

Non-independent mate choice in a fiddler crab: a case of stimulus enhancement

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Abstract Non-independent mate selection occurs when the choice behavior of a female is altered by the interactions between other females and males. In the fiddler crab *Uca mjoebergi*, males court mate-searching females by waving their one greatly enlarged claw. When a female approaches a male, he initiates high-intensity waving. We conducted one natural mate choice experiment and two mate choice experiments using custom-built robotic crabs. We show that the decision of one female to approach a group of males increases the probability that another female will approach and visit a male from the same group. We suggest that this behavior is best explained by the ‘stimulus enhancement’ hypothesis, where the presence of a female near a group of males makes them more likely to be detected by other females due to an increase in male display rate.

Keywords Fiddler crabs · Mate choice copying · Non-independent mate choice · Stimulus enhancement · *Uca mjoebergi*

Introduction

Determining the factors that generate variation in male mating success is fundamental to our understanding of sexual selection (Andersson 1994). Non-independent mate choice, where the choice of one female influences that of another, can potentially increase intrapopulation variation in

male mating success with fewer males gaining a greater proportion of matings. This has important consequences for the strength and direction of sexual selection on male traits (Westneat et al. 2000). Most studies of non-independent mate choice are laboratory based and focus almost exclusively on ‘mate-choice copying’ where the likelihood that a female chooses a male increases after she has observed him being chosen by another female (Dugatkin 1992; Witte and Massmann 2003; Godin et al. 2005; Brown and Fawcett 2005; Mery et al. 2009; Yorzinski and Platt 2010). An early study Dugatkin (1992) showed that female guppies (*Poecilia reticulata*) could remember the identity of males they had previously seen in association with another female and that females found these male more attractive than males they had not been previously seen with a female.

Far fewer studies have looked at another form of non-independent mate choice: stimulus enhancement. Here, the presence of a female near a male or group of males increases male visibility and possibly attractiveness to other females (Westneat et al. 2000). Courtship and copulation often consists of conspicuous displays (Andersson 1994) that attract the attention of other mate-searching females. This increases the likelihood that these females will approach an area and mate with the already courting males, thus resulting in non-independent mate choice (Westneat et al. 2000). Alternatively, females might chose to actively avoid a male or group of males who she has recently seen courting (e.g., to reduce the risk of mating with a sperm-depleted male). To date, no study has specifically tested this hypothesis and the prevalence of this form of non-independent mate choice is unknown.

In the fiddler crab *Uca mjoebergi*, males have one greatly enlarged claw, which they wave at approaching mate-searching females in a conspicuous courtship display

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(Milner et al. 2008, 2010a). During the mating period, receptive females leave their territories and wander through the population, visiting a series of males before eventually selecting a mate (Reaney and Backwell 2007). Males form a cluster around the female and tend to wave in synchrony (Backwell et al. 1998). Female choice is based partly on wave rate, wave leadership, and claw size (Backwell et al. 1999; Reaney and Backwell 2007; Milner et al. 2010b). Once a female selects a male, she enters his burrow, remains inside, and mates with him. Occasionally, however, she mates with him on the surface and then finds another burrow in which to incubate her eggs (unpublished data, Slatyer R.). Regardless of whether mating is in the burrow or on the surface, the conspicuous courtship display could potentially attract the attention of mate-searching females that are not the immediate target of the displaying male/s. This would increase the likelihood that one of the previously courting males or an immediate neighbor obtains a mate.

In this study, we used a natural mate choice experiment to determine whether the presence of a female in a cluster of naturally waving males increased the probability of a second female approaching these males. We then ran a choice experiment using two robotic crabs, one with a female tethered next to it, to determine whether the presence of a female by a male without any effect on male waving might increase the likelihood that he attracts a second mate-searching female. We documented the waving behavior of males that were courting a nearby female and males that were not courting a female. We used this information in the final robotic crab choice experiments. We gave a female the choice between two groups of robotic crabs, neither of whom had a female tethered near it. One group waved in a pattern that mimicked the natural waving of a cluster of males that were courting a nearby female and the other waved in a pattern that mimicked the natural waving behavior of a non-courting male cluster.

Methods

The study was conducted from September to December 2009. *U. mjoebergi* is a small fiddler crab (carapace width <20 mm) that inhabits intertidal mudflats in northern Australia (Reading and Backwell 2007; Fayed et al. 2008). They occur in dense mixed sex colonies (37 ± 17 crabs m^{-2} ; R. Slatyer, L. T. Reaney, and P. R. Y. Backwell, unpublished data) and during the mating period, receptive females leave their territories and wander through the population visiting the burrows of a series of courting males before eventually selecting a mate (Reaney and Backwell 2007). During this period, multiple mate-searching females are commonly seen in close proximity (R. Milner, personal observation).

Documentation of courting and non-courting waving

We videoed 50 groups of naturally occurring males either with or without a female tethered in the center of the cluster ($n=25, 25$). All other females were removed from the area. A 20-s segment of each video was then analyzed and we documented the total number of waves given by each male in the cluster, the number of waves that were given in synchrony with other males from the cluster, and the spatial separation between each male and his nearest neighbor.

Natural mate choice experiment

We selected two identically sized (two to four) groups of males with approximately the same claw lengths (i.e., <5 mm difference between comparative individuals between groups; size matching was performed by eye). The groups were 50–60 cm apart and all other crabs within a 50-cm radius of the two groups were temporarily confined in their burrow after we sealed burrows with a sand plug. A female crab was then tethered with a 2-cm piece of cotton glued to her carapace that was attached to a nail. The nail was embedded in the sediment so that the female was in the middle of one group of males (courting group). The second group of males did not have a female tethered among them (non-courting group). The two groups were <60 cm apart so they were equally disturbed by the presence of the experimenter. After an acclimation period of 2 min for the males, a second female was placed under an opaque plastic container midway between the two groups. Once all males in each group were visible, the container was lifted using a remotely triggered lever. We scored a positive choice if the female moved in a direct line to one of the males in either group and touched or entered the entrance of his burrow. A trial was discarded if the female ran immediately after being released or did not make a choice within 3 min ($N=10$). In total, 20 females made a positive choice.

Female presence effect experiment

We used a custom built robotic crab claw (see Reaney et al. 2008; henceforth ‘robotic crab’) in which each robotic crab produces a claw movement engineered to resemble the wave of a courting male *U. mjoebergi*. The system consisted of a control box and two identical crab units. Each crab unit had a motor housed in a plastic container that controlled the movement of a rigid metal arm. An identical replica claw was attached to each robotic crab arm. All claws were the same size (17 mm). The experiments were run in a cleared area of mudflat within the population. All crabs within 2 m of the choice arena were first removed and released elsewhere on the mudflat.

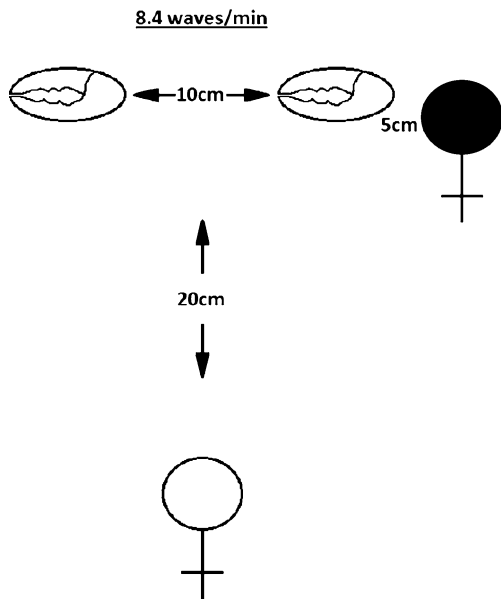


Fig. 1 Diagram showing choice arena for ‘Female presence effect experiment’ (‘model’ female absent vs. model female present). Robotic crab: ; female release point: ♀; tethered ‘model’ female: ♀

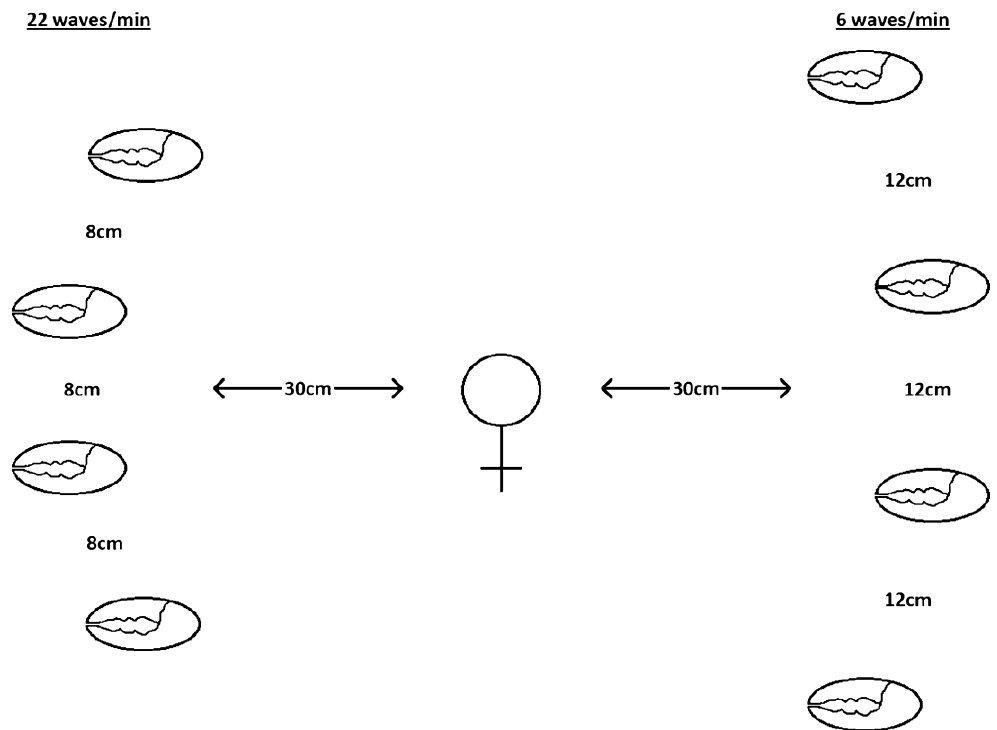
To test whether the presence of a female near a male influences the mate choice decision of another female, we gave 53 focal females a choice between two identical robotic crabs, one of which had a female tethered 5 cm away (to simulate a female visiting a male). The two robotic crabs were placed 10 cm apart and 20 cm from the female release point (Fig. 1). The wave rate was set at 8.4

waves/min, which falls within *U. mjoebergi*’s natural courtship wave rate range and has successfully been used in past studies (see Booksmythe et al. 2008; Milner et al. 2008, 2010b). The females were placed under a clear plastic container at the release site and left for at least three wave cycles. The container was then lifted using a remotely triggered lever. We scored a positive choice if the female moved in a direct line and stopped at the base of a waving robotic unit (for video footage see Reaney et al. 2008). We discarded three trials because the female ran immediately after being released or did not make a choice within 3 min.

Effect of elevated courtship experiment

We used data from the ‘Documentation of courting and non-courting waving’ to create a more natural mate choice experiment in which females were given the choice between a cluster of four robotic crabs that waved in a pattern that either mimicked the natural waving behavior of a courting cluster or a non-courting cluster of males. Neither cluster of robotic crabs had a female tethered near it (for justification, see Results). The four robotic crabs that mimicked courting males waved in synchrony at 22 waves/min and were placed 8 cm apart (Fig. 2). The four robotic crab cluster that mimicked non-courting males waved at 6 waves/min in alternation with each other and were placed 12 cm apart. The two cluster were opposite each other and each was 30 cm from the female release point (to justify values, see results for natural non-courtship waving; Fig. 2).

Fig. 2 Diagram showing choice arena for ‘Effect of elevated courtship experiment’ (courting vs. non-courting). Robotic crab: ; female release point: ♀



In total, we released 33 females and their choice was documented as previously described for the ‘female presence effect experiment’. In total, 30 females made a choice.

In all experiments, we used naturally mate-searching females that had been observed to visit at least one male before being captured and tested. For all mate-choice experiments, any potential side bias was controlled for by alternating the presentation of test stimuli between sides across trials. There was also no detectable side bias (female presence effect experiment: left vs. right, 23: 27; $n=50$, binomial test, $P=0.67$; effect of elevated courtship experiment: left vs. right, 17:13; $n=30$, binomial test, $P=0.59$).

Female preferences were tested with binomial tests (two tailed) with $\alpha=0.05$. To be conservative, two-tailed tests were used because we had no strong prior predictions for female preferences.

Results

Documentation of courting and non-courting waving

The natural waving behavior of courting and non-courting males differed. Courting males waved at a rate of 27.1 ± 6.1 waves/min ($n=52$ courting males/25 clusters) and 89% of the waves given were in synchrony with other males from the cluster. Courting males clustered tightly because they approached the tethered female so that the mean distance between male neighbors reduced to 8.1 ± 3.0 cm ($n=60$ courting males/25 clusters). Non-courting males waved at a much slower rate (3.8 ± 4.4 waves/min, $n=52$ non-courting males/25 clusters) and were far less synchronous (11.5% of waves overlapped those of other males in the group). The non-courting males did not cluster and the mean distance between males was 14.0 ± 6.3 cm ($n=67$ non-courting males/25 clusters).

Natural mate choice experiment

Females that were given a choice between a naturally occurring group of males that were actively waving at a tethered female and a control group of non-courting males, choose the courting males significantly more often (binomial test; $P<0.001$). In 90% of the successful trials ($n=18$ of 20), the focal female moved in a direct line and visited one of the courting males, while in the remaining 10% of the successful trials the female visited a non-courting male.

Female presence effect experiment

Females given a choice between two waving robotic crabs that were identical except that one of them had a female

tethered 5 cm away showed no preference for either male robot. Females choose both robotic crabs equally (25:25; $P=1$, $n=50$).

Effect of elevated courtship experiment

We used the values from the natural waving data to create a choice experiment in which females could choose between two groups of robotic crabs that either mimicked the natural waving behavior of a courting or non-courting group of males. Females were significantly more likely to choose a robotic crab from the group that mimicked courting males (24 of 30; binomial test, $P=0.001$, $n=30$).

Discussion

We have shown that non-independent female mate choice occurs in the field in the fiddler crab *U. mjobergi*. Females preferentially approached a group of males that was actively courting a female over a group that was not courting a female. This result could be due to direct ‘female copying’ in which a female is attracted to a male or group of male because she sees another female near him/them (Godin et al. 2005). Alternatively, it could be due to ‘stimulus enhancement’ in which a female is attracted to a courting male or group of courting males because their displays make them more conspicuous (Westneat et al. 2000). The results of our first mate choice experiment suggest that female copying is unlikely to play a role. The presence of a female near to a robotic crab did not influence her choice of robotic crab. The wave rate used in this experiment was lower than that of males actively courting a female when she is at close range. It is however, still more than twice the rate of non-courting males, and within the range of natural wave rates seen when a female is approaching a group of males. It was clearly a sufficiently high wave rate to attract females to approach the waving robotic crabs (only 3 of 53 females failed to approach a ‘male’). We are therefore confident that our negative result reflects the absence of an effect on female choice of seeing a female near a male, rather than it being an artifact of females perceiving neither male as being sexually active and therefore indifferent to the presence of another female.

The second mate choice experiment suggests that stimulus enhancement can account for the non-independent choices of females. Courting males wave faster, in greater synchrony and in close proximity to each other than non-courting males. Females that were given a choice between two groups of robotic crabs that mimicked the natural waving behavior of either a courting or non-courting group of males were signifi-

cantly more likely to approach a robotic crab from the courting group.

In *U. mjobergi*, the decision of a female to mate with a male is unlikely to directly result in another female mating with the same male. This is because most matings take place within the male's burrow and it can presumably only house a single breeding female (Reading and Backwell 2007). In the rare case where mating on the surface occurs (Slatyer unpublished data) it is unlikely that a female would wait to mate with the courting male suggesting that mate choice copying is an unlikely component of this mating system. Instead, non-independent mate choice is most likely to arise because the elevated rate of waving elicited by one female enhances the likelihood of other males in the group subsequently attracting another female who sees this heightened level of courtship. It should be noted, however, that the effect of 'stimulus enhancement' on female mate choice in *U. mjobergi* is likely to be brief as males begin to slow their wave rate soon after a female either enters a male's burrow to mate or leaves the area (R. Milner, personal observation), presumably because waving is costly (Matsumasa and Murai 2005). Nevertheless, the presence of a female does increase the probability that another female in the near vicinity will approach the same group of courting males (multiple mate-searching females are commonly seen in close proximity; R. Milner, personal observation) and, by extension, increase the mating probability for these males. This will ultimately lead to non-independent female mate choice decisions that could significantly affect the evolution of sexually selected male traits (Gibson and Höglund 1992; Westneat et al. 2000).

Past studies of non-independent mate choice have either ignored or deliberately excluded any influence of stimulus enhancement because they were specifically designed to test for mate choice copying. For example, in a number of studies on guppies, the model female was removed before the focal female was allowed to choose (Dugatkin 1992; Dugatkin and Godin 1992; Briggs et al. 1996; Brooks 1996; LaFleur et al. 1997; Brooks 1999; Vukomanovic and Rodd 2007). This had the effect of eliminating any role for stimulus enhancement in the mate choice decision of the focal female (unless she had a memory of the male assigned the model female as one who courted at a higher rate than the control male, but did not attribute this to the presence of the model female). Given that most studies that investigate non-independent mate choice indirectly control for stimulus enhancement, we still know very little about its prevalence or importance in mate choice. In communally signaling species where a male can not readily mate with two females over a short interval, the extent to which stimulus enhancement is a

factor that determines whether it is adaptive to retain neighbors that might increase a focal male's likelihood of acquiring a mate and/or whether selection favors males adjusting their courtship levels in relation to those of their neighbors remains poorly studied.

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