1 **Selection for conspicuous visual signals in a fiddler crab**

2 Perez D.M. [1]*; and Backwell P.R.Y.[1]

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4 [1] Research School of Biology; The Australian National University; Canberra ACT 0200;

5 Australia

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9 ***Corresponding author**: Daniela Malgarini Perez; Division of Ecology & Evolution;

10 Research School of Biology; The Australian National University; Canberra ACT 0200;

11 Australia.

12 Tel: +61 02 6125 3828

13 Email: dani.malgarini@gmail.com; https://orcid.org/0000-0002-8560-0368

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22 **Abstract**

23 Sexual selection has an undeniable influence in the evolution of the spectacular

24 diversity of courtship signals in the animal kingdom. A long history of study has

25 pointed to mechanisms through which sexual selection can act: it can favour signals that

26 are reliable indicators of species identity or effectively transfer mate quality

27 information. In some species, these mechanisms have the potential to shape signal

28 evolution. This is the case in fiddler crabs. Males court females by waving their

29 sexually dimorphic claw. Females recognise conspecific males by the species-specific

30 display, whilst intraspecific variants of the display appear to be indicators of male

31 quality. We investigated which of these mechanisms prevail by using robotics to test

32 female responses to waves of different heights in the fiddler crab, *Austruca mjoebergi*.

33 We reveal that, although the studied species shares a sympatric habitat, females did not

34 significantly more often approach the species' average signal. We found evidence that

35 more conspicuous, higher signals were more likely to attract females, although the

36 effect was not particularly strong. We discuss our results in the light of other possible

37 scenarios from which sexual selection can act in the evolution of signals.

38

39 Key words: Sexual selection; Signal diversity; Signal evolution; Directional selection;

40 Species recognition.

41

42 **Significance statement:** Sexual selection has strong role in the evolution of courtship

43 signals. A large body of evidence has revealed that mating preferences may favour

44 signals that indicate species identity or mate quality. We study which of these

45 mechanisms is predominant in fiddler crabs. We use robotics to investigate female

46 preference for a highly conspicuous and diverse characteristic of courtship signals. We

47 found that, females most likely do not use the signal for species recognition, but instead

48   favour signals that stand out and indicate mate quality. Our results advocate that

49   directional selection is likely to be predominant, but we suggest that a more complex

50   mosaic of selective forces may influence the evolution of the high interspecific signal

51   diversity in fiddler crabs.

Introduction

Extravagant courtship traits and displays are widespread throughout the animal

kingdom. The high diversity of these signals spurs the question of how and why they

have evolved. The most common explanation is that the choosing sex has preferences

for particular variants of the species-specific signals. These different preferences can act

as pre-mating barriers between species (e.g. Hebets and Papaj 2005; Boul et al. 2007;

Chen et al. 2012) as well as influencing how conspicuous certain aspects in the

attraction signals become. Thus, distinct sexual selection processes may drive the

evolution of courtship traits in different directions.

Taxa that have considerable variability in their courtship signals offer a unique

opportunity to examine the reasons behind their evolution (Ord and Martins 2006). One

such group is the fiddler crabs (Crustacea: Ocypodidae). Males have a single enlarged

claw that is used for fighting and courtship displays, which are quickly stimulated by

female presence. The displays consist of conspicuous circular and vertical wave

motions with the claw often raised above eye-level (Figure 1a). Interestingly, this signal

has a great interspecific diversity with each species presenting its own pattern (Perez et

al. 2012; Salmon et al. 1978; Detto et al. 2006). Females use wave patterns for species

recognition, indicating the coevolution between signal design and receiver's preferences

(Perez and Backwell 2017). Selection towards a stereotyped, or average, signal may

occur if trait variability results in overlaps with heterospecific signals, therefore

jeopardizing effective species recognition (Ryan and Rand 1993; Sætre et al. 1997). In

fact, the vertical displacement of the display proportional to body size is species-

specific in sympatric species, and it was previously suggested that wave amplitude is a

cue for species recognition when species distributions overlap (How et al. 2009). Thus,

as the most variable element of the wave between species, the vertical motion of the

78   display is a promising target in female choice studies (Perez et al. 2012; Perez in prep).

79   This aspect of courtship also represents a highly conspicuous facet of the display under

80   fiddler crab visual ecology (Zeil, Nalbach & Nalbach, 1986; Christy & Salmon, 1991;

81   Land & Layne, 1995; Zeil & Al-Mutairi, 1996; Murai & Backwell, 2006) and the only

82   one to be equally perceived from any sender-receiver orientation (Perez et al. 2012;

83   Araujo et al., 2013).

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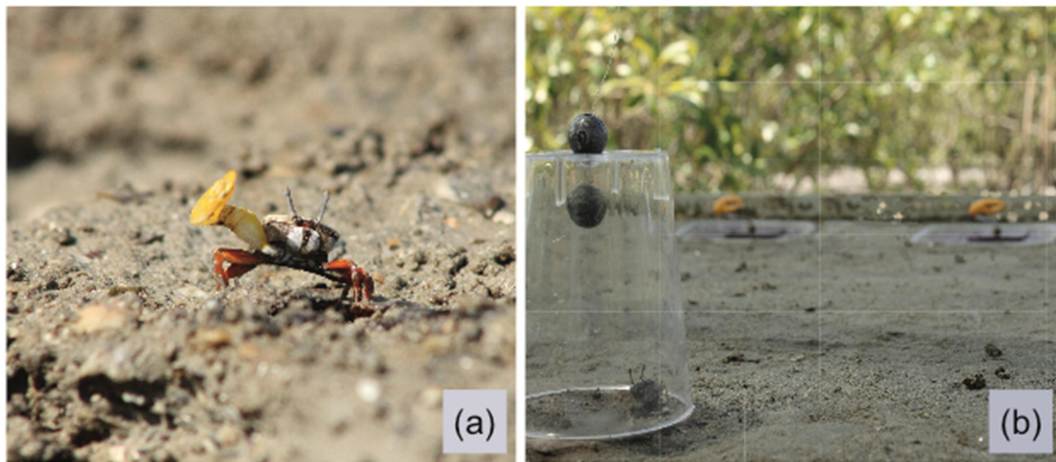
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86   **Fig. 1** Fiddler crab *Austruca mjoebergi* (a) real male waving in his natural habitat (b)

87   robotic males waving in the choice arena being assessed by female inside transparent

88   cup prior to release

89

90   Intraspecific variation in wave displays is also fundamental to mate choice (Jordão et al.

91   2007; Pope 2005; Mowles et al. 2018). Previous studies on wave patterns showed that

92   females of *Afruca tangeri* and *Austruca perplexa* approach males based on the height

93   that the claw is raised during a wave in natural conditions (Oliveira and Custódio 1998;

94   Murai and Backwell 2006). Although the trait is correlated with claw length and body

95   size, females can assess the claw displacement in relation to the body, indicating that

96   females prefer more stimulating signals (Murai and Backwell 2006). High amplitude

97   waves require bigger and more energetic movements and can indicate male quality and

98   potential (Murai and Backwell 2006; Bywater et al., 2018). However, how wave

99   displays are used for species recognition and mate choice is still unclear as these

100   functions can potentially conflict (Pfennig 1998). Thus, we suggest that in species that

101   face high sympatry, females may give priority to species recognition over mate quality

102   assessment.

103

104   This study takes a broad approach into the investigation of fiddler crab signal evolution

105   by sexual selection. We aim to determine the predominant mechanism that shapes

106   courtship signal in fiddler crabs by running our investigations with a well-studied

107   species, *A. mjoebergi* (Detto et al. 2006; Reaney et al. 2008; Callander et al. 2012).

108   Controlled choice experiments, are vital to investigate signal preference with accuracy.

109   We use robotics to effectively manipulate male signals and explore female preferences

110   for the highly conspicuous wave element, wave amplitude (i.e. the extent of claw reach

111   at display apex calculated as a proportion between height above eye level and the total

112   vertical movement of the claw during a wave; see the diagram in Table 1). Thus, we

113   investigate the average and range of wave amplitudes in this species to specifically ask

114   the questions: (1) is wave amplitude a cue for species recognition? A preference for the

115   average value could indicate stabilizing selection for wave characteristics; (2) are

116   females attracted to higher amplitude waves in general? Higher amplitude waves might

117   help females to locate males more clearly or assess their size and potential.

118

Methods

We studied a population of the fiddler crab *Austruca mjoebergi* from August to November in 2013 and 2017 at East Point Reserve, Darwin, Australia (12°24'31.89"S 130°49'49.12"E). Both males and females defend territories around their burrow within a large, mixed-sex population. When ready to mate, a female will leave her territory and move through the population of waving males. Males form small clusters (about 2-6 individuals) around the female, and as she moves, males join in or drop out of the cluster. The female visits one of the males in the cluster by walking towards him and briefly entering his burrow. She then either leaves the male to continue searching, or she accepts the male and remains underground in his burrow. The chosen male enters the burrow and plugs its entrance with sand, where mating occurs.

Wave amplitudes

We calculated the average and range of *A. mjoebergi* wave amplitudes: the proportion of claw elevation above eye level by the total vertical claw movement (see diagram in Table 1). We recorded 56 waving males under natural conditions from a horizontal perspective. We then watched the videos to measure their wave displays following the methodology by Perez and collaborators (2016). The average wave amplitude was 0.26 ± 0.12, similar to the one previously reported, 0.29 ± 0.08 (How et al. 2009). This value overlaps with the wave amplitudes of the two highly sympatric species, *Tubuca elegans* (0.16 ± 0.10) and *T. signata* (0.22 ± 0.05; Booksmythe et al. 2008; How et al. 2009).

Preference experiment

Female preference was tested using custom-built robotic crabs that consist of a twin-cam motor, which moves a small metal arm with a plaster mould of *A. mjoebergi* claw
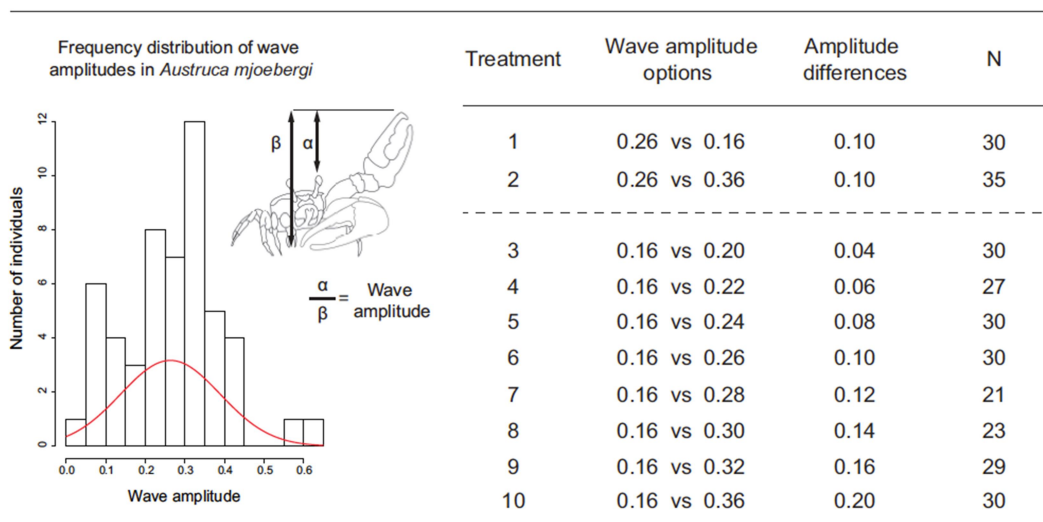
145   attached in a motion that exactly mimics the courtship wave of the species. The motor

146   was remotely controlled to regulate the exact timing of each wave using custom

147   designed software (see Reaney et al. 2008; Holman et al. 2014 for further details of the

148   robotic crabs). The motor was buried under a testing arena with only the metal arm

149   protruded through the arena floor. For all treatments, we used moulds of the same claw,

150   each measuring 2.03 cm, considered an attractive size (Clark and Backwell, 2016), and

151   painted a yellow that matched the natural claw color of this species (see Detto et al.

152   2006 for claw paint). The choice arena mimics the natural conditions explained above

153   and is composed of a raised platform covered with a 0.5cm thick layer of mangrove

154   sediment. The platform was placed in a clearing in the mangroves with a homogenous

155   background of mangrove trees, maintaining the visual scenario of their natural

156   environment (Figure 1b). Females are known to respond well to this experimental

157   setting, which has been used several times in the past to reveal female mate preferences

158   (Perez and Backwell, 2017). We controlled for any confounding variables in our

159   experimental design, by being careful to randomize the position that the stimuli were

160   presented in relation to each other and the surrounding environment.

161

162   The study targeted mate-searching females, which were captured, measured (carapace

163   width in cm) and housed individually in shaded cups containing 0.4 cm deep seawater

164   until used in a choice trial. For each trial, the female was placed at the release point on

165   one end of the test arena, in a small translucent cup that was lifted remotely once the

166   female had seen three waves of the robotic crabs (Figure 1b) (see Reaney et al. 2008 for

167   more details). A choice was considered to be made when the female approach within 5

168   cm of a robotic crab arm. The time until choice was recorded from releasing until

169   approach to a robotic crab arm. Trials were discarded if the female darted, ran to the

170   edge of the arena, or remained stationary for >3 minutes. Each female (total 254) was

171   tested only once and released after the experiment so they could continue mate-

172   searching. To avoid recaptures, females were collected from non-release areas.

173

174   The wave rate of all stimuli was constant at 16.8 waves/minute, and a female was

175   placed equidistant from two robotic crab units (each 20 cm away). The absolute height

176   of the wave can change according to receiver's distance (How et al. 2008), but intense

177   courtship only occurs when the resident can recognize the sex of the approaching crab

178   (from approximately 30 cm; How et al. 2008). Thus, the placement of the female

179   relative to the robotic males was critical. In addition, most choices are made from the

180   releasing point. Thus, although the contrast between claw waving and background

181   changes with female approach, the movement amplitude in relation to body is constant.

182   In all treatments, females were given a choice between two stimuli presented on robotic

183   crab units 15 cm apart. We used robots with distinct wave amplitudes to reproduce the

184   average as well as lower and higher waves that fall within one standard deviation from

185   the average. Height from the ground at claw starting position (i.e. horizontal from the

186   ground) was fixed, and angles of claw movement and wave shape were constant. The

187   data is not vulnerable to noise, as when presented to identical robotic crabs, the choice

188   is extremely close to 1:1 (choice between a pair of synchronous waving robotic crabs

189   and average wave amplitude; two-tailed binomial test: 55:68, $P = 0.28$; Backwell

190   unpublished data).

191

192   We first investigated whether females use wave amplitude as a cue for species

193   recognition (i.e. as a pre-mating barrier). We determine whether there is a preference for

194   the average wave amplitude (0.26) against lower wave amplitude (0.16; Treatment 1, n

195   = 30) and higher wave amplitude (0.36; Treatment 2, n = 35) (Table 1). Following, we

196   investigated if preferences were absolute, and therefore whether sexual selection favors

197 higher (most conspicuous) wave amplitudes in general. To answer this part of our study,

198 we ran a series of experiments where the lowest wave amplitude (0.16) was paired

199 against increasing amplitudes ranging from 0.20 to 0.36 (Treatments 3 to 10). This gave

200 a series of wave amplitude differences (0.04, n = 30; 0.06, n = 27; 0.08, n = 30; 0.10, n

201 = 30; 0.12, n = 21; 0.14, n = 23; 0.16, n = 29; 0.20, n = 30) between the choices

202 presented in each treatment (Table 1). Finally, we investigate if time until choice

203 indicates how certain females are of their preferences. Data collection was randomized

204 between treatments across mating cycles; most of the data (89% of the choices) were

205 collected in 2017. Given the experimental procedure, it was not possible to record data

206 blind.

207

Treatment	Wave amplitude options	Amplitude differences	N
1	0.26 vs 0.16	0.10	30
2	0.26 vs 0.36	0.10	35
3	0.16 vs 0.20	0.04	30
4	0.16 vs 0.22	0.06	27
5	0.16 vs 0.24	0.08	30
6	0.16 vs 0.26	0.10	30
7	0.16 vs 0.28	0.12	21
8	0.16 vs 0.30	0.14	23
9	0.16 vs 0.32	0.16	29
10	0.16 vs 0.36	0.20	30

208

209 **Table 1.** Frequency distribution of wave amplitudes from a sample of *Austruca*

210 *mjoebergi* males. Wave amplitude is calculated as the proportion of wave height at the

211 maximum claw elevation relative to eye-level (α) divided by the total claw elevation

212 (β). Wave amplitudes used in each of the two-choice treatments are presented along

213 with the difference between the choices and the number of trials in each treatment, N.

214 Note that Treatments 1 and 6 are comprised of the same dataset used in the two stages

215 of the investigation, preferences for average wave amplitude (Treatment 1 to 2), and

216 higher amplitudes (Treatments 3 to 10)

217

218 ***Statistical Analyses***

219 To investigate female selection on wave displays, we performed Generalized Linear

220 Models (GLM) and one Linear Model (LM). First, to test female preference for average

221 amplitude against lower and higher waves (Treatments 1 and 2), we ran a GLM with

222 choice (either average or other wave amplitude) as the response variable and treatment

223 as the explanatory variable with a binomial error distribution and logit link function. In

224 the second part of the experiment, we investigated if preference favours higher

225 amplitude displays. We ran a GLM with the response variable as choice for high or low

226 wave option and increasing wave amplitude differences across the treatments as fixed

227 factor with a binomial error distribution and logit link function. Following this, we ran

228 the null GLM where amplitude difference was removed to answer if females selected

229 for higher displays in general. Lastly, we tested if the time until choice differed

230 according to choices for higher or lower wave options and amplitude differences. We

231 transformed the time of response (log_{10}) and regressed it against choice for high or low

232 wave option and amplitude differences (with an interaction between them). We set the

233 reference level as the lowest amplitude difference (0.04; Treatment 3). We considered

234 amplitude differences as a continuous variable due to the increasing contrast between

235 options presented across the treatments 3 to 10 (from 0.04 to 0.2). We conducted all

236 statistical analyses on R-3.3.3 (R Core Development Team 2017).

237

238 ***Ethical Note***

239 This research was approved by the Australian National University Animal Ethics

240 Committee (permit A2015/54). We limited the handling and the amount of time each

11

241   crab was used to no longer than 5 minutes. No crab was injured during the research, and

242   all continued their regular activities after release. The work was conducted under a

243   research permit from the Darwin City Council (permit no. 3648724).

244   ***Data Availability***

245   The datasets during and/or analysed during the current study are available from the

246   corresponding author on reasonable request.

247

248 **Results**

249 In the first part of the experiment, we investigated whether females selectively

250 approached the 'average' signal height. We found that females were not more likely to

251 approach the species-specific average wave height over higher or lower waves (Figure

252 2). Of the 65 trials in total, 34 (52%) chose the average wave amplitude (17 choices in

253 Treatment 1; 17 choices in Treatment 2) and 31 (48%) chose the alternative option (13

254 choices for the lower wave in Treatment 1; 18 choices for the higher wave in Treatment

255 2) (GLM: Estimate = -0.211, Std. Error = 0.500, $P = 0.673$).

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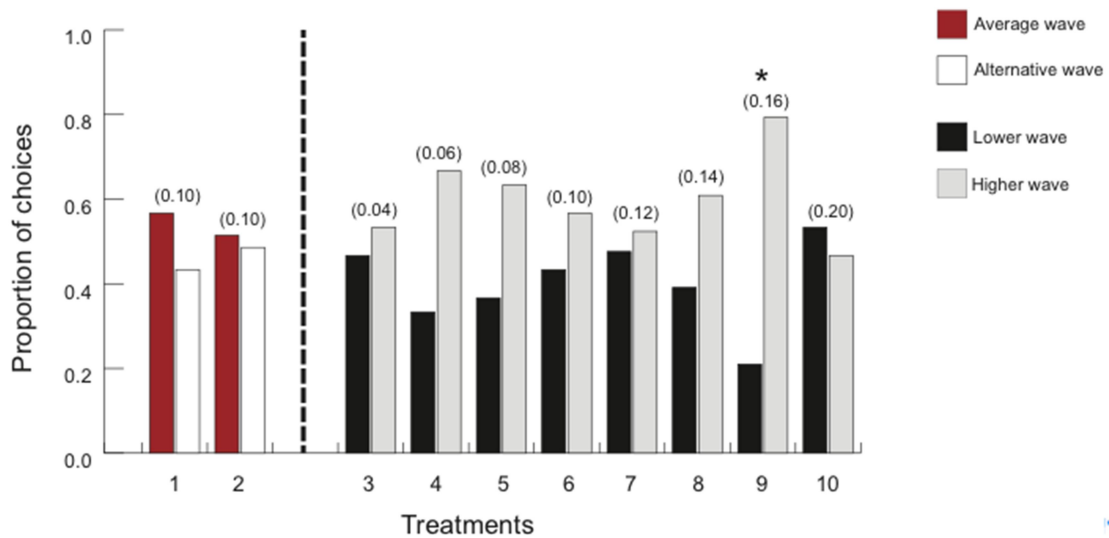
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259 **Fig. 2** Female *Austruca mjoebergi* responses to high and low wave amplitudes labelled

260 by colour. The selected options are proportional to sample sizes across each of the 10

261 treatments indicated by the horizontal axis according to the amplitude differences

262 between the options indicated between brackets. Binomial tests were performed for

263 each treatment individually and significance indicated, thus: *=$P<0.05$

264

265 In the second part of the experiment, we investigated whether females selectively

266 approach higher amplitude signals (Figure 2). We found that females did not

267   significantly approach higher or lower amplitude waves as the amplitude difference

268   increases (GLM: Estimate = -0.017, Std. Error = 0.051, P = 0.738). However, the

269   chance that a random female at a random treatment will pick the higher wave over the

270   lower amplitude wave was significant (GLM: Estimate = 0.364, Std. Error = 0.121, $P <$

271   0.01). Consequently, there was a tendency for females to approach higher waves in

272   general, but an increase in amplitude differences did not affect female behaviour.

273

274   Finally, the time taken to approach a signal was similar when females approached

275   higher ($\bar{x}$ = 36.14, s.d. = 27.79, n = 132) or lower amplitude waves ($\bar{x}$ = 43.06, s.d. =

276   34.29, n = 88) (LM: Estimate= -0.103, Std. Error = 0.204, P = 0.615). Amplitude

277   differences (LM: Estimate= -0.047, Std. Error = 0.345, P = 0.891) did not have a

278   significant effect on the time taken to approach. The response time for the higher option

279   does not significantly differ from the lower option (LM: Estimate = -0.075, Std. Error =

280   0.205, P = 0.713) or as the amplitude differences between options increased (LM:

281   Estimate = 0.011, Std. Error = 0.461, P = 0.980).

282

Discussion

We show that under a set of scenarios from which sexual selection can act in the evolution of signals, *Austruca mjoebergi* females tend to approach higher amplitude wave displays, although this result is driven by one of the treatments (Amplitude difference = 0.16). This tendency did not get stronger as the difference in amplitude between the choices increase. In addition, average wave amplitude was not significantly preferred even though the studied species shares a highly sympatric habitat.

The vertical movement is the most conspicuous motion component of wave displays and is largely responsible for the current variability of courtship in fiddler crabs (Perez et al. 2012; Perez in prep). Wave amplitude, the claw reach above the eye level relative to the entire wave movement, is species-specific (How et al. 2009). The variation around wave amplitude average in *Austruca mjoebergi* males (0.26 ± 0.12) mainly overlaps with two sympatric species, *Tubuca elegans* (0.16 ± 0.10) and *T. signata* (0.22 ± 0.05; Booksmythe et al. 2008; How et al. 2009), which could affect species recognition. Despite this, females did not significantly more often approach the species-specific average wave heights. Two explanations are possible for this finding. First, females do not use only one cue, but the combination of the species-specific cues (for instance wave movement and claw and body colour) to recognize conspecifics in sympatric populations (Salmon et al. 1978; Detto et al. 2006; Perez and Backwell 2017). Second, preferences for the average may be stronger in populations under high predation pressures. When females face greater risks of predation, male assessment must be rapid (Perez et al. 2016). Females of *A. mjoebergi* are not subject to intense predation (Bourdiol et al. 2018) and costs of being picky are lower (Magnhagen 1991). Future studies investigating female preferences in other species will be essential to validate the findings of the present study.

309

310   In search for high quality mates, females may pick males that display costly

311 conspicuous signals with high-energy expenditure (Zahavi 1975). Courtship signal

312 exaggeration is the most predictable direction of evolution via sexual selection, as it

313 improves communication efficiency (Tazzyman et al. 2014). Conspicuous signals in

314 fiddler crabs are predominantly from species with strong sexual selection (How et al.

315 2009) and the studied species showed exceptionally high waves. Although display

316 height and crab size are correlated (Murai et al. 2009), the tendency for females to

317 approach higher amplitude (waves extending above the eye level) show that females can

318 dissociate wave and claw size. Although we had mostly non-significant results, our

319 results tend to follow prior findings in other species of general preferences for high

320 waves (Oliveira and Custódio 1998; deRivera 2005; Murai and Backwell 2006; Murai

321 et al. 2009), but not to increasingly higher values. Furthermore, the spread of wave

322 amplitude values around the average shows that this trait is a possible indicator of male

323 quality. The suggestion that females are attracted to signals that stand-out is still valid

324 since females are also attracted to leading waves (Backwell et al. 1999). Future

325 investigations controlling for other aspects of the display movement, such as speed and

326 lateral sweep, may help to reveal if preference ultimately tends to favour stand-out

327 signals. Due to experimental restrictions with robotic crabs mechanism, this was not

328 possible in the present study.

329

330   Understanding the roles of mate preferences in courtship evolution is a daunting task

331 due to the myriad of study cases in nature and their particularities (Jennions and Petrie

332 1997). For this reason, it is important to take broad investigative approaches to

333 understand variation in sexual choices. The evolution of courtship in fiddler crabs is

334 likely attributed to an interaction with other selective mechanisms not looked at in this

335   study. We encourage prospective research to reveal the magnitude of other selecting

336   factors that shape display diversity (Cornwallis and Uller 2010). For example, the extent

337   to which a signal is perceived in relation to the environment is an essential part in the

338   evolution of signal structure and variability (Hemmi et al. 2006; Klomp et al. 2016;

339   Ramos and Peters 2017).

340

341   The effectiveness of communication between the receiver and the signaller plays an

342   essential role in courtship signal evolution (Kirkpatrick 1987; Endler 1992). The

343   receiver's sensory system is a fundamental evolutionary force upon courtship signals

344   (Ryan 1993, 1998) and, therefore, sexual selection favours those signals that can be

345   perceived by the receiver's pre-existing perceptual bias (West-Eberhard 1979).

346   The preference for wave height is compatible with accurate perception of vertical

347   movements (Zeil et al. 1986; Christy and Salmon 1991; Land and Layne 1995; Zeil and

348   Al-Mutairi 1996; Murai and Backwell 2006). In their flat visual world, fiddler crabs

349   have two visual zones, above and below the line of the horizon (Zeil et al. 1986). In the

350   former, the crabs are sensitive to predator detection (enlarged size or coming from the

351   sky), and in the latter the crabs are accustomed to movements of congeners (Land and

352   Layne 1995). Wave displays break the visual horizon line, which initially alerts the

353   receiver to potential danger, but later can be perceived as a congener's signal (Zeil and

354   Al-Mutairi 1996). Thus, males use vertical movements as sensory traps to stimulate the

355   visual perception of the receiver (Zeil et al. 1986; Oliveira and Custódio 1998; Burford

356   2000).

357

358   The line of visual horizon can act as a threshold, limiting the perception of sexual

359   signals. Consequently, the female's ability to discriminate stimuli may vary, as a signal

360   may be distinctly perceived according to the relative sizes of the sender and receiver,

361 which could favour the intraspecific diversity we found and the non-significant results

362 in most of our treatments (Hingle et al 2001; Ronald et al. 2012). When species biology

363 alludes to phenotype-dependent preferences, it is important to account for mate choice

364 variation to better understand signal diversity (Jennions and Petrie 1997). In stalk-eyed

365 flies, choices are size-dependant as larger females distinguish eyespan differences more

366 accurately and prefer larger males, although females prefer males with large eyespan in

367 general (Hingle et al. 2001). This mechanism may have the power to alter the intensity

368 and direction of sexual selection on courtship (Jennions and Petrie 1997; Widemo and

369 Sæther 1999). This is an important aspect that previous studies on fiddler crab female

370 preference have overlooked (Oliveira and Custódio 1998; deRivera 2005; Murai and

371 Backwell 2006).

372

373 Finally, recent findings revealed that fiddler crab male morphology is linked to claw

374 waving displays (Bywater et al. 2018). Thus, the balance between body parts during

375 display is an essential constraint to wave pattern and reach (Bywater et al. 2018) and,

376 thus, sexual selection not only acts on the behaviour, but on the morphology that is

377 correlated with it. Colour association and background contrast could also influence the

378 patterns and conspicuousness of the signal to the receiver (Detto et al. 2006; McLean et

379 al. 2014; How et al. 2015). Comparing species signals and the receiver perception

380 against the myriad of visual backgrounds should reveal a whole new perspective of how

381 these signals evolved to their present complexity and is another essential and a rich

382 research avenue (Bian et al. 2018).

383

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