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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Introduction

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

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67   coordinated movement (Mancia 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,

competitors that land their punches on their opponent more accurately are more likely to win

(Ashker, 2011). Repeated striking of the opponent also takes place in fights between

European hermit crabs, *Pagurus bernhardus*, over the ownership of empty gastropod shells.

These serve as 'portable burrows' protecting the crabs from predators and buffering them

against variation in the external environment. The opponents take on distinct roles

characterised by different behaviours. The smaller of the two crabs usually adopts the role of

'defender', spending the majority of the fight tightly withdrawn into its shell, resisting the

attempts of its larger opponent, the 'attacker', to evict it by pulling it out of its shell through

the aperture (Fig. 1). In order to secure an eviction, attackers must perform vigorous bouts of

shell rapping. Attackers grasp the shell of the defender using their walking legs. Then they

use their abdominal musculature to repeatedly move their shell towards and away from the

shell of the defender, so that the defender's shell is struck by a rapid succession of raps.

Successful attackers perform more raps per bout of rapping, hit harder and often leave shorter

pauses between bouts of rapping compared to those that give up without evicting the

defender. They also show greater escalation in the rate of rapping compared to attackers that

are unsuccessful, and the differences in the vigour of rapping between the two outcomes

become more marked towards the end of the fight (Briffa et al., 1998). Analysis of post-fight

metabolites indicates that vigorous shell rapping is a challenging behaviour that exceeds the

energetic requirements of routine activity (Briffa & Elwood, 2004). Previous analyses have

focussed on the vigour of shell rapping (Briffa et al. 1998; Briffa & Elwood 2000a; 2000b;

Briffa, Elwood & Russ, 2003) but, as yet, none have addressed the spatial component of the

movements used in shell rapping. A simple measure of the spatial component for shell

rapping is the distance that the attacker moves its shell away from the defender's shell prior

to each strike, which we refer to as 'displacement distance'. Given that shell rapping involves

repeated strikes of the attacker's shell against the defender's we 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.

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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

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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. berhnardus*; 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.

17

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 a 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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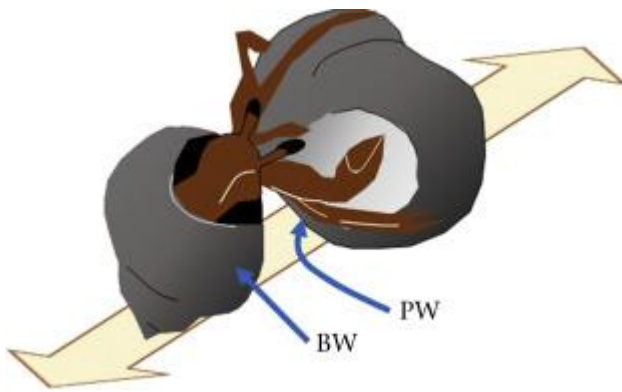
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589   **Figure 1:** Diagrammatic illustration of two hermit crabs engaged in a shell fight. The attacker

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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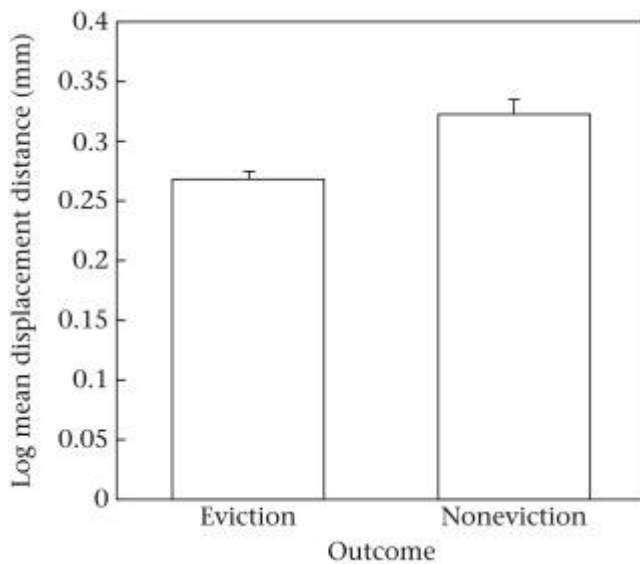
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601   **Figure 2:** The difference in the mean displacement distance of shell rapping performed by

602   attackers between fights that ended in evictions and non-evictions. Error bars show standard
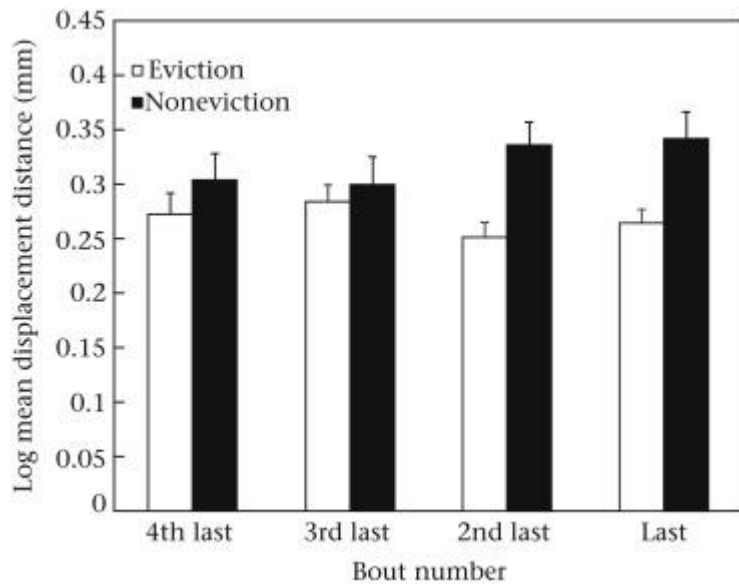
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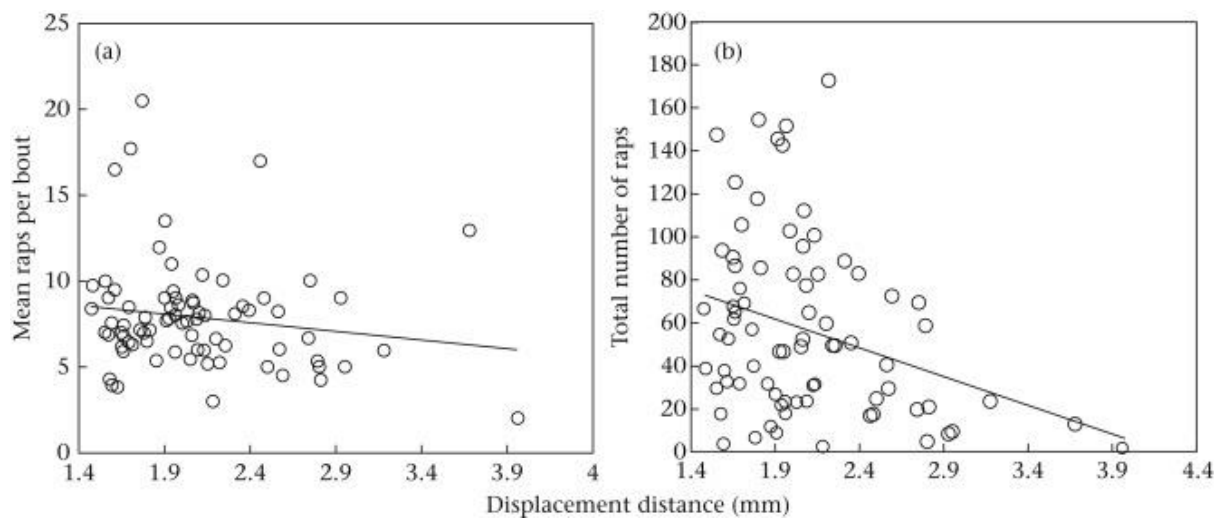
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606   **Figure 3:** The significant negative correlations between displacement distance and (a) the

607   mean number of raps per bout and (b) the total number of raps performed by attackers.

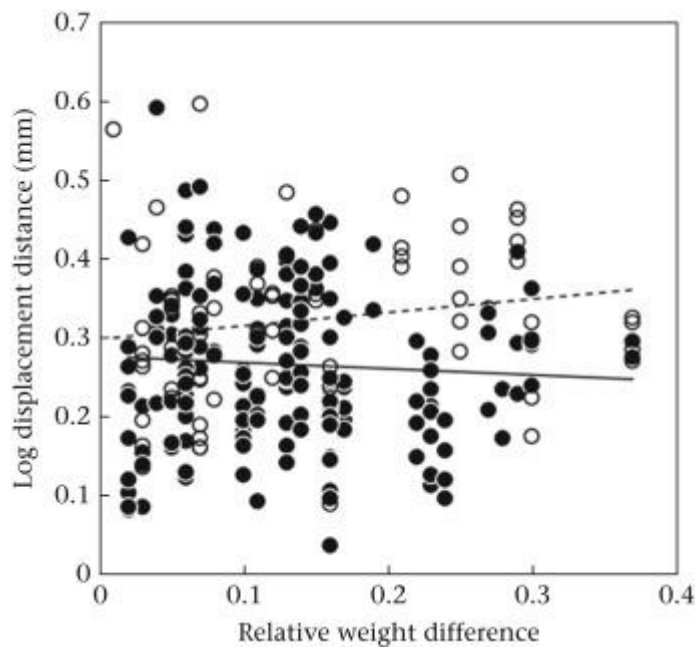608   Regression lines fitted for illustration.

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Figure 4: The change in mean displacement distance across the last four bouts of rapping, for fights that ended in evictions and non-evictions. Error bars show standard errors.
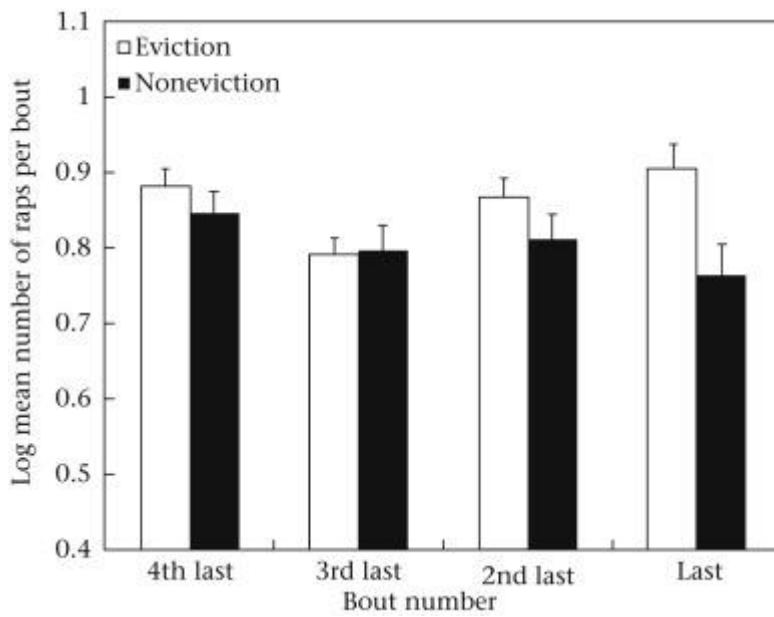
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Figure 5: The correlation between relative weight difference (RWD) and displacement distance for fights that ended in an eviction (solid circles, solid line) and non-evictions (open

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