observer could not be seen by the crabs. The larger crab was placed into the dish first, followed by the smaller crab after a 5 min interval. Each fight was recorded with a GoPro HERO 3+ camera mounted directly above the container. We staged 133 contests. Rapping occurred in 83 of these, but we excluded any fights where the video footage was not of sufficient quality to observe the movements of attackers' shell during rapping. This left a total of 78 fights for analysis. See the Supplementary material for video recordings showing some examples of shell fights.

The temporal pattern of shell rapping was scored from the video recordings using The Observer XT software (Noldus Information Technology, Wageningen, The Netherlands). We also recorded the outcome of each fight (eviction or noneviction). For each rap, individual frames were then extracted from the video recording using KMPlayer software (www.kmplayer.com). These frames were then analysed using ImageJ software (https://imagej.nih.gov/ij) to find the frame with the maximum displacement distance between the attacker's and defender's shells for each rap. Maximum displacement distance was defined as the shortest distance between the outer margin of the body whorl of the attacker's shell and the parietal wall of the defender's shell, the latter being the point of impact on the ventral shell surface of the defender's shell near the aperture (Fig. 1). Displacement distances were calibrated using the average of two marks of known length (3 mm) made on the surface of the attacker's shell, which could be clearly seen in the video recordings. From our record of the temporal pattern of shell rapping we calculated the total number of raps, the number of bouts of rapping, the mean number of raps per bout and the mean duration of pauses between bouts (Briffa et al., 1998). Bouts were defined as being terminated when the duration between two consecutive raps was >1 s (see Briffa & Elwood, 2000a, for details). Previous studies have indicated that the vigour of shell rapping varies from bout to bout and that over the last four bouts of fighting the pattern of change between bouts differs between successful attackers and those that give up without evicting the defender (Briffa et al., 1998). Therefore, we also calculated the number of raps in each of the last four bouts. For displacement distance, we calculated the mean displacement distance overall for each fight and the mean displacement distance for raps in each of the last four bouts of rapping in each fight.

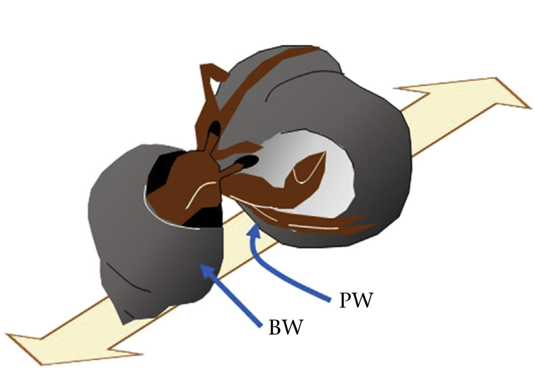

Figure 1. Diagrammatic illustration of two hermit crabs engaged in a shell fight. The attacker is on the left and the defender is on the right. The defender's chelipeds would normally be visible in the aperture of its shell but these are omitted for clarity (the attacker's antennae and antennules are also omitted). During shell rapping the attacker strikes the body whorl (BW) of its shell against the defender's shell adjacent to the parietal wall (PW) of the defender's shell. To effect these strikes, the attacker moves its shell back and forth in the plane indicated by arrows.

Statistical Methods

Displacement distance showed a positive correlation with attacker weight ($\log_{10}$ transformed data), whereby large attackers moved their shells further than smaller attackers (Pearson correlation: $r_{76} = 0.32$, $P < 0.005$). There was also a positive correlation with defender weight ($r_{76} = 0.39$, $P < 0.0005$), such that the displacement distance increased as attackers fought larger defenders. In this study, we sought to minimize the range of size differences between opponents, such that there was a strong correlation between attacker and defender weight ($r_{76} = 0.95$, $P < 0.0001$). Therefore, it would be inappropriate to include both measures (attacker and defender weight) as covariates in the same analysis. We thus compared displacement distance between successful and unsuccessful attackers using an ANCOVA where relative weight difference (RWD) was included as a covariate. This encompasses both attacker and defender weights in a single variable (Briffa et al., 2013). Measures of the vigour of rapping (total raps, total bouts of rapping, mean raps per bout, mean duration of pauses between bouts) were analysed in the same way. All response variables were $\log_{10}$ transformed prior to analysis to improve normality. We used a general linear mixed-effects model to determine whether the displacement distance varied across the last four bouts of fighting and whether any pattern of variation differed between outcomes. The response variable was displacement distance and the fixed factors were bout number (fourth last to last), outcome, RWD and the interactions between these variables. Fight ID was assigned as a random intercept to account for repeated measures of the number of raps per bout within each fight. Degrees of freedom were estimated using the Kenward–Roger method, such that *F* values could be used to infer significance. We also used a similar analysis to investigate changes in the mean number of raps per bout over the last four bouts of rapping. Analyses were performed in the R base package (R Core Team, 2014) and using the lme4 (Bates, Maechler, Bolker, & Walker, 2014) and lmerTest (Kuznetsova, Brockhoff, & Christensen, 2014) packages.

Ethical Note

Using a bench vice to remove the crab from its shell does not injure the crab and no crabs were injured during this experiment. At the end of the experiment, all crabs were fed, we ensured that each had a gastropod shell of suitable size and we returned them to the sea at their point of origin. No licences or permissions are needed to collect hermit crabs and their use in experiments is not covered by any U.K. legislation.

RESULTS

Number of Raps

There was no interaction effect between outcome and RWD on the total number of raps ($F_{1,74} = 0.85$, $P = 0.36$); the interaction effect was therefore removed from the model and the ANCOVA was recalculated with main effects only. The number of raps did not vary with RWD ($F_{1,75} = 1.28$, $P = 0.26$) but attackers that evicted the defender performed more raps than those that failed to evict the defender ($F_{1,75} = 11.59$, $P = 0.001$).

Number of Bouts

There was no interaction effect between outcome and RWD on the total number of bouts ($F_{1,74} = 0.77$, $P = 0.38$); the interaction effect was therefore removed from the model and the ANCOVA was recalculated with main effects only. The number of bouts did not vary with RWD ($F_{1,75} = 0.76$, $P = 0.38$) but attackers that evicted the defender performed more bouts than those that failed to evict the defender ($F_{1,75} = 5.91$, $P = 0.017$).

Number of Raps per Bout

There was no interaction effect between outcome and RWD on the mean number of raps per bout ($F_{1,74} = 0.001$, $P = 0.98$); the interaction effect was therefore removed from the model and the ANCOVA was recalculated with main effects only. The number of raps per bout did not vary with RWD ($F_{1,75} \leq 0.001$, $P = 0.99$) but attackers that evicted the defender performed more raps per bout than those that failed to evict the defender ($F_{1,75} = 4.69$, $P = 0.034$).

Duration of Pauses

There was no interaction effect between outcome and RWD on the mean duration of pauses ($F_{1,64} = 0.11$, $P = 0.75$); the interaction effect was therefore removed from the model and the ANCOVA was recalculated with main effects only. The duration of pauses did not vary with RWD ($F_{1,65} = 0.59$, $P = 0.45$) and there was no difference in pause duration between outcomes ($F_{1,765} = 0.99$, $P = 0.32$). Note that the degrees of freedom for analysis of pauses is lower than for the other response variables because 10 fights only contained one bout and hence had no pauses.

Displacement Distance

There was no interaction effect between outcome and RWD on the displacement distance of the attacker's shell ($F_{1,74} = 0.35$, $P = 0.43$); the interaction effect was therefore removed from the model and the ANCOVA was recalculated with main effects only. Displacement distance did not vary with RWD ($F_{1,74} = 1.21$, $P = 0.28$) but attackers that failed to evict the defender displaced their shells further than those that evicted the defender ($F_{1,75} = 9.21$, $P = 0.003$; Fig. 2). Both the mean number of raps per bout (Pearson correlation: $r_{76} = -0.23$, $P = 0.04$; Fig. 3a) and the total number of raps (Pearson correlation: $r_{76} = -0.39$, $P = 0.0004$; Fig. 3b) decreased with increasing displacement distance. All attackers decide to terminate single bouts of rapping, but the decision to terminate a fight is only made by the subset of attackers that decide to give up. Therefore, we also tested for a correlation between displacement distance and the total number of raps only in fights that ended with a noneviction. In this subset of fights, which had been terminated by the decision of the attacker, there was also a negative correlation between displacement distance and the total number of raps ($r_{21} = -0.56$, $P = 0.009$).

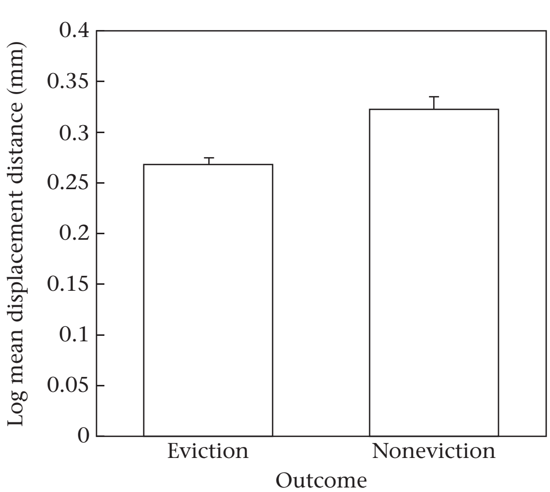

Figure 2. The difference in the mean displacement distance of shell rapping performed by attackers between fights that ended in evictions and nonevictions. Error bars show SEs.

Last Four Bouts

During the last four bouts of rapping there were no overall effects of outcome ($F_{1,\ 212.98} = 1.30$, $P = 0.26$), bout number ($F_{1,192.48} = 0.05$, $P = 0.83$) or RWD ($F_{1,203.22} = 0.06$, $P = 0.81$) on displacement distance, and there was no interaction between bout number and RWD ($F_{1,187.05} = 0.1$, $P = 0.76$). However, a significant interaction between outcome and bout number indicates that for successful attackers the displacement distance decreased, whereas for attackers that gave up without evicting the defender the displacement distance increased across the last four bouts ($F_{1,\ 192.48} = 8.02$, $P = 0.005$; Fig. 4). There was also a significant interaction between outcome and RWD whereby displacement distance increased with RWD for unsuccessful attackers but declined with RWD for successful attackers ($F_{1,\ 203.22} = 4.26$, $P = 0.04$; Fig. 5). There was also a significant three-way interaction between outcome, bout number and RWD ($F_{1,187.05} = 5.56$, $P = 0.02$) indicating that this difference in relationship between RWD and displacement distances between successful and unsuccessful attackers became more marked over successive bouts.

In the analysis of changes in the number of raps per bout over the last four bouts, there was no three-way interaction and no interactions between outcome and RWD or bout number and RWD so these effects were deleted and the model recalculated containing only main effects and the interaction between bout number and outcome. There was no main effect of outcome ($F_{1,229.1} = 1.07$, $P = 0.30$), bout number ($F_{1,195.58} = 0.14$, $P = 0.71$) or RWD ($F_{1,72.48} = 0.0002$, $P = 0.98$). However, a significant interaction between bout number and outcome indicates that for successful attackers the mean number of raps increased across bouts whereas the number of raps declined from bout to bout for attackers that gave up without evicting the defender ($F_{1,195.39} = 8.87$, $P = 0.003$; Fig. 6).

DISCUSSION

As defined by Byers et al. (2010), the repetitive performance of challenging behaviours can vary in terms of both vigour and skill, and our primary means of detecting variation in skill is to analyse its spatial component, i.e. the movement patterns performed (Manica et al., 2017). In the present study, vigour was quantified by the number of raps per bout (rate of activity) and by the total number of raps (duration of activity), while the spatial component of skill was quantified by the displacement distance of the raps. While high vigour is associated with winning a fight it now appears that precise movements are also important. Attackers that failed to evict the defender showed a clear pattern of greater displacement than those that were successful.

One possible explanation for the difference in displacement distance between outcomes is that it is driven by the defensive behaviour of successful defenders that resist eviction. Attackers can monitor their own performance (Edmonds & Briffa, 2016) and displacement distance might correlate with the power supplied to

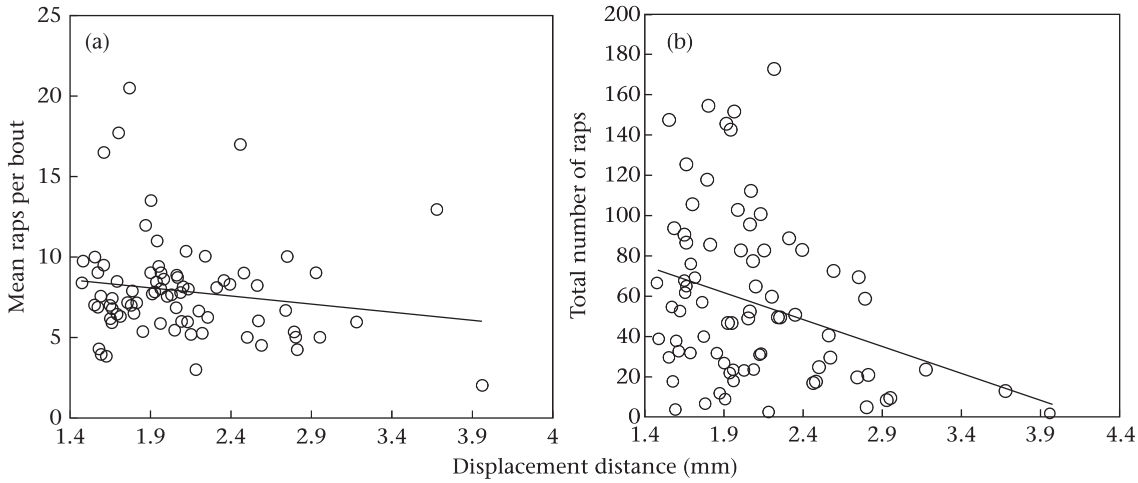

Figure 3. The correlations between displacement distance and (a) the mean number of raps per bout and (b) the total number of raps performed by attackers. Regression lines fitted for illustration.

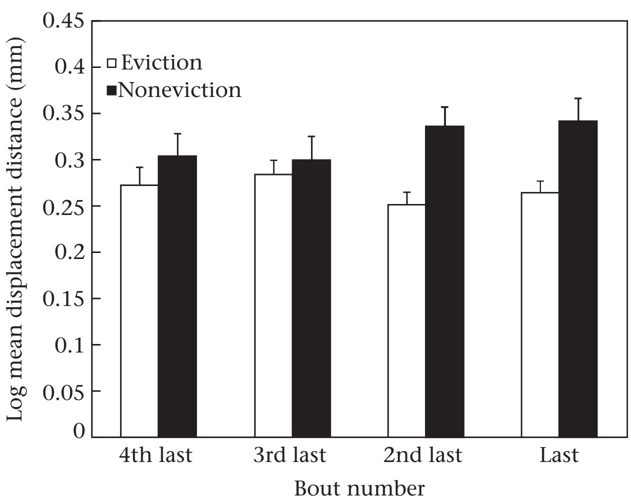

Figure 4. The change in mean displacement distance across the last four bouts of rapping, for fights that ended in evictions and nonevictions. Error bars show SEs.

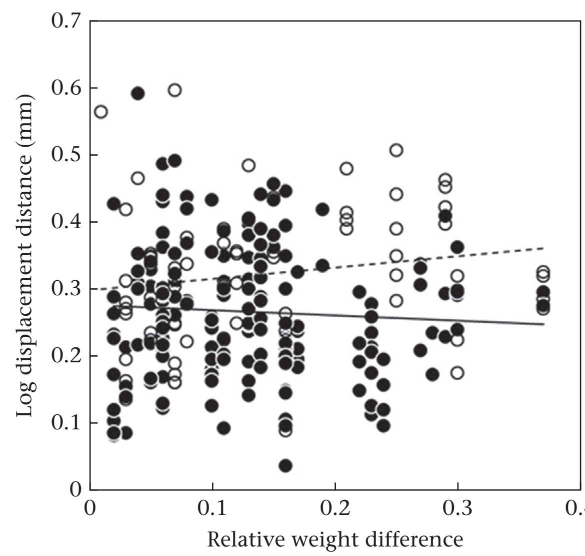

Figure 5. The correlation between relative weight difference and displacement distance for fights that ended in an eviction (solid circles, solid line) and nonevictions (open circles, dashed line), for raps performed during the last four bouts. Regression lines fitted for illustration.

each rap. Greater displacement might therefore represent a strategy that attackers use to try to overcome especially stubborn defenders. We did not assess the power of shell rapping in this study but this explanation seems unlikely. Assuming that the fighting ability of defenders relative to attackers increases as their sizes become more similar (Briffa et al., 1998), then if greater displacement represents a strategy for dealing with high-quality defenders we would expect to see a negative relation between RWD and displacement distance (i.e. as attackers get larger relative to defenders they would be displacing their shells by shorter distances). Across the whole fight there was no correlation between displacement distance and RWD. During the last four bouts where this effect might be expected to be most apparent we did find correlations between RWD and displacement. However, for those attackers that failed to evict the defender displacement increased slightly with RWD such that they displaced further against relatively weaker defenders.

While facultative increases in displacement in response to the fighting ability of defenders seem unlikely, the differences in this spatial component of shell rapping between outcomes are consistent with the idea that successful and unsuccessful attackers differ in the ability to perform well-coordinated motor movements, that is they differ in skill. Although skill and vigour can be distinguished through the definitions suggested by Byers et al. (2010), disentangling the relative contribution of these two components may be less straightforward both in the present study and in other examples. In the present example, both aspects contributed to positive outcomes for attackers. Indeed, individuals that performed more raps also showed low displacement, so it appears that skill and vigour covary, similar to the situation in courtship displays in *V. jacarina* (Manica et al., 2017).

There are two potential explanations for the association between displacement distance and the vigour of shell rapping. First, they could be relatively independent traits, and individuals of high underlying quality can rap skilfully (maintaining short displacement distances) as well as vigorously. Although skill has been understudied in the context of agonistic behaviour there are several examples of enhanced expression across a suite of signalling traits in high-quality individuals. For example, in the sexually selected

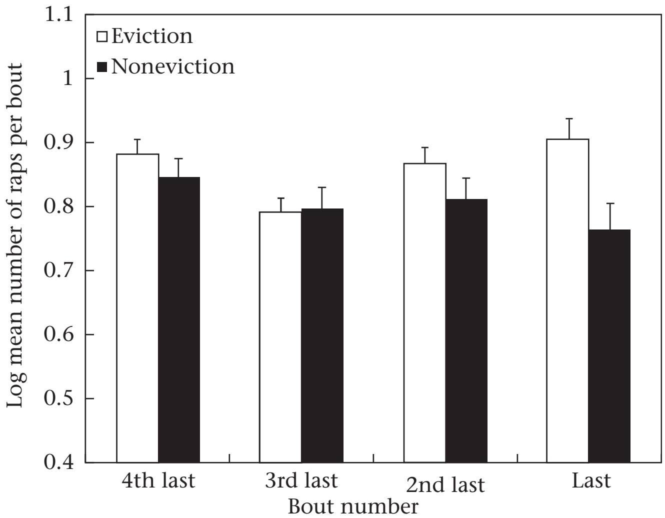

Figure 6. The change in the mean number of raps per bout across the last four bouts of rapping, for fights that ended in evictions and nonevictions. Error bars show SEs.

displays of male fiddler crabs, *Uca tangeri*, males wave their major cheliped and roll mud balls from the sediment that they excavate from their burrows. Males that wave their claws at a greater rate also make mud balls more efficiently and females choose males on the basis of both behaviours (Latruffe, McGregor& Oliveira, 1999). A difference between this example and the current one is that in the fiddler crabs two distinct behaviours are involved in the sexual displays whereas here we focused on two components of the same behaviour. A second explanation is that vigour and displacement distance are functionally linked such that rapping vigorously is dependent upon forming the motor movements skilfully. Shorter displacement distances, for example, could allow smaller intervals between successive raps and hence a greater rate of rapping within each bout, which is known to influence the chance of an eviction (Briffa & Elwood, 2000a). Here, we found that attackers that displaced their shells further performed fewer raps per bout and fewer raps in total, the latter result still being present when only those attackers that decided to give up were included in the analysis. Thus, attackers that rapped with high displacement also decided to terminate both individual bouts of rapping and entire fights sooner than those that rapped with lower displacement. These differences, in the number of raps per bout and persistence in a fight, have been shown to be driven by accumulated energetic costs (Briffa & Elwood, 2004). Therefore, rather than skill and vigour components being traded off against one another as seen for displays in *V. jacarina* (Manica et al., 2017), we suggest a different explanation for the covariation between the vigour and skill of shell rapping in *P. bernhardus*: lower displacement might allow for less energy expenditure per rap. In this case, more raps could be performed before the onset of fatigue, allowing attackers a greater chance of persisting until the defender crosses its own threshold (Briffa & Elwood, 2004) for giving up. Conversely, those attackers that perform the movements less well (by displacing their shell further than is necessary) might be wasting effort, such that they can perform fewer raps before giving up. If skill and vigour are functionally linked they should not be regarded as independent RHP traits. Rather, performing the movements involved in shell rapping skilfully could be necessary for the sustained vigorous rapping that is associated with evictions. These scenarios have parallels with those suggested for the evolution of social competence (Taborsky & Oliveira, 2012). In social settings, including contests, either competence in interactions with other individuals may evolve independently across a range of different behaviours or the expression of social behaviours may show positive covariation. These explanations (independent traits or functionally linked traits) for the link between skill and vigour are not mutually exclusive. Indeed, both are compatible with our result that skill differs between fight outcomes.

In addition to defining skill as performing a challenging activity well, Byers et al. (2010) also suggested that for skill to be an adaptive component of animal signalling it should be assessed by receivers. In the case of shell rapping, shorter displacement distances by attackers were indeed associated with giving-up decisions in the defenders that received shell rapping. Previous studies have shown that defenders that receive vigorous rapping are more likely to give up and our assumption has therefore been that vigour is the key feature that defenders assess (Briffa & Elwood, 2004; Mowles et al., 2009, 2010). Furthermore, vigorous shell rapping appears to inflict direct physiological costs on defenders (as well as on the attackers that perform the raps; Briffa & Elwood, 2004, 2005), potentially because the resulting vibrations of the defender's abdominal muscles cause a reflex stiffening (Chapple, 1993). Nevertheless, defenders still appear to assess the pattern of rapping because those that receive vigorous rapping at the start of the fight give up sooner than those that are eventually evicted but receive weak rapping at the start of the fight (Briffa & Elwood, 2002). While defenders might assess the vigour of rapping, it is improbable that they could visually assess the movement patterns performed by attackers directly, because they spend the shell-rapping phase of the fight withdrawn into their shell and would be unable to observe attackers. Rather, defenders might assess the sustained vigour that short displacement distances allow, rather than the displacement distances per se. Nevertheless, if attackers that rap skilfully, avoiding wasteful effort on longer displacement distances, are better able to sustain vigorous rapping then skilful rapping should still be adaptive even if skill is not directly assessed by defenders. This is perhaps a key difference between the tactile behaviours analysed here and the visual and acoustic displays discussed by Byers et al. (2010) and recently analysed in birds by Manica et al. (2017), where receivers can directly observe (and hear) all aspects of a display.

If displacing the shell too far reduces the chance of evicting the defender, why would some attackers do this? One suggestion for variation in skill is that it reflects underlying differences in individual quality, driven by variation in genes, condition and development, which ultimately drive variation in the neuronal and muscular machinery required for coordinated movement (i.e. motor control; Byers et al., 2010). In addition, skill might be honed as a result of accumulated experiences. For example, in many species individuals with experience of winning a fight are more likely to win subsequent fights (Hsu, 2001; Hsu, Earley, & Wolf, 2006; Hsu & Wolf, 1999). The benefits of experience can even accrue across different contexts. In the hermit crab *Pagurus nigrofascia* prior experience of copulation increases the chance of success in subsequent agonistic encounters (Yasuda, Matsuo, & Wada, 2015). Assuming that larger hermit crabs are older (Lancaster, 1988) and hence more experienced, we found limited evidence that experience might influence skill. In fights where there was an eviction, the displacement distance decreased as the size of attackers relative to defenders increased. In contrast, for attackers that failed to evict the defender, displacement distance increased with increasing relative size of attackers. However, when we compared displacement distance against the absolute size of attackers we found a positive trend, which was probably driven by larger body sizes constraining the crabs to move their abdomens through greater distances. Thus, it may be difficult to determine the effect of experience on displacement distance by using body size as a proxy for experience.

Another possibility is that attackers might vary in their ability to assess the effectiveness of their own shell rapping during a fight. A recent study (Edmonds & Briffa, 2016) has shown that attackers assess the effects of their own raps on the defender and if rapping is ineffective they perform an alternative behaviour, shell rocking, more frequently. Perhaps then, attackers that use short displacement distances are better able to judge the effectiveness of their shell rapping, adjusting the distance towards an optimal displacement as the fight proceeds. Indeed, we found differences in the temporal pattern of variation in displacement distances, between successful and unsuccessful attackers. The behaviour of attackers during the final bouts of the fight is critical to their chances of success. Previous studies (Briffa et al., 1998) and the current one show that successful attackers escalate the vigour of rapping (number of raps per bout) whereas those that give up de-escalate. Here, we showed that for successful attackers the displacement distances decreased during the final four bouts, suggesting adjustments towards smaller displacement distances. However, in unsuccessful attackers, we saw the opposite (and stronger) pattern of an increase in displacement across the final four bouts of rapping in those attackers that failed to evict the defender. In terms of effective shell rapping, this trend mirrors the differences between successful and unsuccessful attackers in terms of vigour during the same critical period of the fight. The decline in vigour is linked to accumulated energetic costs of shell rapping in attackers, such as the accumulation of muscular lactate, and theory predicts de-escalation in the rate of agonistic behaviour as a result of fatigue (Payne & Pagel, 1997). Therefore, the increase in displacement in unsuccessful attackers might also be related to fatigue. Although the links between fighting skill and fatigue have been understudied in animals, they have been analysed to an extent in the context of combat sports in humans. In a study of three-bout boxing contests, offensive skill was defined as the proportion of punches that landed on target (Ashker, 2011). For both winners and losers, the proportion of on-target punches declined across the three bouts of intensive combat (Ashker, 2011). Furthermore, the vigour of punching (number of punches per bout) was maintained across all three bouts for winners but declined for losers (Ashker, 2011). Thus, there are striking similarities between the shell-rapping behaviour of attacking hermit crabs and the punching behaviour of human boxers. In both examples, it appears that skill (displacement distance in hermit crabs and on-target punches in boxers) declines with contest duration, such that the accuracy (as well as the vigour) of agonistic behaviour is reduced by fatigue. If displacement distance indicates wasteful effort, it appears that the amount of effort wasted increases with fatigue levels, perhaps due to a loss of co-ordination in the required motor patterns. The fact that skill levels can both increase and decrease in fights is relevant to the question of how fighting animals make their decisions to give up. If skill is subject to the effects of fatigue, the presence of both patterns (as seen in the current study) lends support to the idea that giving up is based on self-assessment, as models based on this assumption are the only ones compatible with escalation and de-escalation of agonistic behaviour (Payne, 1998; Payne & Pagel, 1997); in contrast, mutual assessment models predict that agonistic behaviour should be performed consistently within phases of a fight (Enquist & Leimar, 1983).

Both vigour and the spatial component of movement patterns involved in shell rapping are important determinants of contest outcomes in hermit crabs. According to the definitions of skill given by Byers et al. (2010), the accuracy of the movement patterns involved in shell rapping reflects the skill of attackers, i.e. their ability to perform a demanding activity well. Nevertheless, our results also indicate that skill and vigour are interlinked, and that both may vary as a result of fatigue. Performing with sustained vigour may be dependent upon the ability to skilfully perform the movements involved. Individuals that waste effort by displacing their shells too far perform fewer raps and are less likely to win the fight. Therefore, we suggest that in the context of animal contests, movement patterns do not need to be directly observed or assessed by opponents for skill to be an important determinant of fight outcomes. There are many other examples of agonistic displays based on repetitive movement patterns where skill, as well as vigour, might be an important correlate of RHP, and further studies into the role of skill during fights could provide new insights into strategic decision making during animal contests. In particular, there is the potential for a greater understanding of how individuals use prior experiences and information gathering within fights to hone their fighting skill, and how these abilities interact with the costs of fighting, which appear critical to the chance of winning.

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Supplementary Material

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