

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

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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 (4th 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

470 **References**

471 Arnott, G. & Elwood, R. W. 2009 Assessment of fighting ability in animal contests. *Anim.*

472 *Behav.* **77**, 991–1004. (doi:10.1016/j.anbehav.2009.02.010)

473 Ashker, S. 2011. Technical and tactical aspects that differentiate winning and losing

474 performances in boxing. *Int. J. Perform. Anal. Sport* **11**, 356-364.

475 Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014 lme4: Linear mixed-effects models

476 using Eigen and S4. R package version 1.0-6. [http://CRAN.R-](http://CRAN.R-project.org/package=lme4)

477 [project.org/package=lme4](http://CRAN.R-project.org/package=lme4).

478 Bridge, A., Elwood, R. W. & Dick, J. T.A. 2000 Imperfect assessment and limited

479 information preclude optimal strategies in male-male fights in the orb-weaving spider

480 *Metellina mengei*. *Proc. Biol. Sci.* **267**, 273–9. (doi:10.1098/rspb.2000.0997)

481 Briffa, M. & Elwood, R. W. 2000a Analysis of the finescale timing of repeated signals: does

482 shell rapping in hermit crabs signal stamina? *Anim. Behav.* **59**, 159–165.

483 (doi:10.1006/anbe.1999.1273)

- 484 Briffa, M. & Elwood, R. W. 2000b The power of shell rapping influences rates of eviction in
485 hermit crabs. *Behav. Ecol.* **11**, 288–293. (doi:10.1093/beheco/11.3.288)
- 486 Briffa, M. & Elwood, R. W. 2002 Power of shell-rapping signals influences physiological
487 costs and subsequent decisions during hermit crab fights. *Proc. Biol. Sci.* **269**, 2331–6.
488 (doi:10.1098/rspb.2002.2158)
- 489 Briffa, M. & Elwood, R. W. 2004 Use of energy reserves in fighting hermit crabs. *Proc. Biol.*
490 *Sci.* **271**, 373–9. (doi:10.1098/rspb.2003.2633)
- 491 Briffa, M. & Elwood, R. W. R. 2005 Rapid change in energy status in fighting animals:
492 causes and effects of strategic decisions. *Anim. Behav.* **70**, 119–124.
493 (doi:10.1016/j.anbehav.2004.10.013)
- 494 Briffa, M. & Elwood, R. W. 2007. Monoamines and decision making during contests in the
495 hermit crab *Pagurus bernhardus*. *Anim. Behav.* **73**, 605–612.
- 496 Briffa, M. & Elwood, R. W. 2009 Difficulties remain in distinguishing between mutual and
497 self-assessment in animal contests. *Anim. Behav.* **77**, 759–762.
498 (doi:10.1016/j.anbehav.2008.11.010)
- 499 Briffa, M. & Elwood, R. W. 2010 Repeated measures analysis of contests and other dyadic
500 interactions: problems of semantics, not statistical validity. *Anim. Behav.* **80**, 583–588.
501 (doi:10.1016/j.anbehav.2010.06.009)
- 502 Briffa, M., Elwood, R. W. & Dick, J. 1998 Analysis of repeated signals during shell fights in
503 the hermit crab *Pagurus bernhardus*. *Proc. R. Soc. B Biol. Sci.* **265**, 1467–1474.
504 (doi:10.1098/rspb.1998.0459)
- 505 Briffa, M., Elwood, R. W. & Russ, J. 2003 Analysis of multiple aspects of a repeated signal:

506 power and rate of rapping during shell fights in hermit crabs. *Behav. Ecol.* **14**, 74–79.
507 (doi:10.1093/beheco/14.1.74)

508 Briffa, M. & Hardy, I. C. W. 2013 Introduction to Animal Contests. In *Animal Contests* (eds
509 I. C. W. Hardy & M. Briffa), pp. 357. Cambridge: Cambridge University Press.

510 Briffa, M., Hardy, I. C. W., Gammell, M. P., Jennings, D. J., Clarke, D. D. & Goubault, M.
511 2013 Analysis of contest data. In *Animal Contests* (eds I. C. W. Hardy & M. Briffa),
512 pp. 47–85. Cambridge: Cambridge University Press.

513 Briffa, M. & Sneddon, L. 2010 Contest behavior. In *Evolutionary Behavioral Ecology* (eds
514 D. Westneat & C. Fox), pp. 246–265. Oxford: Oxford University Press.

515 Briffa, M. & Sneddon, L. 2007 Physiological constraints on contest behaviour. *Funct. Ecol.*
516 **21**, 627–637. (doi:10.1111/j.1365-2435.2006.01188.x)

517 Byers, J.A., Hebets, E. & Podos, J. 2010 Female mate choice based upon male motor
518 performance. *Anim. Behav.* **79**, 771–778. (doi:10.1016/j.anbehav.2010.01.009)

519 Chapple, W. D. 1993 Dynamics of reflex cocontraction in hermit crab abdomen: experiments
520 and a systems model. *J. Neurophysiol.* **69**, 1904–17.

521 Edmonds, E. & Briffa, M. 2016 Weak rappers rock more: hermit crabs assess their own
522 agonistic behaviour. *Biol. Lett.* **12**, 20150884. (doi:10.1098/rsbl.2015.0884)

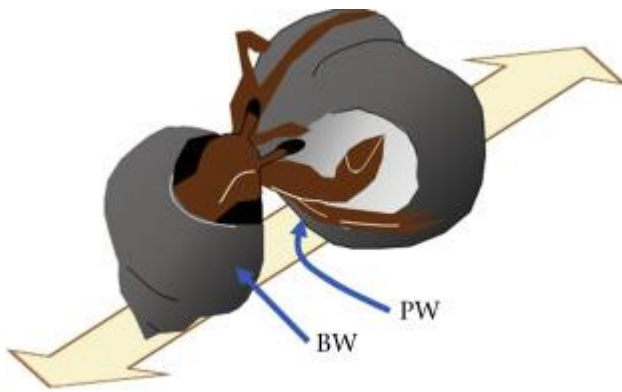
523 Enquist, M. & Leimar, O. 1983 Evolution of fighting behaviour: Decision rules and
524 assessment of relative strength. *J. Theor. Biol.* **102**, 387–410. (doi:10.1016/0022-
525 5193(83)90376-4)

526 Humphries, E., Hebblethwaite, A., Batchelor, T. & Hardy, I.C.W. 2006 The importance of
527 valuing resources: host weight and contender age as determinants of parasitoid wasp

- 528 contest outcomes. *Anim. Behav.* **72**, 891–898. (doi:10.1016/j.anbehav.2006.02.015)
- 529 Huntingford, F. A., Taylor, A. C., Smith, I. P. & Thorpe, K. E. 1995 and physiological
530 studies of aggression swimming crabs in. *J. Exp. Mar. Bio. Ecol.* **193**, 21–39.
- 531 Hsu, Y. 2001 The winner and loser effect: what fighting behaviours are influenced? *Anim.*
532 *Behav.* **61**, 777–786. (doi:10.1006/anbe.2000.1650)
- 533 Hsu, Y., Earley, R. L. & Wolf, L. L. 2006 Modulation of aggressive behaviour by fighting
534 experience: mechanisms and contest outcomes. *Biol. Rev. Camb. Philos. Soc.* **81**, 33–
535 74. (doi:10.1017/S146479310500686X)
- 536 Hsu, Y. & Wolf, L. 1999 The winner and loser effect: integrating multiple experiences. *Anim.*
537 *Behav.* **57**, 903–910. (doi:10.1006/anbe.1998.1049)
- 538 Jennings, D. J., Gammell, M. P., Payne, R. J. H. & Hayden, T. J. 2005 An Investigation of
539 Assessment Games During Fallow Deer Fights. *Ethology* **111**, 511–525.
540 (doi:10.1111/j.1439-0310.2005.01068.x)
- 541 Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. 2014 lmerTest: Tests for random
542 and fixed effects for linear mixed effect models (lmer objects of lme4 package). R
543 Packag. version. , R package version 2.0–6. [http://CRAN.R-](http://CRAN.R-project.org/package=lmerTest)
544 [project.org/package=lmerTest](http://CRAN.R-project.org/package=lmerTest).
- 545 Lancaster, I. 1988 *Pagurus bernhardus* (L.)-an introduction to the natural history of hermit
546 crabs. *F. Stud.* **7**, 189–238.
- 547 Latruffe, C., McGregor, P. & Oliveira, R. 1999 Visual signalling and sexual selection in male
548 fiddler crabs *Uca tangeri*. *Mar. Ecol. Prog. Ser.* **189**, 233–240.
549 (doi:10.3354/meps189233)

- 550 Manica, L.T., Macedo, R.H., Graves, J.A., & Podos, J. Vigor and skill in the acrobatic mating
551 displays of a Neotropical songbird. *Behav. Ecol.* Advance Access published September
552 20, 2016, (doi:10.1093/beheco/arw143)
- 553 Morrell, L., Backwell, P. & Metcalfe, N. 2005 Fighting in fiddler crabs *Uca mjoebergi*: what
554 determines duration? *Anim. Behav.* **70**, 653–662. (doi:10.1016/j.anbehav.2004.11.014)
- 555 Mowles, S. L. & Ord, T. J. 2012 Repetitive signals and mate choice: Insights from contest
556 theory. *Anim. Behav.* **84**, 295–304. (doi:10.1016/j.anbehav.2012.05.015)
- 557 Mowles, S. L., Cotton, P. A. & Briffa, M. 2009 Aerobic capacity influences giving-up
558 decisions in fighting hermit crabs: does stamina constrain contests? *Anim. Behav.* **78**,
559 735–740. (doi:10.1016/j.anbehav.2009.07.003)
- 560 Mowles, S. L., Cotton, P. A. & Briffa, M. 2010 Whole-organism performance capacity
561 predicts resource-holding potential in the hermit crab *Pagurus bernhardus*. *Anim.*
562 *Behav.* **80**, 277–282. (doi:10.1016/j.anbehav.2010.05.004)
- 563 Neave, N., McCarty, K., Freynik, J., Caplan, N., Hönekopp, J. & Fink, B. 2011 Male dance
564 moves that catch a woman’s eye. *Biol. Lett.* **7**, 221–4. (doi:10.1098/rsbl.2010.0619)
- 565 Payne, R. & Pagel, M. 1997 Why do animals repeat displays? *Anim. Behav.* **54**, 109–19.
- 566 Payne, R. 1998 Gradually escalating fights and displays: the cumulative assessment model.
567 *Anim. Behav.* **56**, 651–662.
- 568 R Core Team 2014 R: A Language and Environment for Statistical Computing. R Foundation
569 for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- 570 Sneddon, L. U., Huntingford, F. A. & Taylor, A. C. 1997 Weapon size versus body size as a
571 predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behav.*

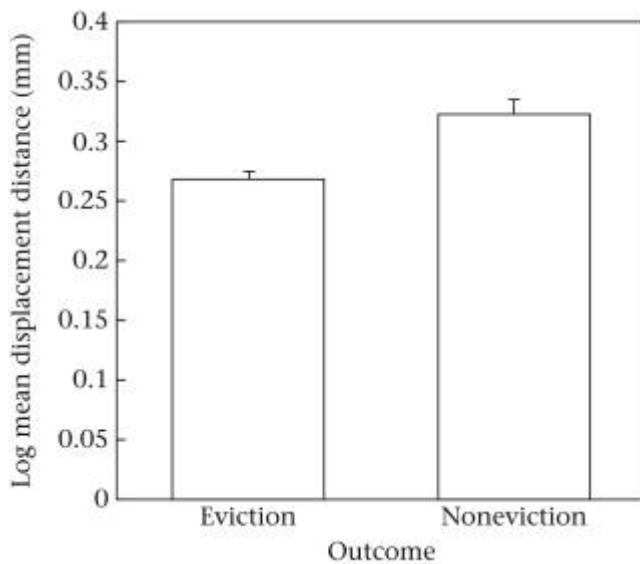
- 572 *Ecol. Sociobiol.* **41**, 237–242. (doi:10.1007/s002650050384)
- 573 Taborsky, B. & Oliveira, R. F. 2012 Social competence: an evolutionary approach. *Trends*
574 *Ecol. Evol.* **27**, 679–688. (doi:10.1016/j.tree.2012.09.003)
- 575 Taylor, P. & Elwood, R.W. 2003 The mismeasure of animal contests. *Anim. Behav.* **65**,
576 1195–1202. (doi:10.1006/anbe.2003.2169)
- 577 Vieira, M. C. & Peixoto, P. E. C. 2013 Winners and losers: a meta-analysis of functional
578 determinants of fighting ability in arthropod contests. *Funct. Ecol.* **27**, 305–313.
579 (doi:10.1111/1365-2435.12051)
- 580 Yasuda, C. I., Matsuo, K. & Wada, S. 2015 Previous mating experience increases fighting
581 success during male-male contests in the hermit crab *Pagurus nigrofascia*. *Behav.*
582 *Ecol. Sociobiol.* **69**, 1287–1292. (doi:10.1007/s00265-015-1941-x)
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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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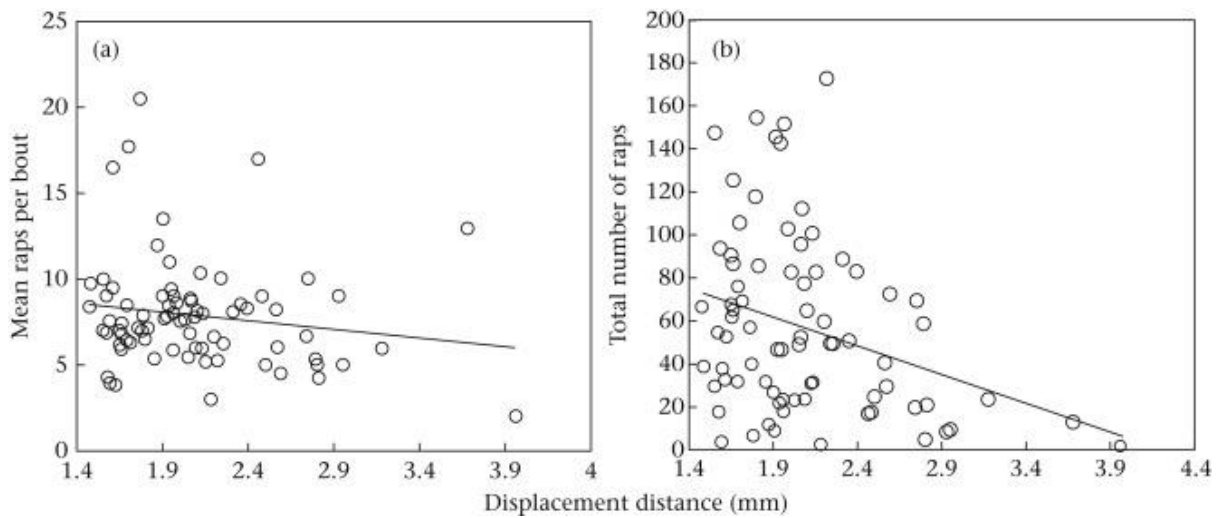
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601 **Figure 2:** The difference in the mean displacement distance of shell rapping performed by
602 attackers between fights that ended in evictions and non-evictions. Error bars show standard
603 errors.

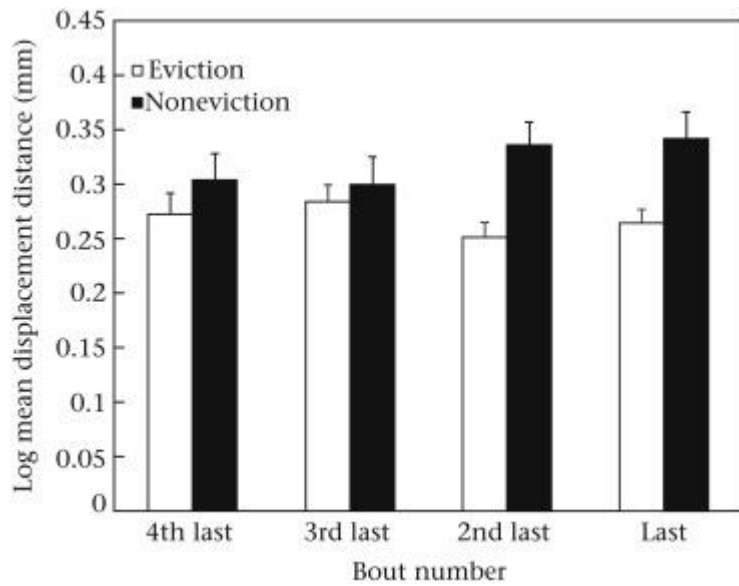
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606 **Figure 3:** The significant negative correlations between displacement distance and (a) the
607 mean number of raps per bout and (b) the total number of raps performed by attackers.
608 Regression lines fitted for illustration.

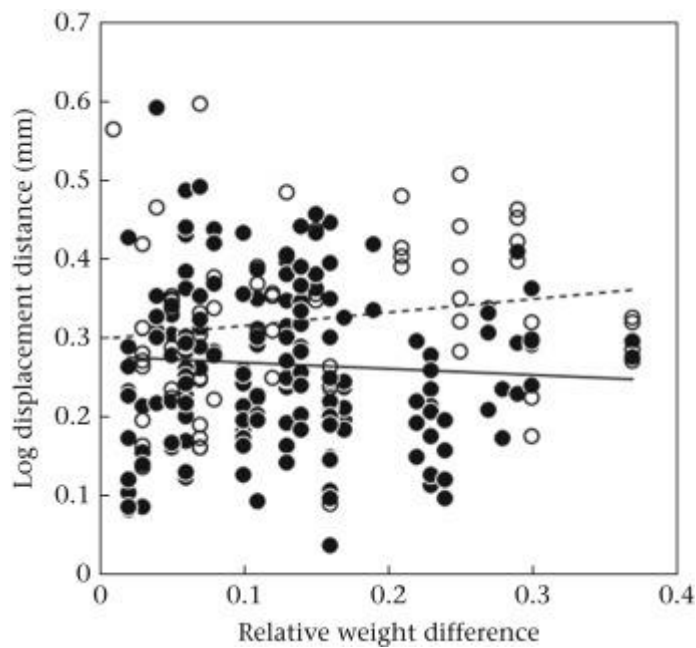
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611 **Figure 4:** The change in mean displacement distance across the last four bouts of rapping, for
 612 fights that ended in evictions and non-evictions. Error bars show standard errors.

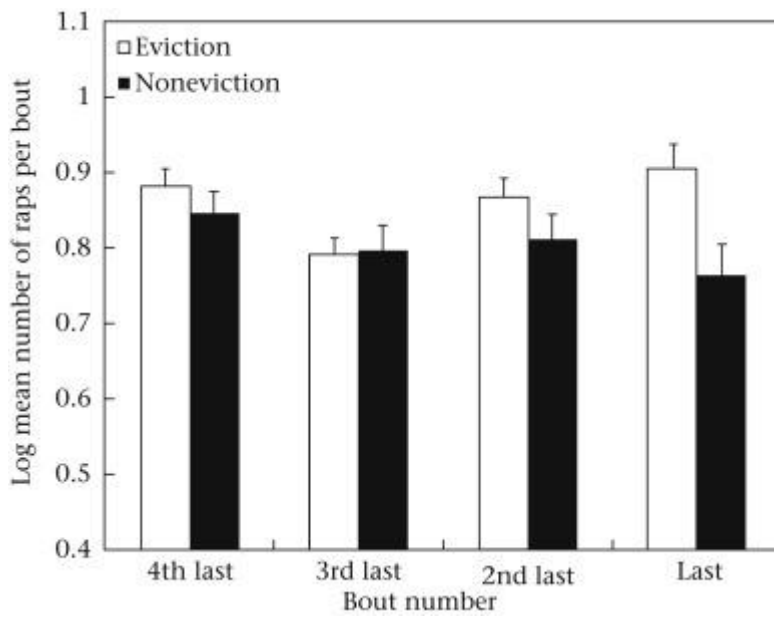
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615 **Figure 5:** The correlation between relative weight difference (RWD) and displacement
 616 distance for fights that ended in an eviction (solid circles, solid line) and non-evictions (open

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