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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.

Keywords: fiddler crab; mate choice; trade-off; travel cost; *Uca mjoebergi*

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-sampling 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 ($\overline{X} \pm \mathrm{SD} = 18.78 \pm 3.7$ 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