



Female fiddler crabs settle for less: the travel costs of mate choice

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Females often have strong preferences for the most attractive males that provide the greatest benefits. However, searching for and sampling potential mates is costly. Females are therefore expected to make an optimizing choice whereby the benefits provided by the male outweigh the cost of choosing him. Consequently males should benefit by minimizing costs experienced by sampling females, or by reducing the ability of females to assess these costs. We investigated the economics of female mate choice in the fiddler crab *Uca mjoebergi* through observation of natural mate-searching behaviour, and by manipulating the costs of choice in a series of two-choice experiments using robotic crabs. Observed females were choosy about their mates, but this selectivity declined when predation risk increased. Experimental females were allowed to choose between males of different attractiveness at a range of distances from the female, with the more attractive male placed further from the female. Females did not travel further to reach a more attractive male except when distances were small. These results suggest that greater attractiveness does not always ensure greater mating success for males, as distant males experience a disadvantage. Male mate-attracting behaviour was then investigated, as male *U. mjoebergi* often leave their territories to approach sampling females, behaviour that may overcome a distance disadvantage. Males closely approached females regardless of their distance from the female. This behaviour is likely to prevent females from making the optimal choice, as they cannot include travel costs in their assessment of males.

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Selecting a mate with the most elaborate ornamentation or the most extravagant display can be costly to females. To locate and reach the most attractive males, females generally need to expend more energy, take greater risks, and pay greater opportunity costs than they would if they were less choosy (Reynolds & Gross 1990). Female selectivity would not occur unless the net benefits outweighed the costs. The extent to which preferences are expressed should therefore vary with the cost of sampling mates (assuming some level of phenotypic plasticity in the behaviour of individuals; e.g. Wong & Jennions 2003).

Mate-searching behaviour has been extensively studied in fiddler crabs (genus *Uca*; Backwell & Passmore 1996; Koga et al. 1998; deRivera et al. 2003) because the

behaviour and ecology of these small intertidal crabs presents a useful and accessible system for addressing mate choice questions. Fiddler crabs live in high-density, mixed-sex populations. Males and females defend small (15 cm diameter) individual territories containing a burrow, which is an essential resource: when threatened by birds or other predators, all crabs in the area retreat rapidly into their respective burrows. They also retreat regularly throughout the day to avoid dehydrating on the scorching mudflat. Male fiddler crabs have a single enlarged claw that they wave to attract females for mating (Crane 1975). Receptive females leave their territories and wander through the population of displaying males, visiting several (up to 106 in one species, deRivera 2005) before selecting a mate. A female selects whom she will visit based on male characteristics such as claw size, wave rate and wave leadership (Backwell & Passmore 1996). If the male is deemed suitable the female will briefly enter and inspect his burrow, basing her final mating decision on the male's

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burrow quality (Backwell & Passmore 1996; Reaney & Backwell 2007). Finding a male who owns a high-quality, structurally sound burrow is extremely important for a receptive female, as this is where she will incubate her eggs (Crane 1975). The quality of the male's burrow can therefore directly affect a female's immediate reproductive success, providing a good reason for females to choose carefully.

The process of mate choice is potentially costly for female fiddler crabs. First, females are more vulnerable than males to some predators (Bildstein et al. 1989; Pratt et al. 2002). Sampling and rejecting several males requires that females travel across the mud surface, which puts them at risk of dehydration and increases the risk of predation. Female fiddler crabs are less selective when the costs of mate choice are high. For example, in *Uca annulipes*, females decrease their selectivity when temporal constraints increase the costs of sampling (Backwell & Passmore 1996). Similarly, in *U. beebei*, females reduce their searching effort under high predation conditions (deRivera et al. 2003). An exception has been found in *U. terpsichores*, where female preference for a male signal increased under increased predation risk. In this case, however, the signal (a sand hood) provided direct benefits to the female in the form of protection from predators (Kim et al. 2007).

Attracting females is potentially very costly for male fiddler crabs. Waving is energetically expensive and occupies large amounts of time that could otherwise be spent on activities such as foraging (Matsumasa & Murai 2005; How et al. 2008). Male courtship behaviour is influenced by food availability in *U. annulipes* and *U. lactea* (Jennions & Backwell 1998; Kim et al. 2008). Furthermore, when a male is waving at a wandering female, he usually leaves his territory and approaches the female (personal observation). This often results in a small group of males gathered around a wandering female. Each of these males, however, leaves his territory unguarded and this increases the risk of losing it to a male intruder.

During mate searching, female fiddler crabs make multiple decisions about whether to bypass a potential mate to reach a more preferred male further away. There is potentially a trade-off between the distance a female is prepared to travel and the male's attractiveness. This is particularly likely when travel costs are elevated. For example, under high predation rates females may limit their search and choose less attractive, more accessible males (Real 1990). Furthermore, if females do make such a trade-off, males might be able to overcome the resulting distance disadvantage by approaching females, thereby concealing the distance to their burrows. The clustering of males around a mate-searching female could prevent her from including information on the distance to a male's burrow in her initial decision to visit him. Males who might otherwise have been discounted because of the distance of their burrow from a female could, in this way, improve their mating success.

Our study was designed to determine whether female fiddler crabs balance the benefits of choosing an attractive mate against the potential costs associated with that choice caused by an increased travel distance.

METHODS

We examined the mate choice behaviour of the fiddler crab *Uca mjoebergi* in their natural mangrove habitat at East Point Reserve in Darwin, Australia. In this species mating activity is restricted to a 9-day period around each neap tide. Data were collected between September and December 2007.

Natural Mate Searching

To determine whether female selectivity declines when predation risk increases, we documented natural mate-searching behaviour by following mate-searching females as they visited successive males. Mate-searching females ($N = 44$) were identified when they were observed inspecting a male's burrow, briefly entering it or putting their legs in it. This is characteristic of sampling behaviour. We tracked each female and recorded the number of males that she passed within 10 cm of, but ignored, before sampling another male's burrow. Each bypassed male was counted only once. Four trials were discarded because the female stopped sampling and took refuge in an abandoned burrow. For 20 females we increased perceived predator presence by moving a plastic bird attached to a thin pole over the sampling area every 30 s at a height of 1 m. To avoid increasing the perceived predation effect over successive trials, we carried out observations over several days and in different areas of the population since the simulated predator created only localized disturbance. Additionally, observations with and without the simulated predator were alternated.

Two-choice Experiments with Robotic Crabs

To establish the preferences of mate-searching females for a male trait, we subjected them to a series of two-choice tests using robotically waving mimics of a male's major claw. Wave leadership was used as the focal trait, as a preference for leading signals has been found in a range of acoustically and visually signalling species (Dyson & Passmore 1988; Greenfield & Roizen 1993). In addition, a recent study of *U. mjoebergi* found that females have a very strong preference for leading waves (Reaney et al. 2008). Mate-searching females, identified when they were observed sampling a male's burrow, were caught and kept in a small amount of water to prevent dehydration. To determine the baseline preference for the focal trait, females ($N = 40$) were allowed to choose between two robotic waving claws of the same claw size (19.4 mm claw length), wave duration (3.6 s) and wave rate (8.4 waves/min), but with one claw having its wave delayed by 1.8 s to create a leader/follower effect between the waving claws. The selected claw length falls within the natural range of claw lengths in the population ($\bar{X} \pm \text{SD} = 18.78 \pm 3.7$ mm, range 7.4–27.5 mm, $N = 930$; P. Backwell, unpublished data).

Each robotic unit consisted of a metal arm driven by a small motor to mimic the wave of a courting male *U. mjoebergi*. The units were powered by a central control, which used tone decoders to control wave timing, sending frequency signals to initiate each wave. Each unit was

controlled by a distinct frequency to enable independent waving. A portable CD player was used to send digital sound files of specific tone sequences to the central control, producing corresponding wave sequences in the robotic units (see Reaney et al. 2008 for further details). Each unit was housed in a plastic container and buried level with the mud surface so that only the lid and protruding arm were visible. Plaster casts of autotomized male claws were painted with yellow oil-based enamel paint (Dulux Tinytin) and attached to each arm. The robotic crabs were placed 5 cm apart and 20 cm from the choosing female (Fig. 1a), who was placed under a small clear plastic cup and allowed to settle before the cup was removed using a remote trigger. Females were exposed to at least two complete waves from each unit before being released. A female's choice was scored as positive if she moved steadily, directly and deliberately to within 2 cm of a waving claw. A trial was discarded if the female ran immediately upon release in any direction (including towards a waving unit), or if the female did not make a choice within 3 min. This increased the likelihood that all choices were made in a mate-searching context.

Once the female preference for leading waves was confirmed in the control trials (see Results below), we repeated the experiment with the unit displaying the leading wave placed at a series of increasingly disadvantageous distances (30 cm, 40 cm, 50 cm) from the choosing female

($N = 40$ in each trial) while the unit displaying the following wave remained at a distance of 20 cm (Fig. 1b–d). To eliminate the possibility of a side bias, for approximately half of the females in each trial the distant, leading unit was placed on the left and the following unit on the right, with these positions reversed for the remaining females.

A further series of trials was then run, in which both the distance between the female and the closer unit and the distance between the two units were varied (5 and 10 cm, 10 and 15 cm, 10 and 20 cm, 20 and 25 cm; $N = 40$ in each trial). Again, the more distant unit always displayed the more attractive, leading wave (Fig. 1e–h) and the distant unit was the left-hand choice for half of the females in each trial and the right-hand choice for the other half. Travel distance was used as a measure of the presumed cost of choice, as the risks associated with time on the surface mean that females should limit the total distance they travel during mate searching.

Assessing female preferences based on choice may reveal limitations of their physiology (i.e. the distance at which males are no longer discernible to a female) or perception (i.e. the leadership effect may not be perceived by the female when waving males are too far apart). To eliminate the possibility that these limitations explained the changes in female choice observed across the other trials, we ran two control trials with the robotic crabs placed 20 cm apart and 50 cm from the choosing female,

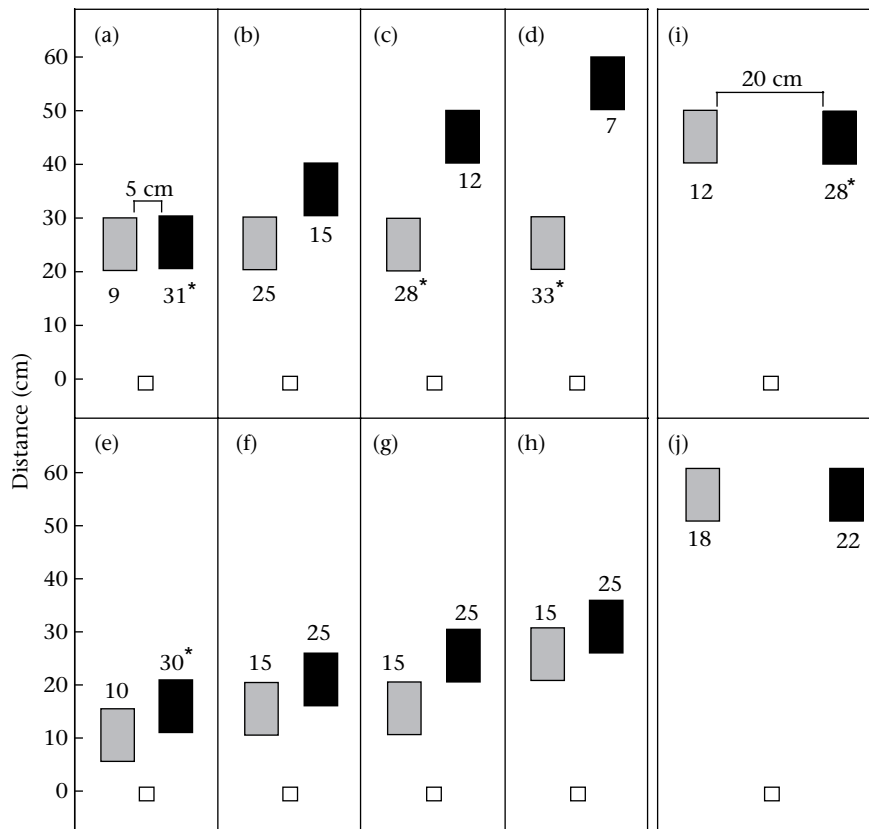


Figure 1. Position of leading wave (black) and following wave (grey) robotic crab units relative to female release point (white square) in the two-choice experiments, and the number of females that chose each unit. An asterisk indicates a significant ($P < 0.05$) female preference for that unit. (a) Both units at 20 cm; (b) 20 and 30 cm; (c) 20 and 40 cm; (d) 20 and 50 cm; (e) 5 and 10 cm; (f) 10 and 15 cm; (g) 10 and 20 cm; (h) 20 and 25 cm; (i) both units at 40 cm, 20 cm apart; (j) both units at 50 cm, 20 cm apart.

and 20 cm apart and 40 cm from the choosing female ($N = 40$ in each trial; Fig. 1i, j).

Females responded well to the robotic crabs. Only 36 of 436 trials were discarded because a female failed to respond. The choices made were extremely clear since females approached the selected robotic crab in a steady and direct path.

Male Courtship Behaviour

To determine whether males alter their territorial behaviour to overcome any distance disadvantage affecting mate attraction, we examined the behaviour of males in the presence of a receptive female. Twenty females were caught and the width of their carapace was measured at the widest point (between the front corners) using dial callipers. Each female was tethered to a nail by a short length (approximately 2 cm) of cotton thread superglued to her carapace. A tethered female was then placed within 30 cm of two or three male burrows. The distances between the female and each of the burrows varied within and between trials. Each male was watched by a separate observer, from the moment they emerged from their burrows and while they approached the female, for a maximum of 5 min. The furthest point reached by each male from his burrow was then marked and the trial ended. For each male, the distance he travelled (from the burrow to the marked point) was measured, as well as the distance from his burrow to the tethered female. We then measured each male's carapace width and claw (propodus) length. A trial was used only if all the focal males waved at the tethered female.

Statistical Analysis

Data from the two-choice experiments were first analysed using binomial tests. To investigate the independent effects of distance to the leading wave from the female release point, and the distance between the leading and following waves, on the proportion of females that chose the leading wave, we ran a general linear model. We used adjusted sum of squares, arcsine transformed the proportion of responses and treated the distance to leader and distance between leader and follower as continuous predictor variables. Each of the 10 experiments contributed a single data point. A Mann–Whitney U test was used to compare the behaviour of control females and of females subjected to an increase in perceived predation risk in the natural mate-searching experiment. The response of males to tethered females was analysed using a general linear mixed model in SPSS version 14.0 (SPSS Inc., Chicago, IL, U.S.A.). In all tests, the alpha level was set at 0.05. All tests were two tailed unless otherwise specified.

RESULTS

Natural Mate Searching

Females did not always sample the burrow of the closest male, bypassing a mean \pm SD of 2.28 ± 3.27 ($N = 40$) males before visiting another male's burrow. However, females ignored significantly fewer males when there was

a perceived increase in predation risk (simulated predator present: $\bar{X} \pm$ SD = 1.3 ± 1.5 males bypassed, $N = 20$) than under natural predation levels (simulated predator absent: $\bar{X} \pm$ SD = 3.3 ± 4.2 males bypassed, $N = 20$; Mann–Whitney U test: $U = 117.5$, $P = 0.02$).

Two-choice Experiments with Robotic Crabs

A significant majority of females (77%) chose the robotic unit that displayed a leading wave when both units were 20 cm from the female release point ($P = 0.001$; Fig. 1a). When the leading wave was moved to be 30 cm from the release point, females showed no significant preference although they tended to choose the closer, following wave (62%; $P = 0.15$; Fig. 1b). Females showed a significant preference for the closer, following wave when the leading wave was 40 cm (70%; $P = 0.02$; Fig. 1c), or 50 cm (82%; $P < 0.001$; Fig. 1d) from the release point.

There was a tendency for females to choose the more distant, leading unit in the 10 versus 15 cm, 10 versus 20 cm and 20 versus 25 cm trials, although none of these were significant (62%; $P = 0.15$ in all cases; Fig. 1f–h). Significantly more females chose the leading wave than the following wave in the 5 versus 10 cm trial (75%; $P = 0.002$; Fig. 1e). Finally, females preferred the leading unit when both units were 40 cm from the release point (70%; $P = 0.02$; Fig. 1i), but showed no significant preference when both units were 50 cm from the release point (55%; $P = 0.64$; Fig. 1j). This shows that females can perceive waving males from a distance of at least 50 cm, and detect wave leadership from a distance of at least 40 cm, even when males are 20 cm apart.

Pooling across the 10 two-choice experiments, we found that the further the leading unit was from the female release point, the less likely the female was to choose the leading unit ($F_{1,7} = 7.207$, $P = 0.031$), and the greater the distance between the leading and following units the more likely the female was to choose the following unit ($F_{1,7} = 30.577$, $P = 0.001$). There was no interaction between distance to leader and distance between leader and follower ($F_{1,6} = 1.50$, $P = 0.267$) and this was removed from the model. The final model was $y = 1.127$ (SE = 0.059) – 0.005 distance to leader (SE = 0.002) – 0.016 distance between leader and follower (SE = 0.003), where y is the arcsine square-root transformation of the proportion of females choosing the leader, and distances are measured in centimetres.

Male Courtship Behaviour

Males can overcome the potential disadvantage of being more distant than their rivals from a female by moving away from their territories and closely approaching mate-searching females. Nearly all males moved to within 5 cm of the tethered female, regardless of their initial distance from her. Neither female nor male size affected how close males came to the female (mixed models: $F_{1,14.9} = 0.55$, $P = 0.47$ and $F_{1,43.8} = 0.57$, $P = 0.46$, respectively). The distance travelled by each male towards the female varied significantly with the distance from the male's burrow to

the female: males who were initially further from the female travelled a greater distance to reach her (mixed model: $F_{1,39.8} = 86.77$, $P < 0.001$; Fig. 2). Removal of two outlying data points only increased the robustness of the result ($F_{1,43} = 204.55$, $P < 0.001$). In short, males did not move a fixed distance from their burrow, but compensated for being more distant by travelling further.

DISCUSSION

Mate-searching female *U. mjoebergi* were choosy about their mates. Under natural conditions, females bypassed an average of 3.3 potential mates before sampling a second male. Females were clearly not mating with the nearest available male and were paying search costs to reach a preferred but more distant male.

When the perceived predation risk was increased by flying a model predator over naturally mate-searching females, they became less selective and bypassed fewer (less than half as many) males. This result concurs with previous experimental studies that have manipulated the overall cost of sampling and comparing mates, and also found reduced female choosiness when sampling was more costly (Alatalo et al. 1988; Milinski & Bakker 1992; Møller 1994; Godin & Briggs 1996). Despite a significant decrease in choosiness, females did not sample the closest male even when threatened. A slightly higher level of threat might have led to a further decrease in choosiness. However, our intention was not to disrupt normal activity when moving the plastic bird over the observation area, but to induce cautious 'freezing' behaviour periodically in all active crabs in the local area, including the focal female. Too high a threat would have caused the crabs to retreat into their burrows and prevented assessment of sampling behaviour.

The two-choice trials using robotic crabs provide a more detailed understanding of the travel costs females are

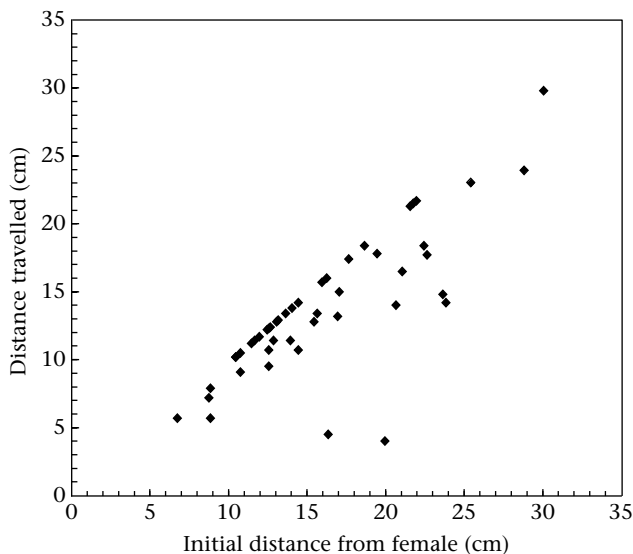


Figure 2. Distances travelled by males from their burrows towards a tethered female, in the male courtship behaviour experiment.

prepared to pay to reach a preferred male. We first demonstrated that there is a strong preference for leading waves when males are at an equal distance from a female. In all of the two-choice trials, the female had the opportunity to view at least two waves by each robotic unit before being released and allowed to make her selection. Although both units would therefore have been equally conspicuous, females strongly preferred the leading wave. It is uncertain why females have a preference for leading waves. In acoustic signalling systems, males producing leading signals are easier to locate and likely to be located more quickly than males producing following, overlapping signals (Greenfield 1994). This is possibly because acoustic leading signals mask, jam or otherwise reduce the perceptibility of following signals (Greenfield & Roizen 1993). Consequently, males producing leading signals experience higher mating success, while females benefit from the decreased costs associated with reducing search time by moving towards more conspicuous signals. However, in visual signalling systems, it is unlikely that leading signals are more easily detected since they do not mask or jam following signals (Backwell et al. 2006). In the experimental protocol we used, females were presented with two waves of equal conspicuity. The reason that females found the leading wave more attractive could be that wave leadership is an indicator of male quality. Male *U. annulipes* that produced more leading waves did so by waving at a faster rate than other males (Backwell et al. 1999). Increased wave leadership is also correlated with male size, display intensity and speed of movement (Backwell et al. 1999, 2006). These traits are likely to indicate the quality of a male as they are more energetically expensive, and might require that a male is in good condition if he is to produce them (Andersson 1994).

In the first series of two-choice trials, the distance from the female to the following wave was maintained at 20 cm while the distance from the female to the preferred, leading wave was increased to 30, 40 or 50 cm. When the leading wave was at 30 cm, females showed no preference for either wave. This indicates a balance between a preference for leadership and against travelling a greater distance. Females were presumably weighing the benefits of selecting their preferred male against the higher costs of reaching him. When the preferred signal was placed at 40 or 50 cm, the balance tipped and the costs outweighed the benefits. Females selected the following male even though he was not the preferred option when all else was equal.

These results indicate that as distances increase, female fiddler crabs become less willing to pay a greater travel cost to approach a more attractive mate. Fiddler crabs have two stages of mate choice, first selecting an attractive male and then assessing the quality of his burrow (Backwell & Passmore 1996; Reaney & Backwell 2007). While a female's choice of burrow will directly affect the hatching success of the eggs she incubates there, choosing a male with a leading wave is not likely to result in direct benefits. Although not tested in *U. mjoebergi*, male phenotypic traits are not correlated with burrow quality in other fiddler crabs (Backwell & Passmore 1996). As our experiment only tested female preferences for a male phenotypic trait, the indirect benefits of a choice were being weighed

against the direct cost. The benefits gained from choosing a male with a leading wave may be insufficient to outweigh the extra travel cost.

The second series of two-choice trials presented females with smaller travel costs than they faced in the first series of trials, with both waves presented at distances of 25 cm from the female or less. In the first of these trials, the leading signal was presented at 10 cm and the following signal at 5 cm from the female release point. Females significantly preferred the more distant, leading signal. However, in all other trials, females showed no significant preference for the leading or the following signal. These results are consistent with wave leadership providing only small, indirect benefits to females. In the 5 versus 10 cm trial, the predicted benefits may have been great enough to outweigh the small additional travel cost, particularly given that the costs were small in absolute terms.

The two-choice trials indicated that greater attractiveness does not always ensure matings for males when the costs of mating with these males are higher. This result is not due to either an inability of females to perceive signals over greater distances or an inability to detect wave leadership from greater distances. This was evident in the control trials in which both signals were presented at 40 cm from the female. Even at this distance, females showed a significant preference for the leading wave that was comparable to the result of the 20 cm control trial. This preference was lost only when the signals were 50 cm away from the female. Therefore in all of the two-choice trials we ran, waving claws were placed at distances that meant they were clearly visible to the female.

How do the results of these trials relate to the natural mating behaviour of *U. mjoebergi*? First, they indicate that males gain some benefit by being closer to a mate-searching female. Having a preferred signal is of little benefit if the male is too far from the female. The final experiment in our study showed that displaying males will leave their territories to approach a mate-searching female closely. This is highly risky behaviour for a male, as he must leave his territory unguarded and open to usurpation by burrowless, wandering crabs. However, the potential mating benefits are great, especially when the male's territory is a long distance from the female. By approaching her, the male prevents the female from incorporating information on travel distance into her decision on which male to visit. This eliminates the potential disadvantage a male faces if his territory is a substantial distance from the female's intended sampling route.

Male concealment of information on the distance to the burrow is a behaviour that functions to deceive females (see *Simple & McComb 1996*). If females cannot assess the travel distance associated with a male, they may choose males who do not provide benefits that outweigh the associated costs. Animal communication theory predicts that when a signaller evolves to overcome receiver discrimination (i.e. the signal becomes dishonest), the receiver should evolve to be more discriminating towards the signaller (*Bradbury & Vehrencamp 1998*). Similarly, sexual conflict theory sees males and females pitted against each other in an evolutionary arms race, predicting that when one sex evolves an advantage over the

other, a counteradaptation should arise in the other sex (*Arnqvist & Rowe 2005*). However, it is difficult to see how female fiddler crabs could successfully respond to the clustering behaviour of males. Males of every quality and condition appear to display the same behaviour. Nearly every male will closely approach a female that catches his attention, regardless of his size or distance from the female. Thus, while a female can still choose the most attractive male in the cluster around her, she cannot ensure that he is the optimal choice. One way that a female might avoid paying more than a male is worth would be to approach only males who are standing by their burrow entrance. However, this may not be a feasible strategy if most males display the clustering behaviour. Another possibility would be for a female to stop following a male if she has travelled as far as his attractiveness warrants. Indeed, mate-searching *U. mjoebergi* females sometimes stop following a waving male to his burrow (*I. Bookmythe*, personal observation). While there could be several reasons for this, it might occur because the benefits expected from the male are outweighed by the travel costs the female will pay by following him any further.

In sum, while female *U. mjoebergi* display a strong preference for leading waves when costs are equal, this preference is no longer expressed when the associated travel costs increase by even a very small amount. To counteract the disadvantage that males consequently experience when they are further from a female's search trajectory, they closely approach sampling females. This clustering behaviour deceives females as to the costs associated with inspecting the burrow of any given male.

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References

- Alatalo, R. V., Carlson, A. & Lundberg, A.** 1988. The search cost in mate choice of the pied flycatcher. *Animal Behaviour*, **36**, 289–291.
- Andersson, M.** 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Arnqvist, G. & Rowe, L.** 2005. *Sexual Conflict*. Princeton, New Jersey: Princeton University Press.
- Backwell, P. R. Y. & Passmore, N. I.** 1996. Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behavioral Ecology and Sociobiology*, **38**, 407–416.
- Backwell, P. R. Y., Jennions, M. D., Christy, J. H. & Passmore, N. I.** 1999. Female choice in the synchronously waving fiddler crab *Uca annulipes*. *Ethology*, **105**, 415–421.
- Backwell, P. R. Y., Jennions, M. D., Wada, K., Murai, M. & Christy, J.** 2006. Synchronous waving in two species of fiddler crabs. *Acta Ethologica*, **9**, 22–25.
- Bildstein, K. L., McDowell, S. G. & Brisbin, I. L.** 1989. Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential vulnerability to avian predation. *Animal Behaviour*, **37**, 133–139.
- Bradbury, J. W. & Vehrencamp, S. L.** 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer Associates.

- Crane, J. 1975. *Fiddler Crabs of the World*. Princeton, New Jersey: Princeton University Press.
- Dyson, M. & Passmore, N. I. 1988. The combined effect of intensity and the temporal relationship of stimuli on phonotaxis in female painted reed frogs *Hyperolius marmoratus*. *Animal Behaviour*, **36**, 1555–1556.
- Godin, J.-G. J. & Briggs, S. E. 1996. Female mate choice under predation risk in the guppy. *Animal Behaviour*, **51**, 117–130.
- Greenfield, M. D. 1994. Cooperation and conflict in the evolution of signal interactions. *Annual Review of Ecology and Systematics*, **25**, 97–126.
- Greenfield, M. D. & Roizen, I. 1993. Katydid synchronous chorusing is an evolutionary stable outcome of female choice. *Nature*, **364**, 618–620.
- How, M. J., Hemmi, J. M., Zeil, J. & Peters, R. 2008. Claw-waving display changes with receiver distance in fiddler crabs, *Uca perplexa*. *Animal Behaviour*, **75**, 1015–1022.
- Jennions, M. D. & Backwell, P. R. Y. 1998. Variation in courtship rate in the fiddler crab *Uca annulipes*: is it related to male attractiveness? *Behavioral Ecology*, **9**, 605–611.
- Kim, T. W., Christy, J. H. & Choe, J. C. 2007. A preference for a sexual signal keeps females safe. *PLoS ONE*, **2**, e422. doi:10.1371/journal.pone.0000422.
- Kim, T. W., Sakamoto, K., Henmi, Y. & Choe, J. C. 2008. To court or not to court: reproductive decisions by male fiddler crabs in response to fluctuating food availability. *Behavioral Ecology and Sociobiology*, **62**, 1139–1147.
- Koga, T., Backwell, P. R. Y., Jennions, M. D. & Christy, J. H. 1998. Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proceedings of the Royal Society of London, Series B*, **265**, 1385–1390.
- Matsumasa, M. & Murai, M. 2005. Changes in blood glucose and lactate levels in male fiddler crabs: effects of aggression and claw waving. *Animal Behaviour*, **69**, 569–577.
- Milinski, M. & Bakker, T. C. M. 1992. Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. *Proceedings of the Royal Society of London, Series B*, **250**, 229–233.
- Møller, A. P. 1994. *Sexual Selection and the Barn Swallow*. Oxford: Oxford University Press.
- Pratt, A. E., McLain, D. K. & Kirschstein, K. 2002. Intrageneric predation by fiddler crabs in South Carolina. *Journal of Crustacean Biology*, **22**, 59–68.
- Real, L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist*, **136**, 376–405.
- Reaney, L. T. & Backwell, P. R. Y. 2007. Temporal constraints and female preference for burrow width in the fiddler crab, *Uca mjoebergi*. *Behavioral Ecology and Sociobiology*, **61**, 1515–1521.
- Reaney, L. T., Sims, R. A., Sims, S. W. M., Jennions, M. D. & Backwell, P. R. Y. 2008. Experiments with robots explain synchronized courtship in fiddler crabs. *Current Biology*, **18**, 62–63.
- Reynolds, J. D. & Gross, M. R. 1990. Costs and benefits of female mate choice: is there a lek paradox? *American Naturalist*, **136**, 230–243.
- deRivera, C. E. 2005. Long searches for male-defended breeding burrows allow female fiddler crabs, *Uca crenulata*, to release larvae on time. *Animal Behaviour*, **70**, 289–297.
- deRivera, C. E., Backwell, P. R. Y., Christy, J. H. & Vehrencamp, S. L. 2003. Density affects female and male mate searching in the fiddler crab, *Uca beebei*. *Behavioral Ecology and Sociobiology*, **53**, 72–83.
- Semple, S. & McComb, K. 1996. Behavioural deception. *Trends in Ecology & Evolution*, **11**, 434–437.
- Wong, B. B. M. & Jennions, M. D. 2003. Costs influence male mate choice in a freshwater fish. *Proceedings of the Royal Society of London Series B (Supplement)*, **270**, S36–S38.