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

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Abstract

Sexual selection has an undeniable influence in the evolution of the spectacular diversity of courtship signals in the animal kingdom. A long history of study has pointed to mechanisms through which sexual selection can act: it can favour signals that are reliable indicators of species identity or effectively transfer mate quality information. In some species, these mechanisms have the potential to shape signal evolution. This is the case in fiddler crabs. Males court females by waving their sexually dimorphic claw. Females recognise conspecific males by the species-specific display, whilst intraspecific variants of the display appear to be indicators of male quality. We investigated which of these mechanisms prevail by using robotics to test female responses to waves of different heights in the fiddler crab, *Austruca mjoebergi*. We reveal that, although the studied species shares a sympatric habitat, females did not significantly more often approach the species' average signal. We found evidence that more conspicuous, higher signals were more likely to attract females, although the effect was not particularly strong. We discuss our results in the light of other possible scenarios from which sexual selection can act in the evolution of signals.

Key words: Sexual selection; Signal diversity; Signal evolution; Directional selection; Species recognition.

Significance statement: Sexual selection has strong role in the evolution of courtship signals. A large body of evidence has revealed that mating preferences may favour signals that indicate species identity or mate quality. We study which of these mechanisms is predominant in fiddler crabs. We use robotics to investigate female preference for a highly conspicuous and diverse characteristic of courtship signals. We 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.

52 **Introduction**

53 Extravagant courtship traits and displays are widespread throughout the animal
54 kingdom. The high diversity of these signals spurs the question of how and why they
55 have evolved. The most common explanation is that the choosing sex has preferences
56 for particular variants of the species-specific signals. These different preferences can act
57 as pre-mating barriers between species (e.g. Hebets and Papaj 2005; Boul et al. 2007;
58 Chen et al. 2012) as well as influencing how conspicuous certain aspects in the
59 attraction signals become. Thus, distinct sexual selection processes may drive the
60 evolution of courtship traits in different directions.

61
62 Taxa that have considerable variability in their courtship signals offer a unique
63 opportunity to examine the reasons behind their evolution (Ord and Martins 2006). One
64 such group is the fiddler crabs (Crustacea: Ocypodidae). Males have a single enlarged
65 claw that is used for fighting and courtship displays, which are quickly stimulated by
66 female presence. The displays consist of conspicuous circular and vertical wave
67 motions with the claw often raised above eye-level (Figure 1a). Interestingly, this signal
68 has a great interspecific diversity with each species presenting its own pattern (Perez et
69 al. 2012; Salmon et al. 1978; Detto et al. 2006). Females use wave patterns for species
70 recognition, indicating the coevolution between signal design and receiver's preferences
71 (Perez and Backwell 2017). Selection towards a stereotyped, or average, signal may
72 occur if trait variability results in overlaps with heterospecific signals, therefore
73 jeopardizing effective species recognition (Ryan and Rand 1993; Sætre et al. 1997). In
74 fact, the vertical displacement of the display proportional to body size is species-
75 specific in sympatric species, and it was previously suggested that wave amplitude is a
76 cue for species recognition when species distributions overlap (How et al. 2009). Thus,
77 as the most variable element of the wave between species, the vertical motion of the

display is a promising target in female choice studies (Perez et al. 2012; Perez in prep). This aspect of courtship also represents a highly conspicuous facet of the display under fiddler crab visual ecology (Zeil, Nalbach & Nalbach, 1986; Christy & Salmon, 1991; Land & Layne, 1995; Zeil & Al-Mutairi, 1996; Murai & Backwell, 2006) and the only one to be equally perceived from any sender-receiver orientation (Perez et al. 2012; Araujo et al., 2013).

Fig. 1 Fiddler crab *Austruca mjoebergi* (a) real male waving in his natural habitat (b) robotic males waving in the choice arena being assessed by female inside transparent cup prior to release

Intraspecific variation in wave displays is also fundamental to mate choice (Jordão et al. 2007; Pope 2005; Mowles et al. 2018). Previous studies on wave patterns showed that females of *Afruca tangeri* and *Austruca perplexa* approach males based on the height that the claw is raised during a wave in natural conditions (Oliveira and Custódio 1998; Murai and Backwell 2006). Although the trait is correlated with claw length and body size, females can assess the claw displacement in relation to the body, indicating that females prefer more stimulating signals (Murai and Backwell 2006). High amplitude

waves require bigger and more energetic movements and can indicate male quality and potential (Murai and Backwell 2006; Bywater et al., 2018). However, how wave displays are used for species recognition and mate choice is still unclear as these functions can potentially conflict (Pfennig 1998). Thus, we suggest that in species that face high sympatry, females may give priority to species recognition over mate quality assessment.

This study takes a broad approach into the investigation of fiddler crab signal evolution by sexual selection. We aim to determine the predominant mechanism that shapes courtship signal in fiddler crabs by running our investigations with a well-studied species, *A. mjoebergi* (Detto et al. 2006; Reaney et al. 2008; Callander et al. 2012). Controlled choice experiments, are vital to investigate signal preference with accuracy. We use robotics to effectively manipulate male signals and explore female preferences for the highly conspicuous wave element, wave amplitude (i.e. the extent of claw reach at display apex calculated as a proportion between height above eye level and the total vertical movement of the claw during a wave; see the diagram in Table 1). Thus, we investigate the average and range of wave amplitudes in this species to specifically ask the questions: (1) is wave amplitude a cue for species recognition? A preference for the average value could indicate stabilizing selection for wave characteristics; (2) are females attracted to higher amplitude waves in general? Higher amplitude waves might help females to locate males more clearly or assess their size and potential.

119 **Methods**

120

121 We studied a population of the fiddler crab *Austruca mjoebergi* from August to
122 November in 2013 and 2017 at East Point Reserve, Darwin, Australia (12°24'31.89"S
123 130°49'49.12"E). Both males and females defend territories around their burrow within
124 a large, mixed-sex population. When ready to mate, a female will leave her territory and
125 move through the population of waving males. Males form small clusters (about 2-6
126 individuals) around the female, and as she moves, males join in or drop out of the
127 cluster. The female visits one of the males in the cluster by walking towards him and
128 briefly entering his burrow. She then either leaves the male to continue searching, or she
129 accepts the male and remains underground in his burrow. The chosen male enters the
130 burrow and plugs its entrance with sand, where mating occurs.

131

132 ***Wave amplitudes***

133 We calculated the average and range of *A. mjoebergi* wave amplitudes: the proportion
134 of claw elevation above eye level by the total vertical claw movement (see diagram in
135 Table 1). We recorded 56 waving males under natural conditions from a horizontal
136 perspective. We then watched the videos to measure their wave displays following the
137 methodology by Perez and collaborators (2016). The average wave amplitude was 0.26
138 ± 0.12 , similar to the one previously reported, 0.29 ± 0.08 (How et al. 2009). This value
139 overlaps with the wave amplitudes of the two highly sympatric species, *Tubuca elegans*
140 (0.16 ± 0.10) and *T. signata* (0.22 ± 0.05 ; Booksmythe et al. 2008; How et al. 2009).

141

142 ***Preference experiment***

143 Female preference was tested using custom-built robotic crabs that consist of a twin-
144 cam motor, which moves a small metal arm with a plaster mould of *A. mjoebergi* claw

attached in a motion that exactly mimics the courtship wave of the species. The motor was remotely controlled to regulate the exact timing of each wave using custom designed software (see Reaney et al. 2008; Holman et al. 2014 for further details of the robotic crabs). The motor was buried under a testing arena with only the metal arm protruded through the arena floor. For all treatments, we used moulds of the same claw, each measuring 2.03 cm, considered an attractive size (Clark and Backwell, 2016), and painted a yellow that matched the natural claw color of this species (see Detto et al. 2006 for claw paint). The choice arena mimics the natural conditions explained above and is composed of a raised platform covered with a 0.5cm thick layer of mangrove sediment. The platform was placed in a clearing in the mangroves with a homogenous background of mangrove trees, maintaining the visual scenario of their natural environment (Figure 1b). Females are known to respond well to this experimental setting, which has been used several times in the past to reveal female mate preferences (Perez and Backwell, 2017). We controlled for any confounding variables in our experimental design, by being careful to randomize the position that the stimuli were presented in relation to each other and the surrounding environment.

The study targeted mate-searching females, which were captured, measured (carapace width in cm) and housed individually in shaded cups containing 0.4 cm deep seawater until used in a choice trial. For each trial, the female was placed at the release point on one end of the test arena, in a small translucent cup that was lifted remotely once the female had seen three waves of the robotic crabs (Figure 1b) (see Reaney et al. 2008 for more details). A choice was considered to be made when the female approach within 5 cm of a robotic crab arm. The time until choice was recorded from releasing until approach to a robotic crab arm. Trials were discarded if the female darted, ran to the edge of the arena, or remained stationary for >3 minutes. Each female (total 254) was

tested only once and released after the experiment so they could continue mate-searching. To avoid recaptures, females were collected from non-release areas.

The wave rate of all stimuli was constant at 16.8 waves/minute, and a female was placed equidistant from two robotic crab units (each 20 cm away). The absolute height of the wave can change according to receiver's distance (How et al. 2008), but intense courtship only occurs when the resident can recognize the sex of the approaching crab (from approximately 30 cm; How et al. 2008). Thus, the placement of the female relative to the robotic males was critical. In addition, most choices are made from the releasing point. Thus, although the contrast between claw waving and background changes with female approach, the movement amplitude in relation to body is constant. In all treatments, females were given a choice between two stimuli presented on robotic crab units 15 cm apart. We used robots with distinct wave amplitudes to reproduce the average as well as lower and higher waves that fall within one standard deviation from the average. Height from the ground at claw starting position (i.e. horizontal from the ground) was fixed, and angles of claw movement and wave shape were constant. The data is not vulnerable to noise, as when presented to identical robotic crabs, the choice is extremely close to 1:1 (choice between a pair of synchronous waving robotic crabs and average wave amplitude; two-tailed binomial test: 55:68, $P = 0.28$; Backwell unpublished data).

We first investigated whether females use wave amplitude as a cue for species recognition (i.e. as a pre-mating barrier). We determine whether there is a preference for the average wave amplitude (0.26) against lower wave amplitude (0.16; Treatment 1, $n = 30$) and higher wave amplitude (0.36; Treatment 2, $n = 35$) (Table 1). Following, we investigated if preferences were absolute, and therefore whether sexual selection favors

higher (most conspicuous) wave amplitudes in general. To answer this part of our study, we ran a series of experiments where the lowest wave amplitude (0.16) was paired against increasing amplitudes ranging from 0.20 to 0.36 (Treatments 3 to 10). This gave a series of wave amplitude differences (0.04, n = 30; 0.06, n = 27; 0.08, n = 30; 0.10, n = 30; 0.12, n = 21; 0.14, n = 23; 0.16, n = 29; 0.20, n = 30) between the choices presented in each treatment (Table 1). Finally, we investigate if time until choice indicates how certain females are of their preferences. Data collection was randomized between treatments across mating cycles; most of the data (89% of the choices) were collected in 2017. Given the experimental procedure, it was not possible to record data blind.

Table 1. Frequency distribution of wave amplitudes from a sample of *Austruca mjoeborgi* males. Wave amplitude is calculated as the proportion of wave height at the maximum claw elevation relative to eye-level (α) divided by the total claw elevation (β). Wave amplitudes used in each of the two-choice treatments are presented along with the difference between the choices and the number of trials in each treatment, N. Note that Treatments 1 and 6 are comprised of the same dataset used in the two stages

of the investigation, preferences for average wave amplitude (Treatment 1 to 2), and higher amplitudes (Treatments 3 to 10)

Statistical Analyses

To investigate female selection on wave displays, we performed Generalized Linear Models (GLM) and one Linear Model (LM). First, to test female preference for average amplitude against lower and higher waves (Treatments 1 and 2), we ran a GLM with choice (either average or other wave amplitude) as the response variable and treatment as the explanatory variable with a binomial error distribution and logit link function. In the second part of the experiment, we investigated if preference favours higher amplitude displays. We ran a GLM with the response variable as choice for high or low wave option and increasing wave amplitude differences across the treatments as fixed factor with a binomial error distribution and logit link function. Following this, we ran the null GLM where amplitude difference was removed to answer if females selected for higher displays in general. Lastly, we tested if the time until choice differed according to choices for higher or lower wave options and amplitude differences. We transformed the time of response ($\log_{10}$) and regressed it against choice for high or low wave option and amplitude differences (with an interaction between them). We set the reference level as the lowest amplitude difference (0.04; Treatment 3). We considered amplitude differences as a continuous variable due to the increasing contrast between options presented across the treatments 3 to 10 (from 0.04 to 0.2). We conducted all statistical analyses on R-3.3.3 (R Core Development Team 2017).

Ethical Note

This research was approved by the Australian National University Animal Ethics Committee (permit A2015/54). We limited the handling and the amount of time each

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

Results

In the first part of the experiment, we investigated whether females selectively approached the ‘average’ signal height. We found that females were not more likely to approach the species-specific average wave height over higher or lower waves (Figure 2). Of the 65 trials in total, 34 (52%) chose the average wave amplitude (17 choices in Treatment 1; 17 choices in Treatment 2) and 31 (48%) chose the alternative option (13 choices for the lower wave in Treatment 1; 18 choices for the higher wave in Treatment 2) (GLM: Estimate = -0.211, Std. Error = 0.500, $P = 0.673$).

Fig. 2 Female *Austruca mjoebergi* responses to high and low wave amplitudes labelled by colour. The selected options are proportional to sample sizes across each of the 10 treatments indicated by the horizontal axis according to the amplitude differences between the options indicated between brackets. Binomial tests were performed for each treatment individually and significance indicated, thus: $*=P<0.05$

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

study. We encourage prospective research to reveal the magnitude of other selecting factors that shape display diversity (Cornwallis and Uller 2010). For example, the extent to which a signal is perceived in relation to the environment is an essential part in the evolution of signal structure and variability (Hemmi et al. 2006; Klomp et al. 2016; Ramos and Peters 2017).

The effectiveness of communication between the receiver and the signaller plays an essential role in courtship signal evolution (Kirkpatrick 1987; Endler 1992). The receiver's sensory system is a fundamental evolutionary force upon courtship signals (Ryan 1993, 1998) and, therefore, sexual selection favours those signals that can be perceived by the receiver's pre-existing perceptual bias (West-Eberhard 1979). The preference for wave height is compatible with accurate perception of vertical movements (Zeil et al. 1986; Christy and Salmon 1991; Land and Layne 1995; Zeil and Al-Mutairi 1996; Murai and Backwell 2006). In their flat visual world, fiddler crabs have two visual zones, above and below the line of the horizon (Zeil et al. 1986). In the former, the crabs are sensitive to predator detection (enlarged size or coming from the sky), and in the latter the crabs are accustomed to movements of congeners (Land and Layne 1995). Wave displays break the visual horizon line, which initially alerts the receiver to potential danger, but later can be perceived as a congener's signal (Zeil and Al-Mutairi 1996). Thus, males use vertical movements as sensory traps to stimulate the visual perception of the receiver (Zeil et al. 1986; Oliveira and Custódio 1998; Burford 2000).

The line of visual horizon can act as a threshold, limiting the perception of sexual signals. Consequently, the female's ability to discriminate stimuli may vary, as a signal may be distinctly perceived according to the relative sizes of the sender and receiver,

which could favour the intraspecific diversity we found and the non-significant results in most of our treatments (Hingle et al 2001; Ronald et al. 2012). When species biology alludes to phenotype-dependent preferences, it is important to account for mate choice variation to better understand signal diversity (Jennions and Petrie 1997). In stalk-eyed flies, choices are size-dependant as larger females distinguish eyespan differences more accurately and prefer larger males, although females prefer males with large eyespan in general (Hingle et al. 2001). This mechanism may have the power to alter the intensity and direction of sexual selection on courtship (Jennions and Petrie 1997; Widemo and Sæther 1999). This is an important aspect that previous studies on fiddler crab female preference have overlooked (Oliveira and Custódio 1998; deRivera 2005; Murai and Backwell 2006).

Finally, recent findings revealed that fiddler crab male morphology is linked to claw waving displays (Bywater et al. 2018). Thus, the balance between body parts during display is an essential constraint to wave pattern and reach (Bywater et al. 2018) and, thus, sexual selection not only acts on the behaviour, but on the morphology that is correlated with it. Colour association and background contrast could also influence the patterns and conspicuousness of the signal to the receiver (Detto et al. 2006; McLean et al. 2014; How et al. 2015). Comparing species signals and the receiver perception against the myriad of visual backgrounds should reveal a whole new perspective of how these signals evolved to their present complexity and is another essential and a rich research avenue (Bian et al. 2018).

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