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Female choice over short and long distances: neighbour effects

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Abstract Fiddler crabs live at high densities and mate-searching females encounter many males at varying distances. Who is the ideal neighbour for a male? There could be a trade-off if having neighbours that invest more in sexual signals increases the rate at which females initially move towards a focal male, but thereafter decrease the likelihood that he is chosen rather than his neighbour. We used robotic crabs to test whether female choice for focal males (identical claw size/courtship wave rate) varied depending on the relative investment in sexual signals of their two neighbours and the distance at which she first saw the males. The neighbours' phenotype did not affect which of two focal males she initially approached from long-range (50 cm). When a female initially saw a trio of males at a close-range (20 cm), she preferentially chose the focal male over neighbours that invested less in sexual signals (smaller claw/slower wave rate), but did not show a preference for the focal male over neighbours that invested more in sexual signals (larger claw/faster wave rate). However, a female that started to approach a focal male with neighbours that invest more in sexual signals from 50 cm was significantly less likely to choose the focal male than when she first saw the trio at 20 cm. Our results suggest that the initial distance at which males are seen partly determines how neighbours' sexual signals affect male mating success. In general, if larger males can retain smaller neighbours they might therefore increase their mating success.

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Introduction

Does it matter, in communally displaying species, who a male displays next to? In these species, a male's mating success depends on the likelihood that a female initially moves towards him (i.e. long-range attraction), and thereafter whether she chooses him over a neighbour. At close-range, females should choose the male who invests more in sexual signals (for example in display rate or through strategic allocation of display effort; see Patricelli and Krakauer 2009) from within a set of males. All else being equal, males should therefore benefit from having neighbours who invest less in sexual signals. Simultaneously however, having neighbours that invest more in sexual signals might increase the likelihood that a female will initially approach a displaying group of males from a distance if she responds to the total stimulation provided by a set of males. These choices are not limited to communally displaying species and are analogous to situations where males decide the distance at which to call from other males (e.g. spatial separation of calling males in field crickets; Mhatre and Balakrishnan 2006 and anurans; Schwartz and Gerhardt 1989; Bee 2008; Richardson and Lengagne 2010). How do these two processes interact? Additionally, does female mate choice among the same set of males differ depending on the distance from which she starts her approach towards them?

A female's final mate choice decision is likely to depend on the initial choice of which set of males to approach. In visual communication systems, mate choice processes that require females to assess males from a distance will involve

more males. The greater complexity of this choice situation can decrease the ability of females to identify the most highly ornamented or vigorously displaying male and lead to mate choice errors (Hutchinson 2005) (by error we mean an incorrect ranking of males compared to what females would generate if they had perfect information about each male for the traits that are the target of female choice). In general, females choosing among males at close-range only evaluate each male relative to his immediate competitors and not the wider population (comparative evaluation sensu Bateson and Healy 2005). The smaller number of males being viewed increases the likelihood that the female chooses the male who she ranks as the most attractive (i.e. reduces error). Even at close-range there is, however, still the potential for female error. In general, the ability to detect a fixed difference between two stimuli is proportional to the absolute magnitude of the stimuli ('Weber's law' see Shettleworth 1998). From a focal male's perspective, the relative cost of having neighbours that invest more in sexual signalling should therefore depend on his absolute level of sexual signalling (Cohen 1984; Jennions and Petrie 1997).

In practice, females first encounter sets of males from varying distances, and it is possible that this affects mate choice. For example, in acoustic systems, the approach distance affects female choice under both natural and experimental conditions in barking treefrogs (*Hyla gratiosa*; Murphy and Gerhardt 2002). Similarly, in highly visual systems such as those of fiddler crabs (*Uca mjoebergi*) females have been shown to have stronger mating preferences when they are required to travel a short rather than a long distance to reach prospective mates (Booksmythe et al. 2008). Alternatively, a greater initial distance could provide more time for a female to evaluate each male and increase her ability to identify the most attractive male (Chittka et al. 2009). Selection could also favour a sensory mechanism whereby females 'lock in' on a single male so as not to be distracted by the many males visible when approaching from a distance (i.e. akin to the 'cocktail party effect'; for such a mechanism in acoustic communication systems see Pollack 1988; Römer and Krusch 2000). Given that it might be more difficult to rank the visual traits of males from a distance (e.g. the apparent size difference between a large and small male is reduced when they are viewed from a greater distance due to Weber's law), 'locking in' could reduce any larger male advantage.

Determining what factors affect female choice from sets of males at close and long-range is difficult using observational data. First, the spatial distribution of males is rarely random so that some choice situations are more difficult to document. Second, the identity of neighbours can change a male's investment in courtship. Aside from

lekking species (e.g. Durães et al. 2009) where it is possible to take advantage of the division of choice into long-range choice among leks and short-range choice between males on a lek, very few studies have examined how female mate choice criteria change with distance from males in other types of mating systems (but see Sun et al. 2000; Kostarakos et al. 2008; Murphy 2008; Leonard and Hedrick 2010). To date, no study has examined this effect using an experimental approach in a species where males use visual sexual signals to court females. This is important because the perceptual constraints placed on signallers and receivers vary among different sensory systems. For example, the masking of calls by other individuals (e.g. Gerhardt and Klump 1988; Wollerman 1999) is a key problem to signal detection in acoustic systems, but it is not a constraint in visual communication systems.

We used custom-built robotic crab claws (henceforth 'robotic crabs') to experimentally manipulate the identity of a male's neighbours in *U. mjoebergi*. We tested whether: (1) over a long-range (50 cm), the relative investment in sexual signals by two neighbours will affect the likelihood that a female (a) moves towards a focal male of standardised phenotype and (b) then chooses him rather than either of his neighbours; (2) whether the mating success of a focal male differs when a female initially sees him and his two neighbours at close-range (20 cm) compared to when she began her approach from 50 cm. Finally, we document natural mate choice and the identity of a male's immediate competitors in the field.

Materials and methods

Study species

The fiddler crab *U. mjoebergi* inhabits dense, mixed-sex colonies. Both sexes hold territories centred on a burrow. Before mating, a female will leave her territory and wander through the population in search of a mate. Males court mate-searching females by waving their major claw. Females visit a courting male by approaching him and briefly entering his burrow. The likelihood that a male will mate depends on three factors. First, whether a female is attracted towards the area of the mudflat where he lives. This could depend on abiotic factors (e.g. soil type, amount of shade and surface water) and/or social composition (e.g. mean size of males in the area and their density) that might influence long-range attraction of females. Second, once a female is close enough to males to be able to discriminate between them (20 cm), she chooses which males to visit based on claw size, wave rate and display synchrony. Previous studies have shown that females prefer to approach males with larger claws (Reaney 2009; Milner et

al. 2010) and males who wave at a faster rate (Reaney et al. 2008; Reaney 2009). Males make a substantial investment into their sexual signals. For example, the claw-waving displays of male fiddler crabs (genus, *Uca*) are known to be condition-dependent (Jennions and Backwell 1998) and as larger, and therefore, heavier claws, are harder to display, only higher quality males can cope with the greater energetic costs of sustaining an elevated wave rate (Murai et al. 2009).

Third, the decision to stay in the burrow and mate is based on its suitability as an incubation site for her eggs (Reaney and Backwell 2007). Burrow mating occurs over a 5–6 day period in each semi-lunar cycle so that females can release their larvae at a time in the tidal cycle that maximises offspring survival (Morgan and Christy 1995; Morgan and Christy 1997; Christy 2003). Females remain in the male's burrow until the next nocturnal spring tide when they then release their larvae (Morgan and Christy 1997; Christy 2003).

A male's burrow is therefore a vital resource, which is vigorously defended against intruders and encroaching neighbours. Intriguingly, however, larger males appear to retain smaller neighbours by helping them to defend their burrow from intermediate sized intruders (Backwell and Jennions 2004). Males that engage in these defensive coalitions decrease the costs associated with renegotiating territorial boundaries with a new, potentially stronger, neighbour (Backwell and Jennions 2004; Detto et al. 2010). It is not yet known if males only compete against their immediate territorial neighbours during mate choice or whether some males also temporarily vacate their own territories and move onto those of adjoining males to get closer enough to court a mate-searching female.
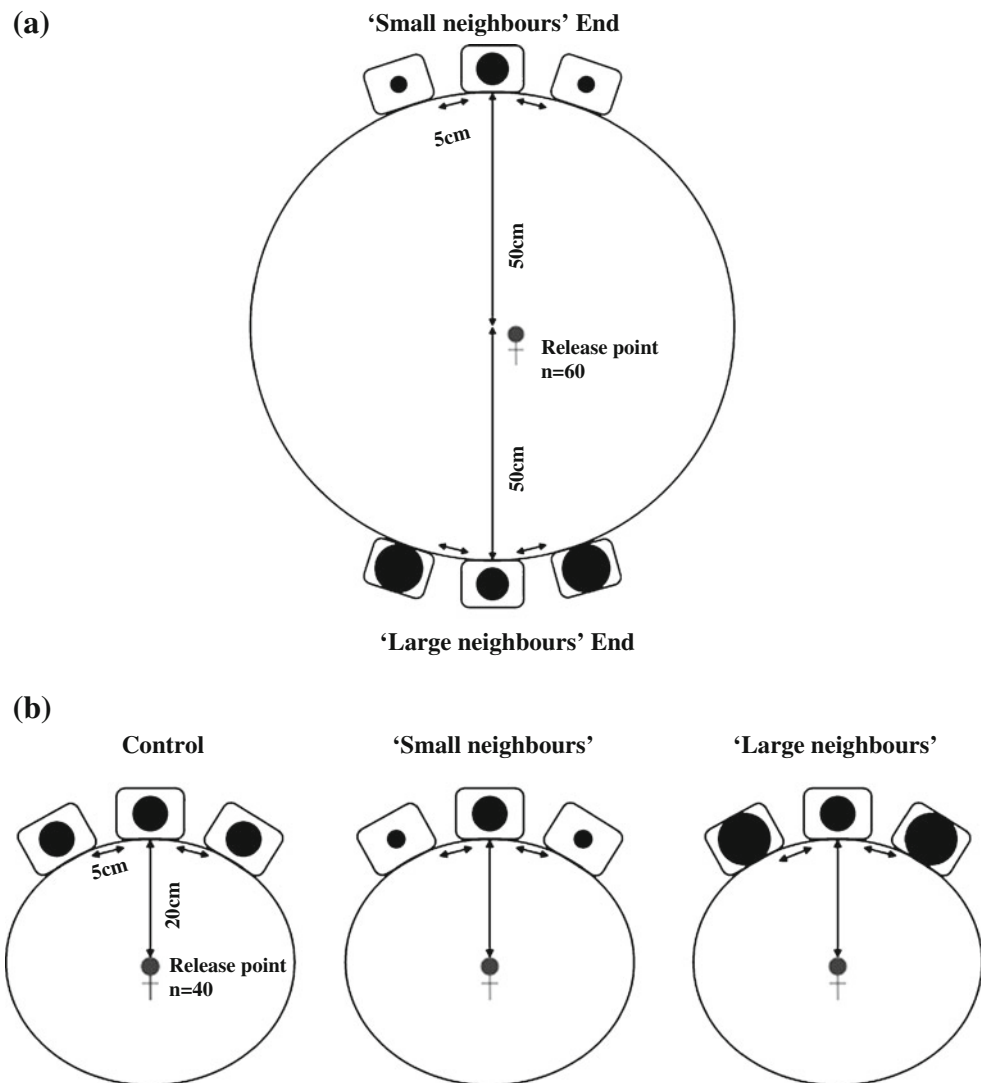
Experimental design

We used robotic crabs to test female mating preferences. Each robot is a motorized unit embedded in the sediment with a metal rod protruding above the surface. The rod is fitted with a painted claw replica made from the mould of an autotomized claw. The motor makes the claw move in a pattern that mimics courtship waving (see Reaney et al. 2008 for a video recording of the robotic crabs). We conducted mate choice experiments on an area of mudflat that was cleared of resident crabs ('test arena'). We captured mate-searching females that we had previously seen visit at least one male. Each female was individually placed in a transparent release container and allowed to observe two complete waving cycles (duration 14.4 s) by the robots (hereafter 'males') before being released. We scored a positive choice if she directly approached to within 2 cm of a male. A trial was terminated if the female did not choose after 3 min.

Fieldwork was conducted in Darwin, Australia, from October–December 2009, during the 5–6 day mating period of each semi-lunar tidal cycle. We ran four robotic crab experiments (one long-range treatment and three short-range treatments) to test whether female choice of focal males changed depending on the distance from which she first saw him, the identity of his neighbours and the interaction between approach distance and neighbour identity.

Long-range choice experiment

Females ($n=60$) were given a choice between two focal males on opposite sides of the test arena on an arc 50 cm from the female release point (Fig. 1a). This distance is within the range at which females will approach a group of males in a direct path in the field (personal observation S.C.). Previous work has shown that female *U. mjoebergi* can discriminate between two courting males from up to 40–50 cm away (Booksmythe et al. 2008). Each focal male was flanked by two neighbours 5 cm on either side of him. The central 'focal' male always had an 18-mm long claw and waved at 8.4 waves/min. One focal male was flanked by two neighbours with 14-mm claws and lower wave rates (4.2 waves/min) (hereafter, for brevity, 'small neighbours'). The other focal male was flanked by two neighbours with 22-mm claw and a higher wave rate (16.8 waves/min) (hereafter for brevity 'large neighbours'). All claw sizes were designed to cover the natural distribution of sexually mature males in the study population. The focal male's wave rate (8.4 waves/min) was chosen as it is close to the population average (Milner et al. 2010) and has been successfully used in previous work with robotic crabs in this species (Booksmythe et al. 2008; Milner et al. 2010). The slower and faster wave rates of the 'small' and 'large' neighbouring males respectively, were selected to ensure synchronous waving. This is necessary to remove any wave leadership effect on female choice (Reaney et al. 2008). Both claw size and wave rate were varied to increase the difference in male attractiveness as both traits are known to affect female choice. Waving is highly synchronous in *U. mjoebergi* but this does not require that all males in a group wave at an identical rate. This is possible because males sometimes 'miss' a wave in a bout of group synchrony. Consequently, on average, males must wave at a rate that is an integer multiple of the mean wave rate to maintain the observed pattern of synchronous waving. The wave rate range we used is therefore biologically realistic. For example, in the 'large neighbour' trials, the two neighbouring males waved twice as fast as the central focal male. This meant the focal male missed a wave and all three males waved in perfect synchrony on every second wave.

Fig. 1 a Long-range experiment. b short-range experiment; *small black circles*=14-mm claw; 4.2 waves/min male; *medium black circles*=18-mm claw; 8.4 waves/min male; *large black circles*=22-mm claw; 16.8 waves/min male

(a)

'Small neighbours' End

5cm

50cm

♀ Release point
n=60

50cm

'Large neighbours' End

(b)

Control   'Small neighbours'   'Large neighbours'

5cm

20cm

♀ Release point
n=40

Short-range choice experiment

In each of three treatments, females chose among three males (n=40 females/treatment). The males were on one side of the arena 5 cm from each other on an arc 20 cm from the female release point (Fig. 1b). A distance of 20 cm has been used in several previous experiments utilising robotic crabs (e.g. Booksmythe et al. 2008; Reaney 2009; Milner et al. 2010) and is consistent with a distance in the field at which females have the potential to evaluate three or four males that are more or less the same distance from her (personal observation S.C.). In each treatment, the central 'focal' male was identical to those used in the long-range experiment (i.e. 18-mm claw/8.4 waves/min). In the 'control' treatment, the two neighbours were identical to the focal male. In the 'small neighbour' treatment, the focal male had two 'small neighbours'. In the 'large neighbour' treatment, the focal male had two 'large neighbours'. The claw size and wave rate of all three classes of males (focal,

'small neighbours' and 'large neighbours') were identical in the long- and short-range experiments. Females were tested in one to three treatments (but only once per treatment). The interval between trials was a minimum of 5 min. We controlled for any order effects by randomising the order of presentation.

Natural female mating behaviour

To identify a courting male's immediate competitors in the field, we tracked 50 mate-searching females until they visited a male. A visit is a prerequisite to final mate choice, and a higher visitation rate increases a male's likelihood of mating (Backwell and Passmore 1996). Observations were made over ~1,000 m² of mudflat. After each recorded visit, we relocated to avoid following the same female twice. We noted: (1) how many waving males surrounded the female; (2) whether males were residents or had left their own territory to court her; (3) whether the visited male courted

from inside his territory or moved off it to court (i.e. the female would have to bypass other males to reach his burrow).

Statistical analysis

In the long-range choice experiment, we used a binomial test ($q=0.5$) to test whether females preferentially approached the 'large neighbour' set of males. We then separately tested whether the focal male was preferentially chosen within each trio of males using a 2x2 Chi-square test against the observed frequencies from the short-range control treatment (i.e. using the latter accounts for any centre/side bias).

To test for a potential order effect on the preferences of females that were used in all three short-range treatments ($n=26$ females), we first ran a general linear model including the interaction between treatment and order and the main effects of order and treatment, with the response variable being whether or not the focal male was chosen. We also tested for a significant side/centre bias in control treatment trials using a goodness of fit test (1:1:1). As there was no effect of either (see Results), we then tested whether there was a difference among the three short-range treatments in how often the focal male versus either of his neighbours was chosen using a 3 (treatments)×2 (focal/neighbour) Chi-square test. There was a significant difference (see Results), so we conducted two additional 2x2 Chi-square tests to test whether the proportion of females choosing the focal male differed between the control and small neighbour and control and larger neighbour treatments. This is almost equivalent to a binomial test where $q=0.33$ (i.e. 1:2 ratio of focal-to-neighbour) but is statistically conservative because we used the observed control treatment frequencies (X:Y ratio) rather than assuming the absence of bias towards central males.

Finally, we ran two 2x2 Chi-square tests to test whether the likelihood that the focal male was chosen differed between the short-range choice and long-range choice experiments in cases where a female approached a large neighbour set of males and a small neighbour set of males, respectively. All 2x2 Chi-square tests were run using Yates correction. Tests were conducted using SPSS 19.0 with $\alpha_{2\text{-tailed}}=0.05$.

Results

Long-range choice experiment

There was no significant difference in the proportion of females that approached the 'large' or 'small' neighbour set of males from 50 cm (binomial, $p=0.90$; $n=60$).

Females significantly preferred the focal male once they approached a small neighbour set of males ($\chi_1^2=4.74$, $p=0.03$) but showed no preference for the focal male when they approached a large neighbour set of males ($\chi_1^2=2.24$, $p=0.13$; Fig. 2a).

Short-range choice experiment

There was no interaction between treatment and presentation order ($\chi_4^2=3.75$, $p=0.44$) and no effect of order itself ($\chi_2^2=1.06$, $p=0.59$) on the subset of 26 females that were reused in all three short-range treatments. The likelihood of the central, focal male being chosen varied depending on
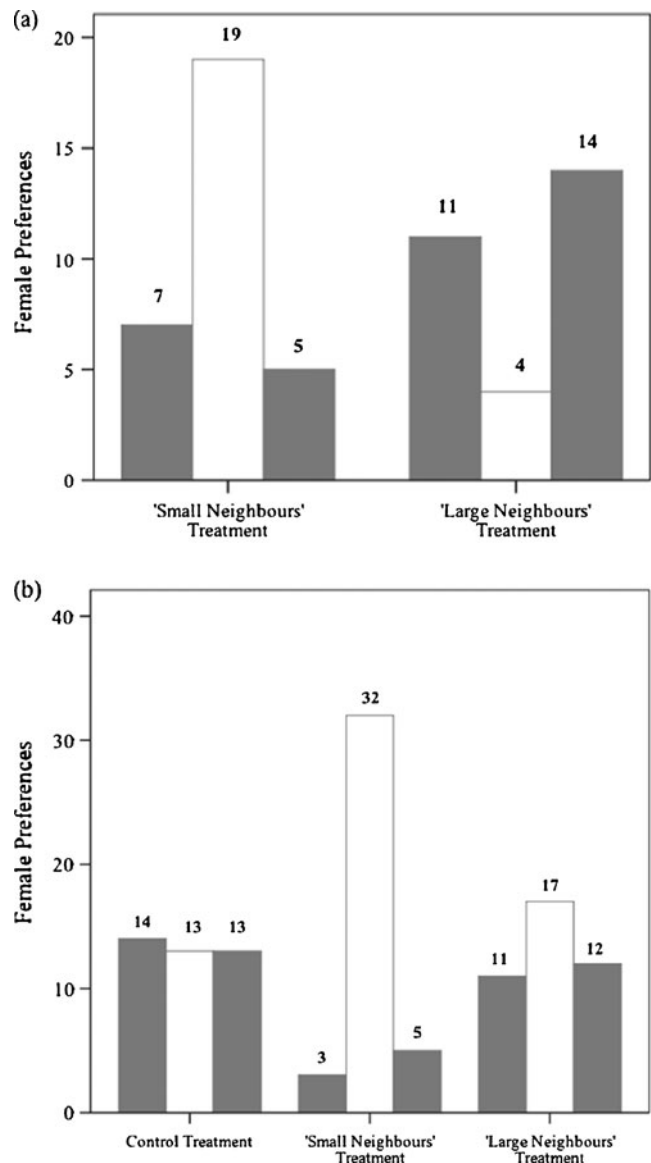

Fig. 2 Number of females which chose the focal male (*white bars*) and neighbouring rival males (*grey bars*) across each of the treatments in the (**a**) long- and (**b**) short-range trials

the identity of his neighbours ($\chi_2^2=20.09$, $p<0.001$; Fig. 2b). In the control treatment, there was no significant preference for males in any of the three positions ($\chi_2^2=0.05$, $p=0.98$, $n=40$) (i.e. no detectable side/centre bias). In the 'small neighbour' treatment, females significantly preferred the focal male who had a larger claw and faster wave rate than his neighbours ($\chi_1^2=16.46$, $p<0.001$). In the 'large neighbour' treatment, however, there was no discrimination against the focal male even though he had a smaller claw and lower wave rate than his neighbours ($\chi_1^2=0.48$, $p=0.49$).

Short-range versus long-range choice

There was no difference in the strength of preference for the focal male between the short- and long-range experiments when the female was approaching a 'small neighbour' set of males ($\chi_1^2=2.17$, $p=0.14$). In both cases, females strongly preferred the focal male. The preference for neighbours was, however, significantly stronger in the long- than short-range trials after approaching a 'large neighbour' set of males ($\chi_1^2=5.53$, $p=0.02$).

Natural choice

We observed 184 males court 50 mate-searching females. Of these, 159 males (86.4%) courted from their own territory, while 25 temporarily left their territory. Consequently, courting males primarily competed against immediate neighbours. When both immediate neighbours ($n=59$) and more distant males ($n=25$) courted, the males that left their territory were more likely to be chosen by females but not significantly so (40% versus 20.3%; $\chi_1^2=3.51$, $p=0.06$). This suggests that attractive males more often leave their territory to court females or that when males leave their territory they court more vigorously (i.e. increase their display effort).

Discussion

The identity of the focal male's neighbours did not affect the likelihood that a female approached his group from a distance. Almost equal numbers of females approached a focal male with 'small' versus 'large' neighbours. Therefore, despite the greater stimulation of having faster waving/larger males in a group, females at 50 cm from two sets of males did not seem to use information about the males' sexual signals to decide which set of males to approach. This suggests that there is no long-range benefit to a courting male from having 'larger' neighbours. It remains to be determined whether differences in claw size and wave rate vary in their effect on signal perception over

longer distances (e.g. differences in wave rate might be more conspicuous than those in claw size from a greater distance). In our study however, claw size and wave rate positively covaried so there is no evidence to indicate that wave rate affected the ability to distinguish between the two sets of males. Any preference for males with a higher wave rate would only be enhanced because these males also had larger claws. So what are the potential costs of larger, faster waving neighbours, and do they vary depending on the distance from which females approach males? The answer is important in determining whether mate choice based on close-range choice can be extrapolated to what happens when females choose from a greater distance. Depending on the average distance at which females first see males in the field this will also influence the strength of selection on males to act in ways that increase the likelihood that their neighbours have phenotypes that increase the focal male's mating success (see Leonard and Hedrick 2009).

At close-range, females clearly used information about male sexual signals to decide who to approach. They significantly preferred males with a higher wave rate and larger claw, although this preference weakened with the absolute magnitude of the competing males' sexual signals. Similarly, once a female started to move towards a set of males in the long-range trial, she preferentially chose the focal male if he had 'small neighbours' but did not show a preference if he had 'large neighbours'. These results suggest that the female choice decision in *U. mjoebergi* is made at a distance between 20 to 50 cm from the males. This is consistent with previous work in this species showing that females showed preferences for wave leadership when first viewing a pair of males at 40 cm, but not when viewing them at 50 cm (Booksmythe et al. 2008).

When we compared the strength of female preferences for the focal male over short and long distances, there was no difference when the focal male had 'smaller neighbours', but the preference was significantly weaker in long-range trials when the focal male had 'larger neighbours'. It should be noted, however, that in neither case (i.e. in neither the long- or short-range trials for the 'large neighbour' treatment) was the preference for the focal male significantly different from the null expectation. Even so, the initial distance at which females make their mate choice decision is clearly important from a male perspective because a focal male's chances of mating are more adversely affected if the female first saw the males from more than 20 cm away. These results are biologically meaningful in *U. mjoebergi* as females can sometimes first encounter displaying males from short distances. Although the mudflat is generally flat given the small size of these crabs, there are numerous visual barriers to seeing males in the 20–50 cm distance range (bearing in mind that females do not seem to discriminate between males seen from >50 cm).

For example, females might first see a set of males when they climb out of a shallow depression (e.g. pits dug by larger crabs and shrimp or rainwater puddles) or from behind a tree root. The increased cost of having larger, faster waving neighbours when females have continual visual access to the set of males as they approach from 50 cm onward might be partly attributable to the increased time it takes a female to approach a group from a greater distance. This might allow a female to more accurately rank males based on their claw size and wave rate.

The fact that there was no change in the strength of the female preference for the focal male with distance when approaching a 'smaller neighbour' set of males could be due to females being better at discriminating the relative magnitude of sexual signals when the absolute expression of these traits is lower. For example, it is probably more difficult for a female to rank males with 18- and 22-mm long claws than those with 14- and 18-mm long claws (i.e. Weber's law). If it is easier for females to rank males with smaller neighbours, then the observed effect of long-range choice is likely to be weaker. Alternatively, the marginal benefits of mating with larger/faster waving males might decline with the absolute level of sexual signalling so that female preferences are an asymptotic function of male size/wave rate.

Our data suggest that males can increase their mating success by choosing their neighbours. In practice, however, is there any way in which males can influence who they have as neighbours? One answer is through the formation of defensive coalitions. In some fiddler crabs, males help smaller neighbours to retain their territories by assisting them in repelling intruders (Backwell and Jennions 2004; Detto et al. 2010). In our field study, we noted that males mainly compete with their immediate neighbours during courtship. Together with our finding that males experience a cost when they have larger, faster waving neighbours (and there is no compensatory increase due to a higher mean rate of long-distance attraction of females to sets of larger males), our results suggest that larger males might protect smaller neighbours and thereby benefit during mate choice. Similarly, recent findings show that less attractive male house finches, *Carpodacus mexicanus*, can improve their pairing success by shifting into new social groupings (Oh and Badyaev 2010).

In sum, males should ideally retain smaller neighbours. This does not appear to reduce their mating success by decreasing the long-range attraction of females towards a male, and it increases the male's likelihood of mating when females are choosing among a few males from a short distance away. The effect of neighbour identity is likely to be far more important for smaller and/or slower waving males as they are more strongly discriminated against by females due to the non-linear, asymptotic relationship between male size and attractiveness. Ironically, however, small males are least able to manipulate the composition of their neighbourhood; only larger males can engage in defensive coalitions that increase the likelihood of retaining smaller neighbours.

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