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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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1 **Motor pattern during fights in the hermit crab *Pagurus bernhardus*: Evidence for the**  
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21 **Abstract**

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

36 **Key words:** Contest, fight, skill, vigour, RHP, decision-making

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## 42 **Introduction**

43 A key determinant of victory in a contest is the difference in fighting ability, or resource  
44 holding potential (RHP) between opponents (Humphries et al., 2006) and the importance of  
45 RHP variation has been clearly demonstrated among arthropods in particular (Vieira &  
46 Peixoto, 2013). Therefore, efforts have been made to uncover the traits that might influence  
47 RHP. Intuitively, larger individuals should be better at fighting and overall body size is  
48 commonly used as a proxy for RHP (Briffa, Hardy, Gammell, Jennings, Clarke & Goubault,  
49 2013). In contests where weapons are used, for example, larger individuals should have larger  
50 and potentially more powerful weapons (Sneddon, Huntingford & Taylor, 1997). Even in  
51 non-injurious contests weapons may be used in static displays (e.g. Huntingford, Taylor,  
52 Smith & Thorpe, 1995; Sneddon et al. 1997) or dynamic displays (e.g. Bridge, Elwood &  
53 Dick, 2000; Morrell, Backwell & Metcalfe, 2005) that advertise RHP through costly  
54 repetition (Payne and Pagel 1997; Payne 1998). The rate and duration of repetitive displays is  
55 usually described as the *vigour* of the display (Briffa & Elwood 2004; Byers, Hebets & Podos  
56 2010). In contests, winners tend to display more vigorously than losers, and in some cases  
57 winners escalate in vigour as the fight progresses (Briffa, Elwood & Dick, 1998; Briffa &  
58 Elwood, 2000a; Jennings, Gammell, Payne & Hayden, 2005). In addition to variation in the  
59 ability to perform vigorously, fighting animals might vary in their ability to perform these  
60 movements in a coordinated and precise way, an attribute described as *skill*. Thus, *vigour* is  
61 the ability to perform energetically expensive motor acts repeatedly whilst *skill* is defined as  
62 the ability to perform these challenging actions ‘well’ (Byers et al. 2010). A challenging  
63 action is one that requires precise activation and coordination of motor units, exceeding the  
64 requirements of routine activities (Byers et al. 2010; Manica et al. 2016) While both skill and  
65 vigour can be constrained by energetic demands, skill is also subject to constraints that may  
66 arise from biomechanics, muscle architecture and the development of a capacity for

67 coordinated movement (Manica et al. 2016), which is assumed to be related to neurological  
68 development (Byers et al. 2010).

69         In these distinctions between vigour and skill, it seems that there is some overlap  
70 between the two concepts as both may be constrained by physiological systems and by  
71 energy demands, and both are linked to *temporal* variation in behaviour. However, skill, thus  
72 defined, also encompasses an element that is absent in respect of vigour. This is variation in  
73 the *spatial* component of expressed behaviour, that is, in the patterns of the movements  
74 performed. Therefore, analyses that seek to determine whether skill is functionally significant  
75 should focus on analysis of variation in movement patterns. Typically, these movement  
76 patterns can be compared between individuals that achieve an outcome and those that fail to  
77 achieve an outcome that is dependent upon the behaviour in question.

78         It has already been suggested that the spatial component of motor coordination can  
79 yield information on individual quality in other contexts where one individual attempts to  
80 convince another to make a decision in the sender's favour. During courtship, females can be  
81 attracted to males that display skilfully as well as vigorously (Byers et al. 2010). For instance,  
82 in dancing displays, an element of human courtship behaviour, males that perform specific  
83 dance moves in a coordinated way are more successful at attracting females than clumsier  
84 dancers (Neave, McCarty, Freynik, Caplan, Hönekopp & Fink, 2011). In the leap displays of  
85 blue-black grassquits, *Volatinia jacarina*, the male birds perform an elaborate combination of  
86 jumps and vocalisations. Success is determined not only by the number of jumps (vigour) but  
87 also by the height of jumping (Manica et al. 2016). Although it is difficult to determine what  
88 traits constrain jump height it was suggested that the ability to perform well-coordinated  
89 motor movements should contribute to jump height, such that it might represent a correlate of  
90 skill. Interestingly, leap rate is negatively correlated with leap height. This correlation is  
91 unlikely to be driven by the fact that higher jumps take longer to perform because the birds

92 do not jump continuously, leaving pauses between consecutive jumps that are of greater than  
93 the time spent aloft. Therefore, this negative correlation represents a potential trade-off  
94 between these two components of the display (Manica et al. 2016).

95         Although contests are not necessarily a result of sexual selection (Briffa & Sneddon,  
96 2007; 2010; Briffa & Hardy, 2013), agonistic behaviours show clear parallels with sexually  
97 selected displays, as both involve decisions (Mowles & Ord, 2012) based on challenging  
98 activities (Briffa & Sneddon, 2007). Thus, if skill is an important feature of courtship  
99 displays there is also the potential for skill to differ between the winners and losers of  
100 contests. In fact, current contest theory implies that skill could be important for two reasons.  
101 First, fights might be settled by a process of ‘mutual assessment’ whereby each opponent  
102 provides its rival with information on its RHP (Taylor & Elwood, 2003; Arnott & Elwood,  
103 2009; Briffa & Elwood, 2009). Here, the loser only decides to give up when it has determined  
104 that it is the weaker individual by assessing its opponent’s behaviour, and the performance of  
105 challenging motor patterns could yield information on individual quality (Byers et al., 2010).  
106 Second, fights might be settled through ‘self-assessment’ (Taylor & Elwood, 2003; Arnott &  
107 Elwood, 2009; Briffa & Elwood, 2009) where giving up decisions are not dependent on  
108 information about the opponent’s RHP. Here, the loser is the first individual to reach a cost  
109 threshold, the maximum limit of costs that an individual is either willing or able to bear.  
110 Thus, repeated signals demonstrate stamina and the contest is won by the individual with  
111 greater endurance (although in the case of injurious fights, the injuries may also contribute to  
112 the accumulation of costs, see Payne 1998; Briffa & Elwood 2009). In this case skill could be  
113 important because performing the behaviour efficiently could delay the onset of fatigue.

114         We do not yet know whether skill contributes to the outcome of animal contests in  
115 either of these two ways. In contrast, well-coordinated motor patterns are known to influence  
116 outcomes in the analogous situation of combat sports in humans. During boxing, for example,

117 competitors that land their punches on their opponent more accurately are more likely to win  
118 (Ashker, 2011). Repeated striking of the opponent also takes place in fights between  
119 European hermit crabs, *Pagurus bernhardus*, over the ownership of empty gastropod shells.  
120 These serve as ‘portable burrows’ protecting the crabs from predators and buffering them  
121 against variation in the external environment. The opponents take on distinct roles  
122 characterised by different behaviours. The smaller of the two crabs usually adopts the role of  
123 ‘defender’, spending the majority of the fight tightly withdrawn into its shell, resisting the  
124 attempts of its larger opponent, the ‘attacker’, to evict it by pulling it out of its shell through  
125 the aperture (Fig. 1). In order to secure an eviction, attackers must perform vigorous bouts of  
126 shell rapping. Attackers grasp the shell of the defender using their walking legs. Then they  
127 use their abdominal musculature to repeatedly move their shell towards and away from the  
128 shell of the defender, so that the defender’s shell is struck by a rapid succession of raps.  
129 Successful attackers perform more raps per bout of rapping, hit harder and often leave shorter  
130 pauses between bouts of rapping compared to those that give up without evicting the  
131 defender. They also show greater escalation in the rate of rapping compared to attackers that  
132 are unsuccessful, and the differences in the vigour of rapping between the two outcomes  
133 become more marked towards the end of the fight (Briffa et al., 1998). Analysis of post-fight  
134 metabolites indicates that vigorous shell rapping is a challenging behaviour that exceeds the  
135 energetic requirements of routine activity (Briffa & Elwood, 2004). Previous analyses have  
136 focussed on the vigour of shell rapping (Briffa et al. 1998; Briffa & Elwood 2000a; 2000b;  
137 Briffa, Elwood & Russ, 2003) but, as yet, none have addressed the spatial component of the  
138 movements used in shell rapping. A simple measure of the spatial component for shell  
139 rapping is the distance that the attacker moves its shell away from the defender’s shell prior  
140 to each strike, which we refer to as ‘displacement distance’. Given that shell rapping involves  
141 repeated strikes of the attacker’s shell against the defender’s we expect that there should be

142 an optimal displacement distance. Displacement distances that are too short might reduce the  
143 impact of individual raps but distances that are too long could make rapping inefficient,  
144 effectively wasting effort.

145         If skill contributes to RHP in hermit crabs, there should be variation among attackers  
146 in displacement distance, corrected for crab size. These differences in displacement distance  
147 should influence the decision of defenders to give up leading to a difference between fight  
148 outcomes (evictions and non-evictions). Since shell rapping is a demanding activity (Briffa &  
149 Elwood, 2004; Mowles, Cotton & Briffa 2009; 2010) we should see covariation between  
150 displacement distance and vigour, either because the two components are traded-off or  
151 because efficient movements delay the onset of fatigue. Third, if the spatial component of  
152 shell rapping is constrained by energetic state, we should see temporal changes in  
153 displacement distance as the fights progress, and winners should be better at maintaining  
154 optimal displacement compared to losers. Such relations between displacement distance,  
155 vigour and outcomes would indicate that the spatial component of skill influences fight  
156 outcomes and hence access to a critical resource.

157

## 158 **Materials and methods**

### 159 *Collecting crabs and staging fights*

160 Hermit crabs were collected from Hannafore Point in Looe, Cornwall, UK between February  
161 and May 2014. The crabs were kept in groups of 70-100 individuals in 80 litre tanks of aerated  
162 seawater at 15°C in a 12h:12h light:dark cycle. They were fed *ad libitum* on white fish. Crabs  
163 were removed from their gastropod shells by carefully cracking the shell in a bench vice. Only  
164 male crabs that had not recently moulted, and that were free of missing appendages and obvious



165 parasites were used. All other individuals were provided with a new shell and returned to the  
166 sea.

167 Each crab was weighed and then allocated to a pair consisting of a larger (potential  
168 attacker) and smaller (potential defender) crab. The larger crab of each pair was provided with  
169 a shell that was 50% of its preferred shell weight. The smaller crab was given a shell that was  
170 100% of the larger crab's preferred shell weight. Preferred shell weights were obtained from  
171 regression equations derived from a previous shell selection experiment (Briffa & Elwood  
172 2005). Following provision of the new shell each crab was placed into a 12cm diameter plastic  
173 dish containing seawater as above, and allowed to acclimate to the new shell for 15-20 hours.  
174 Following this period, fights were staged in an identical plastic container, which was placed  
175 behind the one-way mirror of an observation chamber, such that the observer could not be seen  
176 by the crabs. The larger crab was placed into the dish first, followed by the smaller crab after  
177 a 5-minute interval. Video recordings of each fight were made using a GoPro HERO 3+ camera  
178 mounted directly above the container. One hundred and thirty-three contests were staged.  
179 Rapping occurred in eighty-three of these, but any fights where the video footage was not of  
180 sufficient quality to observe the movements of attackers' shell during rapping were excluded.  
181 This left a total of 78 fights for analysis.

182 The temporal pattern of shell rapping was scored from the video recordings using The  
183 Observer XT software. We also recorded the outcome of each fight (eviction or non-eviction).  
184 For each rap, individual frames were then extracted from the video recording using KMPlayer  
185 software. These frames were then analysed using ImageJ software to find the frame with the  
186 maximum displacement distance between the attacker's and defender's shells for each rap.  
187 Maximum displacement distance was defined as the shortest distance between the outer margin  
188 of the body whorl of the attacker's shell and the parietal wall of the defender's shell, the latter  
189 being the point of impact on the ventral shell surface of the defender's shell near the aperture.

190 Displacement distances were calibrated using the average of two marks of known length (3mm)  
191 made on the surface of the attacker's shell, which could be clearly seen in the video recordings.  
192 From our record of the temporal pattern of shell rapping we calculated the total number of raps,  
193 the number of bouts of rapping, the mean number of raps per bout, and the mean duration of  
194 pauses between bouts (Briffa et al. 1998). Bouts were defined as being terminated when the  
195 duration between two consecutive raps was >1s (see Briffa and Elwood 2000a for details).  
196 Previous studies have indicated that the vigour of shell rapping varies from bout to bout and  
197 that over the last four bouts of fighting the pattern of change between bouts differs between  
198 successful attackers and those that give up without evicting the defender (Briffa et al. 1998).  
199 Therefore, we also calculated the number of raps in each of the last four bouts. For displacement  
200 distance, we calculated the mean displacement distance overall for each fight and the mean  
201 displacement distance for raps in each of the last four bouts of rapping in each fight.

202

### 203 *Statistical methods*

204 Displacement distance unsurprisingly showed a positive correlation with attacker weight ( $\log_{10}$   
205 transformed data), whereby large attackers moved their shells further than smaller attackers  
206 (Pearson correlation:  $r_{76} = 0.32$ ,  $P < 0.005$ ). There was also a positive correlation with defender  
207 weight ( $r_{76} = 0.39$ ,  $P < 0.0005$ ), such that the displacement distance increased as attackers  
208 fought larger defenders. In this study we sought to minimise the range of size differences  
209 between opponents, such that there was a strong correlation between attacker and defender  
210 weight ( $r_{76} = 0.95$ ,  $P < 0.0001$ ). Therefore, it would be inappropriate to include both measures  
211 (attacker and defender weight) as covariates in the same analysis. We thus compared  
212 displacement distance among successful and unsuccessful attackers using an ANCOVA (where  
213 relative weight difference (RWD), which encompasses both attacker and defender weights in

214 a single variable (Briffa et al., 2013), was included as a covariate. Measures of the vigour of  
215 rapping (total raps, total bouts of rapping, mean raps per bout, mean duration of pauses between  
216 bouts) were analysed in the same way. All response variables were  $\log_{10}$  transformed prior to  
217 analysis to improve normality. We used a general linear mixed effects model to determine  
218 whether the displacement distance varied across the last four bouts of fighting and whether any  
219 pattern of variation differed between outcomes. The response variable was displacement  
220 distance and the fixed factors were bout number (4<sup>th</sup> last to last), outcome, relative weight  
221 difference and the interactions between these variables. Fight ID was assigned a random  
222 intercept in order to account for repeated measures of the number of raps per bout within each  
223 fight. Degrees of freedom were estimated using the Kenward-Roger method, such that  $F$ -values  
224 could be used to infer significance. We also used a similar analysis to investigate changes in  
225 the mean number of raps per bout over the last four bouts of rapping. Analyses were performed  
226 in the R base package (R Core Team, 2014) and using the lme4 (Bates, Maechler, Bolker &  
227 Walker, 2014) and lmerTest (Kuznetsova, Brockhoff & Christensen, 2014).

## 228 *Ethical Note*

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

## 234 **Results**

235 There was no interaction effect between outcome and RWD on the total number of raps ( $F_{1,74}$   
236 = 0.85,  $P = 0.36$ ), therefore the interaction effect was removed from the model and the  
237 ANCOVA was recalculated with main effects only. The number of raps did not vary with RWD

238 ( $F_{1,75} = 1.28, P = 0.26$ ) but attackers that evicted the defender performed more raps than those  
239 that failed to evict the defender ( $F_{1,75} = 11.59, P = 0.001$ ). There was no interaction effect  
240 between outcome and RWD on the total number of bouts ( $F_{1,74} = 0.77, P = 0.38$ ), therefore the  
241 interaction effect was removed from the model and the ANCOVA was recalculated with main  
242 effects only. The number of bouts did not vary with RWD ( $F_{1,75} = 0.76, P = 0.38$ ) but attackers  
243 that evicted the defender performed more bouts than those that failed to evict the defender ( $F_{1,75}$   
244  $= 5.91, P = 0.017$ ). There was no interaction effect between outcome and RWD on the mean  
245 number of raps per bout ( $F_{1,74} = 0.001, P = 0.98$ ), therefore the interaction effect was removed  
246 from the model and the ANCOVA was recalculated with main effects only. The number of  
247 raps per bout did not vary with RWD ( $F_{1,75} = <0.001, P = 0.99$ ) but attackers that evicted the  
248 defender performed more raps per bout than those that failed to evict the defender ( $F_{1,75} = 4.69,$   
249  $P = 0.034$ ). There was no interaction effect between outcome and RWD on the mean duration  
250 of pauses ( $F_{1,64} = 0.11, P = 0.75$ ), therefore the interaction effect was removed from the model  
251 and the ANCOVA was recalculated with main effects only. The duration of pauses did not vary  
252 with RWD ( $F_{1,65} = 0.59, P = 0.45$ ) and there was no difference in pause duration between  
253 outcomes ( $F_{1,765} = 0.99, P = 0.32$ ). Note that the degrees of freedom for analysis of pauses is  
254 lower than for the other parameters because 10 fights only contained one bout and hence had  
255 no pauses. There was no interaction effect between outcome and RWD on the displacement  
256 distance of the attacker's shell ( $F_{1,74} = 0.35, P = 0.43$ ), therefore the interaction effect was  
257 removed from the model and the ANCOVA was recalculated with main effects only.  
258 Displacement distance did not vary with RWD ( $F_{1,74} = 1.21, P = 0.28$ ) but attackers that failed  
259 to evict the defender displaced their shells further than those that evicted the defender ( $F_{1,75} =$   
260  $9.21, P = 0.003$ ) (Fig. 2). Both the mean number of raps per bout (Pearson correlation:  $r_{76} = -$   
261  $0.23, P = 0.04$ ; Fig. 3a) and the total number of raps (Pearson correlation:  $r_{76} = -0.39, P =$   
262  $0.0004$ ; Fig. 3b) decreased with increasing displacement distance. All attackers decide to

263 terminate single bouts of rapping, however the decision to terminate a fight is only made by  
264 the subset of attackers that decide to give up. Therefore, we also tested for a correlation between  
265 displacement distance and the total number of raps only in fights that ended with a non-eviction.  
266 In this subset of fights, that had been terminated by the decision of the attacker, there was also  
267 a negative correlation between displacement distance and the total number of raps ( $r_{21} = -0.56$ ,  
268  $P = 0.009$ ).

269 During the last four bouts of rapping there were no overall effects of outcome ( $F_{1,212.98}$   
270  $= 1.30$ ,  $P = 0.26$ ), bout number ( $F_{1,192.48} = 0.05$ ,  $P = 0.83$ ) or RWD ( $F_{1,203.22} = 0.06$ ,  $P = 0.81$ )  
271 on displacement distance, and there was no interaction between bout number and RWD  
272 ( $F_{1,187.05} = 0.1$ ,  $P = 0.76$ ). However, a significant interaction between outcome and bout number  
273 indicates that for successful attackers the displacement distance decreased, whereas for  
274 attackers that gave up without evicting the defender the displacement distance increased across  
275 the last four bouts ( $F_{1,192.48} = 8.02$ ,  $P = 0.005$ ) (Fig. 4). There was also a significant interaction  
276 between outcome and RWD whereby displacement distance increased with RWD for  
277 unsuccessful attackers but declined with RWD for successful attackers ( $F_{1,203.22} = 4.26$ ,  $P =$   
278  $0.04$ ) (Fig. 5). There was also a significant three-way interaction between outcome, bout  
279 number and RWD ( $F_{1,187.05} = 5.56$ ,  $P = 0.02$ ) indicating that this difference in relationships  
280 between RWD and displacement distances between successful and unsuccessful attackers  
281 became more marked over successive bouts.

282 In the analysis of changes in the number of raps per bout over the last 4 bouts, there  
283 was no three-way interaction and no interactions between outcome and RWD or bout number  
284 and RWD so these effects were deleted and the model recalculated containing only main effects  
285 and the interaction between bout number and outcome. There was no main effect of outcome  
286 ( $F_{1,229.1} = 1.07$ ,  $P = 0.30$ ), bout number ( $F_{1,195.58} = 0.14$ ,  $P = 0.71$ ) or RWD ( $F_{1,72.48} = 0.0002$ ,  
287  $P = 0.98$ ). However, a significant interaction between bout number and outcome indicates that

288 for successful attackers the mean number of raps increased across bouts whereas the number  
289 of raps declined from bout to bout for attackers that gave up without evicting the defender  
290 ( $F_{1,195.39} = 8.87, P = 0.003$ ) (Fig. 6).

291

## 292 **Discussion**

293 As defined by Byers et al. (2010) the repetitive performance of challenging behaviours can  
294 vary in terms of both vigour and skill, and our primary means of detecting variation in skill is  
295 to analyse its spatial component, i.e. the movement patterns performed (Manica et al., 2016).  
296 In the present study, vigour is quantified by the number of raps per bout (rate of activity) and  
297 by the total number of raps (duration of activity), whilst the spatial component of skill is  
298 quantified by the displacement distance of the raps. While high vigour is associated with  
299 winning a fight it now appears that precise movements are also important. Attackers that  
300 failed to evict the defender showed a clear pattern of greater displacement compared to those  
301 that were successful.

302 One possible explanation for the difference in displacement distance between  
303 outcomes is that it is driven by the defensive behaviour of successful defenders that resist  
304 eviction. Attackers can monitor their own performance (Edmunds & Briffa 2016) and  
305 displacement distance might correlate with the power supplied to each rap. Greater  
306 displacement therefore might represent a strategy that attackers use in an attempt to overcome  
307 especially stubborn defenders. We did not assess the power of shell rapping in this study but  
308 this explanation seems unlikely. Assuming that the fighting ability of defenders relative to  
309 attackers increases as their sizes become more similar (Briffa et al. 1998), then if greater  
310 displacement represents a strategy for dealing with high quality defenders we would expect to  
311 see a negative relation between RWD and displacement distance (i.e. as attackers get larger

312 relative to defenders they would be displacing their shells by shorter distances). Across the  
313 whole fight these was no correlation between displacement distance and RWD. During the  
314 last 4 bouts where this effect might be expected to be most apparent we did find correlations  
315 between RWD and displacement. However, for those attackers that failed to evict the  
316 defender displacement increased slightly with RWD such that they displaced further against  
317 relatively weaker defenders.

318         Whilst facultative increases in displacement in response to the fighting ability of  
319 defenders seem unlikely, the differences in this spatial component of shell rapping between  
320 outcomes are consistent with the idea that successful and unsuccessful attackers differ in the  
321 ability to perform well-coordinated motor movements, that is they differ in skill. Although  
322 skill and vigour can be distinguished through the definitions suggested by Byers et al. (2010)  
323 disentangling the relative contribution of these two components may be less straightforward  
324 (2010) both in the present study and in other examples. In the present example, both aspects  
325 contribute to positive outcomes for attackers. Indeed, individuals that performed more raps  
326 also showed low displacement, so it appears that skill and vigour co-vary, similar to courtship  
327 displays in *V. jacarina* (Manica et al., 2016).

328         There are two potential explanations for the association between displacement  
329 distance and the vigour of shell rapping. First, they could be relatively independent traits, and  
330 individuals of high underlying quality can rap skilfully (maintaining short displacement  
331 distances) as well as vigorously. Although skill has been understudied in the context of  
332 agonistic behaviour there are several examples of enhanced expression across a suite of  
333 signalling traits in high quality individuals. For example, in the sexually selected displays of  
334 male fiddler crabs, *Uca tangerii*, males wave their major cheliped and roll mud balls from the  
335 sediment that they excavate from their burrows. Males that wave their claws at a greater rate  
336 also make mud balls more efficiently and females choose males on the basis of both

337 behaviours (Latruffe, McGregor & Oliveira, 1999). A difference between this example and  
338 the current one is that in the fiddler crabs there are two distinct behaviours involved in the  
339 sexual displays whereas here we focus on two components of the same behaviour. A second  
340 explanation is therefore that vigour and displacement distance are functionally linked such  
341 that rapping vigorously is dependent upon forming the motor movements skilfully. Shorter  
342 displacement distances, for example, could allow smaller intervals between successive raps  
343 and hence a greater rate of rapping within each bout, which is known to influence the chance  
344 of an eviction (Briffa & Elwood 2000a). Here, we found that attackers that displaced their  
345 shells further performed fewer raps per bout and fewer raps in total, the latter result still being  
346 present when only those attackers that decided to give up were included in the analysis. Thus,  
347 attackers that rap with high displacement also decide to terminate both individual bouts of  
348 rapping and entire fights sooner than those that rap with lower displacement. These  
349 differences, in the number of raps per bout and persistence in a fight, have been shown to be  
350 driven by accumulated energetic costs (Briffa & Elwood 2004). Therefore, rather than skill  
351 and vigour components being traded off against one another as seen for displays in *V.*  
352 *jacarina* (Manica et al. 2016), we suggest a different explanation for the covariation between  
353 the vigour and skill of shell rapping in *P. bernhardus*; lower displacement might allow for  
354 less energy expenditure per rap. In this case more raps could be performed delaying the onset  
355 of fatigue in attackers and thus allowing them a greater chance of persisting until the defender  
356 crosses its own threshold (Briffa & Elwood 2004) for giving up. Conversely, those attackers  
357 that perform the movements less well (by displacing their shell further than is necessary)  
358 might be wasting effort, such that they can perform fewer raps before giving up. If skill and  
359 vigour are functionally linked they should not be regarded as independent RHP traits. Rather,  
360 performing the movements involved in shell rapping skilfully could be necessary for the  
361 sustained vigorous rapping that is associated with evictions. These scenarios have parallels



362 with those suggested for the evolution of social competence (Taborsky & Olivera, 2012). In  
363 social settings, including contests, competence in interactions with other individuals may  
364 evolve independently across a range of different behaviours, or the expression of social  
365 behaviours may show positive covariation. These explanations (independent traits or  
366 functionally linked traits) for the link between skill and vigour are not mutually exclusive.  
367 Indeed, both are compatible with our result that skill differs between fight outcomes.

368         In addition to defining skill as performing a challenging activity well, Byers et al.  
369 (2010) also suggest that for skill to be an adaptive component of animal signalling it should  
370 be assessed by receivers. In the case of shell rapping lower displacement distances by  
371 attackers are indeed associated with giving up decisions in the defenders that receive shell  
372 rapping. Previous studies have shown that defenders that receive vigorous rapping are more  
373 likely to give up and our assumption has therefore been that vigour is the key feature that  
374 defenders assess (Briffa & Elwood, 2004; Mowles et al., 2009; 2010). Furthermore, vigorous  
375 shell rapping appears to inflict direct physiological costs on defenders (as well as on the  
376 attackers that perform the raps) (Briffa & Elwood, 2004; 2005), potentially because the  
377 resulting vibrations of the defender's abdominal muscles cause a reflex stiffening (Chapple,  
378 1993). Nevertheless, defenders still appear to assess the pattern of rapping because those that  
379 receive vigorous rapping at the start of the fight give up sooner compared with defenders that  
380 are eventually evicted but receive weak rapping at the start of the fight (Briffa & Elwood  
381 2002). In contrast, it is improbable that defenders could visually assess the movement  
382 patterns performed by attackers directly, because they spend the shell rapping phase of the  
383 fight withdrawn into their shell and would be unable to observe the movements of attackers.  
384 Rather, defenders might assess the sustained vigour that short displacement distances allow,  
385 rather than the displacement distances *per se*. Nevertheless, if attackers that rap skilfully,  
386 avoiding wasteful effort on larger displacement distances, are better able to sustain vigorous

387 rapping then skilful rapping should still be adaptive even if skill is not directly assessed by  
388 defenders. This is perhaps a key difference between the tactile behaviours analysed here and  
389 the visual and acoustic displays discussed by Byers et al. (2010) and recently analysed in  
390 birds (Manica et al. 2016), where receivers can directly observe (and hear) all aspects of a  
391 display.

392         If displacing the shell too far reduces the chance of evicting the defender, why would  
393 some attackers do this? One suggestion for variation in skill is that it reflects underlying  
394 differences in individual quality, driven by variation in genes, condition and development,  
395 which ultimately drive variation in the neuronal and muscular machinery required for  
396 coordinated movement (i.e. motor control) (Byers et al. 2010). In addition, skill might be  
397 honed as a result of accumulated experiences. For example, in many species individuals with  
398 experience of winning a fight are more likely to win subsequent fights (Hsu, 2001; Hsu &  
399 Wolf 1999; Hsu, Earley & Wolf, 2006). The benefits of experience can even accrue across  
400 different contexts. In the hermit crab *P. nigrofascia* prior experience of copulation increases  
401 the chance of success in subsequent agonistic encounters (Yasuda, Matsuo, & Wada, 2015).  
402 Assuming that larger hermit crabs are older (Lancaster, 1998) and hence more experienced,  
403 we found limited evidence that experience might influence skill. In fights where there was an  
404 eviction, the displacement distance decreased as the size of attackers relative to defenders  
405 increased. In contrast, for attackers that failed to evict the defender, displacement distance  
406 increased with increasing relative size of attackers. However, when we compared  
407 displacement distance against the absolute size of attackers we found a positive trend, which  
408 was most likely driven by larger body sizes constraining the crabs to move their abdomens  
409 through greater distances. Thus, it may be difficult to determine the effect of experience on  
410 displacement distance by using body size as a proxy for experience.

411 Another possibility is that attackers might vary in their ability to assess the  
412 effectiveness of their own shell rapping during a fight. A recent study (Edmonds & Briffa,  
413 2016) has shown that attackers assess the effects of their own raps on the defender and if  
414 rapping is ineffective they perform a greater frequency of an alternative behaviour, shell  
415 rocking. Perhaps then attackers that use short displacement distances are better able to judge  
416 the effectiveness of their shell rapping, adjusting the distance towards an optimal  
417 displacement as the fight proceeds. Indeed, we found differences in the temporal pattern of  
418 variation in displacement distances, between successful and unsuccessful attackers. The  
419 behaviour of attackers during the final bouts of the fight is critical to their chances of success.  
420 Previous studies (Briffa et al. 1998) and the current data show that successful attackers  
421 escalate the vigour of rapping (number of raps per bout) whereas those that give up de-  
422 escalate. Here, we show that for successful attackers the displacement distances decrease  
423 during the final four bouts, suggesting adjustments towards smaller displacement distances.  
424 However, in unsuccessful attackers, we saw the opposite (and stronger) pattern of an increase  
425 in displacement across the final four bouts of rapping in those attackers that failed to evict the  
426 defender. In terms of effective shell rapping, this trend mirrors the differences between  
427 successful and unsuccessful attackers in terms of vigour during the same critical period of the  
428 fight. The decline in vigour is linked to accumulated energetic costs of shell rapping in  
429 attackers, such as the accumulation of muscular lactate, and theory predicts de-escalation in  
430 the rate of agonistic behaviour as a result of fatigue (Payne & Pagel, 1997). Therefore, the  
431 increase in displacement in unsuccessful attackers might also be related to fatigue.  
432 Although the links between fighting skill and fatigue have been understudied in animals, they  
433 have been analysed to an extent in the context of combat sports in humans. In a study of  
434 three-bout boxing contests, offensive skill was defined as the proportion of punches that  
435 landed on target (Ashker, 2011). For both winners and losers, the proportion of on-target

436 punches declined across the three bouts of intensive combat (Ashker, 2011). Furthermore, the  
437 vigour of punching (number of punches per bout) was maintained across all three bouts for  
438 winners but declined for losers (Ashker, 2011). Thus, there are striking similarities between  
439 the shell rapping behaviour of attacking hermit crabs and the punching behaviour of human  
440 boxers. In both examples it appears that skill (displacement distance in hermit crabs and on-  
441 target punches in boxers) declines with contest duration, such that the accuracy (as well as the  
442 vigour) of agonistic behaviour is reduced by fatigue. If displacement distance indicates  
443 wasteful effort, it appears that the amount of effort wasted increases with fatigue levels,  
444 perhaps due to a loss of coordination in the required motor patterns. The fact that skill levels  
445 can both increase and decrease in fights is relevant to the question of how fighting animals  
446 make their decisions to give up. If skill is subject to the effects of fatigue, the presence of  
447 both patterns (as seen in the current data) lends support to the idea that giving up is based on  
448 self-assessment, as models based on this assumption are the only ones compatible with  
449 escalation and de-escalation of agonistic behaviour (Payne & Pagel 1997; Payne 1998); in  
450 contrast, mutual assessment models predict that agonistic behaviour should be performed  
451 consistently within phases of a fight (Enquist & Leimar 1983).

452         Both vigour and the spatial component of movement patterns involved in shell  
453 rapping are important determinants of contest outcomes in hermit crabs. According to the  
454 definitions of skill given by Byers et al. (2010) the accuracy of the movement patterns  
455 involved in shell rapping reflects the skill of attackers, i.e. their ability to perform a  
456 demanding activity well. Nevertheless, our data also indicate that skill and vigour are  
457 interlinked, and that both may vary as a result of fatigue. Performing with sustained vigour  
458 may be dependent upon the ability to skilfully perform the movements involved. Individuals  
459 that waste effort by displacing their shells too far perform fewer raps and are less likely to  
460 win the fight. Therefore, we suggest that in the context of animal contests, movement patterns

461 do not need to be directly observed or assessed by opponents for skill to be an important  
462 determinant of fight outcomes. There are many other examples of agonistic displays based on  
463 repetitive movement patterns where skill as well as vigour might be an important correlate of  
464 RHP, and further studies into the role of skill during fights could provide new insights into  
465 strategic decision-making during animal contests. In particular, there is the potential for a  
466 greater understanding of how individuals use prior experiences and information gathering  
467 within fights to hone their fighting skill, and how these abilities interact with the costs of  
468 fighting, which appear critical to the chance of winning.

469

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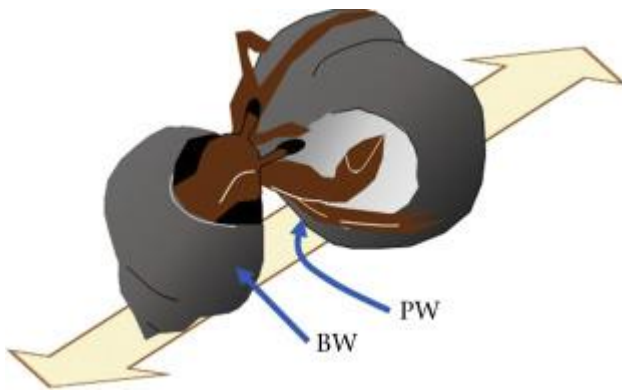
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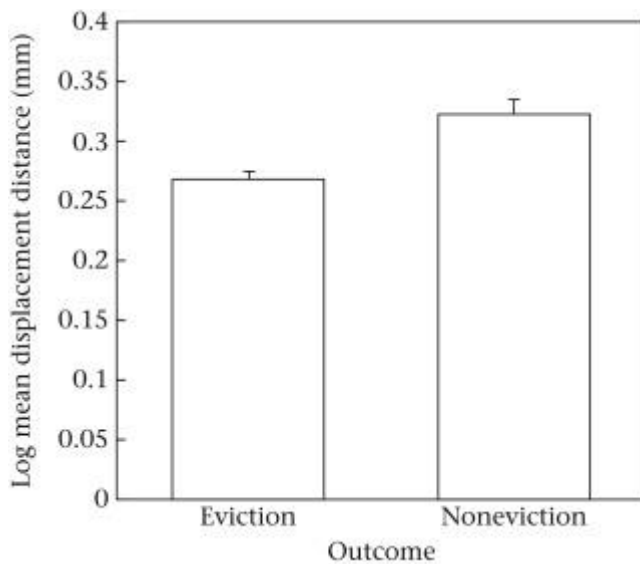
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588

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

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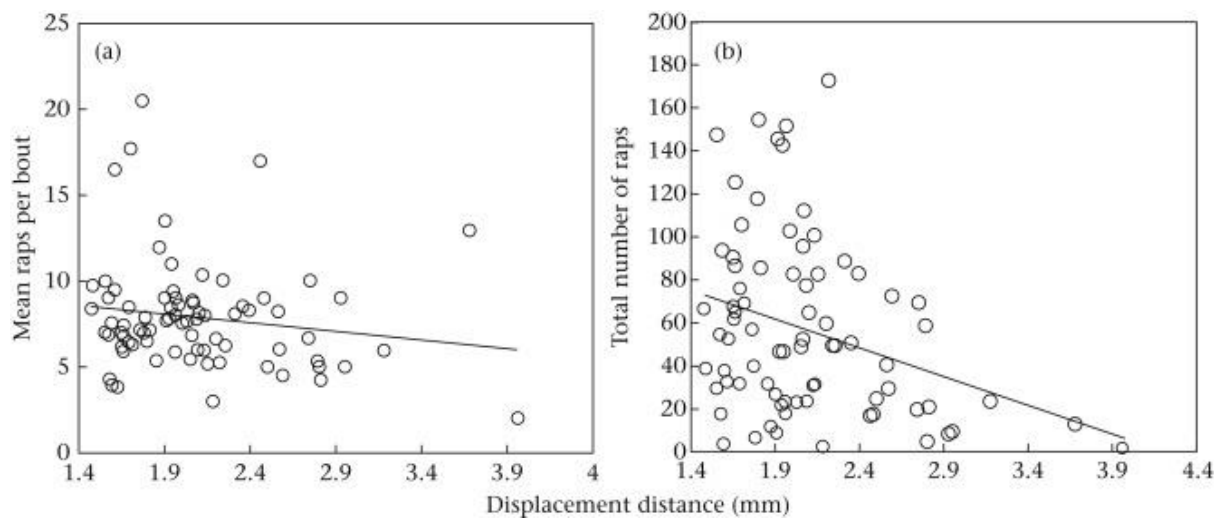
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601 **Figure 2:** The difference in the mean displacement distance of shell rapping performed by  
602 attackers between fights that ended in evictions and non-evictions. Error bars show standard  
603 errors.

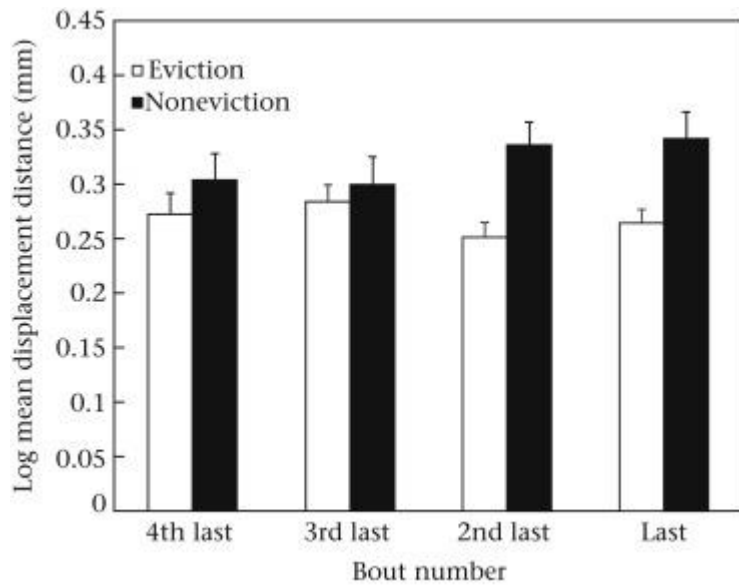
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606 **Figure 3:** The significant negative correlations between displacement distance and (a) the  
607 mean number of raps per bout and (b) the total number of raps performed by attackers.  
608 Regression lines fitted for illustration.

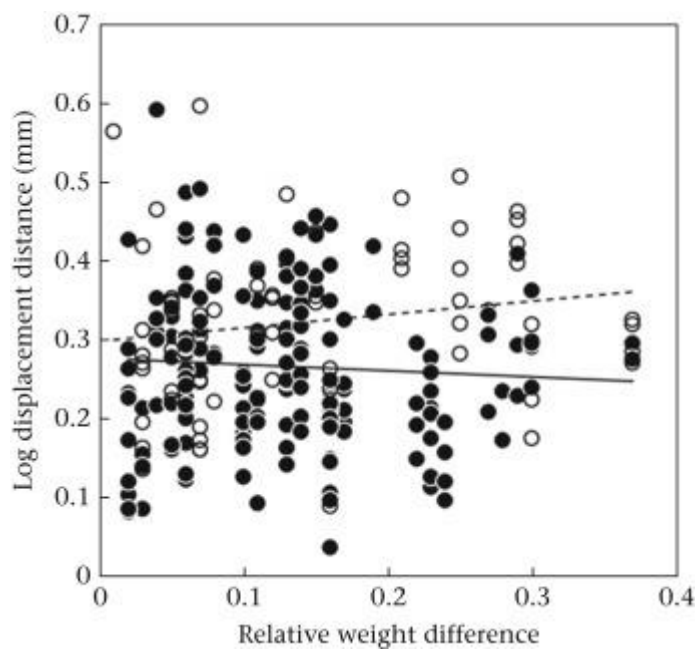
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611 **Figure 4:** The change in mean displacement distance across the last four bouts of rapping, for  
 612 fights that ended in evictions and non-evictions. Error bars show standard errors.

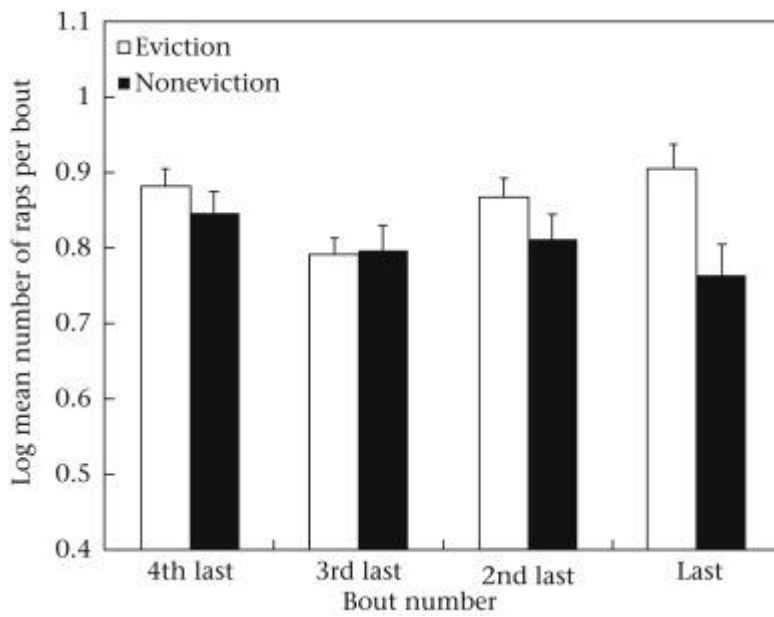
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615 **Figure 5:** The correlation between relative weight difference (RWD) and displacement  
 616 distance for fights that ended in an eviction (solid circles, solid line) and non-evictions (open

617 circles, dashed line), for raps performed during the last four bouts. Regression lines fitted for  
618 illustration.



619

620 **Figure 6:** The change in the mean number of raps per bout across the last four bouts of  
621 rapping, for fights that ended in evictions and non-evictions. Error bars show standard errors.

622

623 **Highlights**

- 624 • Fight behaviour varies in vigour fighting skill has yet to be analysed
- 625 • Skill describes the precision of coordinated movement
- 626 • Victorious hermit crabs displaced their shells by less distance than losers
- 627 • Displacement distance varied with vigour and as fights progressed
- 628 • Skill as well as vigour contributes to fighting ability in hermit crabs