



Male fiddler crabs prefer conspecific females during simultaneous, but not sequential, mate choice

Isobel Booksmythe*, Michael D. Jennions, Patricia R.Y. Backwell

Evolution, Ecology & Genetics, Research School of Biology, The Australian National University

ARTICLE INFO

Article history:

Received 22 July 2010
Initial acceptance 6 September 2010
Final acceptance 5 January 2011
Available online 7 February 2011
MS. number: 10-00498R

Keywords:

fiddler crab
male mate choice
mate discrimination
sequential mate choice
species recognition
Uca

Mate choice is potentially beneficial whenever prospective mates vary in quality, but when mates are encountered sequentially the cost of rejecting a current mating opportunity affects the net benefit of choosiness by lowering the mating rate. There is, however, no reduction in mating rate when choosing among potential mates that are encountered simultaneously. In general, mating with a heterospecific is costly as the resultant offspring are of low fitness. It is often argued that males, unlike females, will court and even mate with heterospecifics because the lost opportunity cost is minimal if they rarely encounter potential mates. In the fiddler crab *Uca mjoebergi*, we show that, in a natural situation, where females arrived sequentially males were equally likely to court conspecifics and heterospecifics. Females were released individually into the population, and nearly every male they passed performed a courtship waving display whether the female was conspecific or heterospecific. Taken alone, this result implies that males exhibit no species discrimination. However, in an experimental setting where males simultaneously viewed a conspecific and a heterospecific female, males waved faster and for longer at conspecific females, and attempted to mate more often with conspecifics. This indicates that *U. mjoebergi* males can discriminate between conspecific and heterospecific females and prefer to court conspecifics when given a choice. We used mate choice among rather than within species (to maximize variation in mate quality) to illustrate the need to distinguish between simultaneous and sequential mate choice when quantifying mating preferences.

© 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Species recognition constitutes the most basic form of mate choice. Mating with heterospecifics can entail such costs as the production of nonviable or less successful hybrid offspring, wasted gametes, sperm depletion and squandered breeding resources. Even where the risk of actually mating is low, misdirected courtship also wastes time, energy and resources. More generally, each heterospecific mating removes an animal from the mating pool and decreases the rate at which it will encounter, court and eventually mate with conspecifics (Peterson et al. 2005). The magnitude of this opportunity cost will depend on the likelihood that a prospective conspecific mate will be encountered before recuperating from courting or mating with a heterospecific.

Many studies indicate that males and females differ in their propensity to discriminate between species during mate choice, reflecting differences in mating costs (e.g. Saetre et al. 1997; Svensson et al. 2007; Kozak et al. 2009). It is argued that the cost of a heterospecific mating is higher for the sex with greater parental investment owing to a longer 'time out' after mating which generates a larger

mating opportunity cost (Trivers 1972). As females typically provide more parental care than males, they are expected to show greater mate discrimination against heterospecifics (Wirtz 1999). In addition, Bateman gradients (regression of fitness on mating rate) are usually steeper for males than females, indicating that males pay a greater cost if they lower their mating rate by rejecting mates (Jennions & Kokko 2010).

Male mate choice is expected to occur when females vary in quality and male investment per mating is relatively high (Kozak et al. 2009). For example, sexually dimorphic wing coloration in the damselfly *Calypteryx virgo* gives males a substantially greater risk of avian predation during courtship compared to females; in this species males show greater discrimination against heterospecifics than females (Svensson et al. 2007). Despite the generally strong relationship between male fitness and mating rate, rejecting some females is beneficial if it increases the mean value per mating (e.g. Härdling et al. 2008). In the case of species discrimination, variation in female quality is at its most extreme. While it seems that avoiding heterospecific courtship must be beneficial owing to the extremely low value of heterospecific mates, many factors affect the costs of misdirected courtship. These include the strength of female discrimination (Kozak et al. 2009), and the number and distribution of conspecifics and heterospecifics (Gröning & Hochkirch 2008). Mate

* Correspondence: I. Booksmythe, Research School of Biology, The Australian National University, Building 116, Daley Road, Canberra, ACT 0200, Australia.

E-mail address: isobel.booksmythe@anu.edu.au (I. Booksmythe).

availability strongly affects whether or not male mate choice evolves. For example, when females are limited a male's chance of not mating increases, so the cost of mate choice (i.e. rejecting a mating opportunity) is higher (Barry & Kokko 2010). Furthermore, the pattern of mate encounter has major implications for the benefits of discrimination (Kokko & Ots 2006). When mates are encountered simultaneously, even small differences in the profitability of different mating opportunities can make mate choice beneficial. When mates are encountered sequentially, however, choice becomes more costly, as it involves rejecting a current mating opportunity for an uncertain future gain in mate quality (Barry & Kokko 2010). Thus even if some matings entail large costs, the level of mate discrimination can be very low when mates are encountered sequentially (Kokko & Ots 2006). In accordance with this prediction, male sticklebacks, *Gasterosteus aculeatus*, preferred to court the larger of two dummy females presented in a simultaneous choice experiment, but courted both dummies equally when they were presented sequentially (Rowland 1982). Encounter regime similarly affected female preferences for larger males in sailfin mollies, *Poecilia latipinna* (MacLaren & Rowland 2006).

In fiddler crab (genus *Uca*) populations, each individual defends a small territory containing a burrow that is an important shelter and breeding resource. All species display remarkable sexual dimorphism: females have two small feeding claws, whereas in males one claw is greatly enlarged (up to 50% of their body weight) and used as a weapon and a sexual ornament. *Uca mjoebergi* is an Australian species in which males wave the enlarged claw in a conspicuous courtship display to attract females to their burrows to mate. Receptive females abandon their own territories and wander through the population, bypassing many waving males before choosing to inspect a burrow, and sampling several males' burrows before finally choosing a mate (Reaney & Backwell 2007). This mating system means that males encounter prospective mates sequentially. As the operational sex ratio is highly male biased (Reading & Backwell 2007), a male would rarely have more than one receptive female at a time in his immediate vicinity.

Although the geographical distributions of fiddler crab species overlap, populations are usually monospecific owing to species-specific habitat requirements. However, some localized sympatry occurs. At East Point Reserve (Darwin, Northern Territory) a population of mainly *U. mjoebergi* also contains low numbers of three other fiddler crab species (*Uca signata*, *Uca elegans* and *Uca vomeris*). While *U. mjoebergi* are found consistently over a 0.25 ha area (approximate density 37 ± 17 crabs/m²; R. Slatyer, L. T. Reaney & P. R. Y. Backwell, unpublished data), the distribution of the other species appears very patchy in this area. *Uca signata* are similar in size to *U. mjoebergi*, while the remaining two species are substantially larger (largest recorded carapace width: *U. mjoebergi* = 16.4 mm, *U. signata* = 18.4 mm, *U. elegans* = 26.6 mm, *U. vomeris* = 29.2 mm, Crane 1975). *Uca mjoebergi* and *U. signata* differ noticeably, however, in the coloration of the male claw: those of *U. mjoebergi* are bright yellow, while *U. signata* claws are mainly white with an orange-red manus. *Uca mjoebergi* females prefer conspecific males to *U. signata* males (Detto et al. 2006), but anecdotal evidence suggests that males will court heterospecific females. Female *U. signata* and *U. mjoebergi* are very similar in colour to the human eye, but differ in relative eyestalk length and the shape of the frontal carapace (Crane 1975). As fiddler crab vision does not involve high resolving power or acuity (Detto et al. 2006), it is unclear whether males can perceive these species differences unless females are close. Indiscriminate courtship could impose substantial costs on *U. mjoebergi* males whenever heterospecific females are common, given the high energetic costs of waving (Matsumasa & Murai 2005). Time spent courting heterospecifics will also reduce opportunities for males to court conspecifics if males cannot discriminate between the species.

There is, however, evidence for male mate choice in *U. mjoebergi*, as males preferentially court larger conspecific females (Reading & Backwell 2007).

Here we studied a sympatric pair of fiddler crab species in which species discrimination by females has been shown (Detto et al. 2006). We investigated whether males recognize and reject heterospecific females, and whether this depends on the context in which choice occurs. Specifically, do males court conspecific and heterospecific females equally (1) when females are encountered sequentially and (2) when females are encountered simultaneously?

METHODS

Courtship of *U. mjoebergi* and *U. signata* females by *U. mjoebergi* males was measured to determine whether courting males differentiate between the species when mates are encountered sequentially. Fifteen *U. mjoebergi* and 15 *U. signata* resident females were caught and individually released into the population at least 2 m from their territory, and visually tracked for 5 min. The number of *U. mjoebergi* males within 20 cm of the female and the number of these that directed courtship waves at the female were recorded. Females were then recaptured and measured using dial callipers (± 0.1 mm carapace width). We used general linear models in SPSS 17.0 (SPSS Inc., Chicago, IL, U.S.A.) to explain variation in the number of courting males per female, with species identity, female size and number of males passed as predictor variables. All interaction terms were nonsignificant ($P > 0.4$) and removed from the final model.

To determine whether male *U. mjoebergi* prefer conspecific to heterospecific females in a simultaneous choice scenario, 47 *U. mjoebergi* males were allowed to choose between size-matched (< 1 mm difference) *U. mjoebergi* and *U. signata* females. Each male was tested once, using a different pair of females. Resident males were randomly selected and visually isolated from the population with a barrier 5 cm high and 30 cm in diameter. Females were tethered (1 cm of thread glued to the carapace and tied to a nail pressed into the sediment) randomly on opposite sides of the male's burrow, 10 cm from the entrance. Once the male emerged from his burrow we filmed him for 5 min using a video camera mounted directly above the enclosure. We noted the time spent courting each female, the time spent attempting to mate with each female, the number of waves directed at each female and the wave rate to each female (waves/s calculated from a 20 s video sample beginning with the first wave to a female). We used Wilcoxon signed-ranks tests to compare paired data, and log-likelihood ratio (LLR) tests, Fisher's exact tests and binomial tests for binary data. All tests are two tailed with $\alpha = 0.05$.

RESULTS

Nearly all males waved when a female passed within 20 cm. The number of waving males was therefore closely related to the number of males a female passed. Female size had an additional small, but significant, positive effect on the number of waving males (Table 1). Female species identity did not affect the number of males that waved (Fig. 1): conspecific and heterospecific females both provoked

Table 1

General linear model to predict the number of males waving at a wandering female over a 5 min period

	Parameter estimate (SE)	F	df	P
Species	-0.050 (0.306)	0.027	1, 24	0.871
Female size	0.275 (0.132)	4.335	1, 24	0.048
Number of males passed	1.016 (0.025)	1662.111	1, 24	<0.001

N = 30 females.

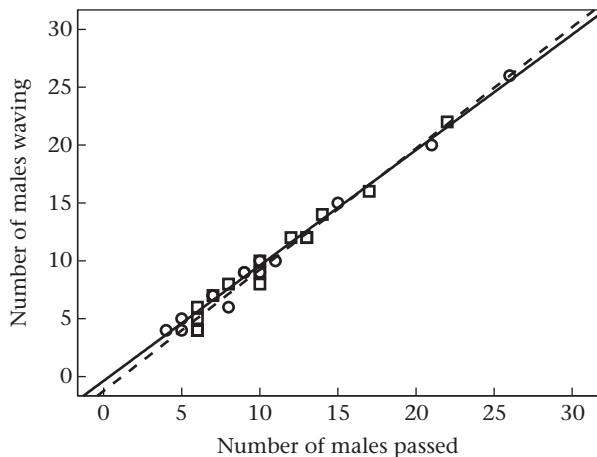


Figure 1. Male waving response to *U. mjoebergi* females (circles and solid line; $Y = 0.997X - 0.372$) and *U. signata* females (squares and dashed line; $Y = 1.048X - 1.241$). The lines do not differ in slope ($F_{1,22} = 0.710$, $P = 0.408$).

the same waving response from *U. mjoebergi* males when females were encountered singly (i.e. sequential exposure to females).

Seven simultaneous choice trials in which the male did not court or attempt to mate with either female were discarded, leaving 40 trials in which the male courted (waved to) or attempted to mate with at least one female. The male courted at least one female in 39 trials, and both females in 21 trials. The male attempted to mate with at least one female in 24 trials, and both females in three trials.

The male emerged from the burrow facing the *U. mjoebergi* female in 28 of 40 trials (binomial test: $P = 0.017$) and initially courted the *U. mjoebergi* female in 27 of 40 trials (binomial test: $P = 0.038$). Males were more likely to court first the female they faced on emerging (LLR = 29.153, $df = 1$, $P < 0.001$). Importantly, however, the species of the female initially courted did not affect the likelihood that the male courted both females during the trial (LLR = 0.636, $df = 1$, $P = 0.425$). In total, the male courted the *U. mjoebergi* female in 34 trials and the *U. signata* female in 26 trials (Fisher's exact test: $P = 0.069$).

Males spent longer courting *U. mjoebergi* females (median, lower–upper quartiles: 56 s, 6.75–108.5) than *U. signata* females (15 s, 0–56; Wilcoxon signed-ranks test: $Z = 2.316$, $N = 40$, $P = 0.021$). They also directed more waves at *U. mjoebergi* (16, 3.5–35.75) than *U. signata* females (5, 0–18; $Z = 2.640$, $N = 40$, $P = 0.008$). When waving at *U. mjoebergi* females, male wave rate was faster (0.3 waves/s, 0.2–0.36) than when waving at *U. signata* females (0.2 waves/s, 0–0.3; $Z = 2.45$, $N = 40$, $P = 0.014$).

The male attempted to mate with the *U. mjoebergi* female in 20 trials and the *U. signata* female in seven trials (Fisher's exact test: $P = 0.004$). Mating attempts with *U. mjoebergi* females also lasted longer (14 s, 0–113.5) than those with *U. signata* females (0 s, 0–0; $Z = 3.272$, $N = 40$, $P = 0.001$).

DISCUSSION

When male *U. mjoebergi* encountered a single female that passed within 20 cm of them (i.e. a sequential mate choice scenario) they did not differentiate between conspecifics and heterospecifics. Almost every male waved at the female regardless of species. This suggests that the cost of indiscriminate courtship is small compared to the risk of missing an opportunity to attract a conspecific female. During mating periods, male fiddler crabs wave whenever they detect a female. Males that have lost their major claw, juvenile males and hermit crabs can also occasionally provoke courtship (I. Booksmythe, personal observation; see also Booksmythe et al. 2010). Although waving is energetically costly (Matsumasa &

Murai 2005), the costs of indiscriminate waving might be reduced if a waving group, triggered by any stimulus, attracts more receptive females through its increased conspicuousness (R. Milner, unpublished data).

When simultaneously presented with females of both species (tethered 10 cm away), males waved significantly more at conspecifics. Furthermore, males waved significantly faster when courting a conspecific. These results indicate that, contrary to the conclusion one might draw from male courtship when females are encountered sequentially, males can differentiate between conspecifics and heterospecifics, and prefer to court conspecifics. Even so, males that initially courted a conspecific were as likely to court both females during the trial as males that initially courted a heterospecific. If males can discriminate between species, why spend time courting heterospecifics? This is possibly because of a limitation of our experimental design: female response might assist males in identifying receptive conspecifics, but tethered females cannot approach or retreat from a courting male. Failure to retreat might indicate that a female is a suitable mate, encouraging a male to continue courtship; failure to follow a courting male back to his burrow might prompt him to investigate alternative mating possibilities. Such behavioural cues could be as important as morphological characters for male species recognition in *U. mjoebergi*. Our results on actual mating attempts corroborate this interpretation. Although male *U. mjoebergi* were far more likely to attempt to mate with a tethered *U. mjoebergi* than *U. signata* female, seven males still attempted to mate with a heterospecific. This indicates that, even at close range, species discrimination is imperfect.

The simultaneous choice experiment suggests that male *U. mjoebergi* prefer to court conspecific females. Why then was discrimination absent in the natural courtship situation when males only encountered one female? We propose that heterospecific courtship does not impose large direct costs on *U. mjoebergi* males, particularly in the absence of an immediate alternative mating opportunity. If, however, a male is simultaneously faced with more than one female, his discriminatory abilities are sufficient to allow him to favour a conspecific female. It might be easier to recognize a heterospecific female when a conspecific female is present as a direct comparison, than to recognize a heterospecific female in isolation (Shettleworth 1998). Several factors are likely to lower the costs of heterospecific courtship for *U. mjoebergi* males. First, female *U. mjoebergi* show strong species recognition ability based on claw colour (Detto et al. 2006). The species-specific claw coloration and courtship displays of male fiddler crabs, which are the subject of female mate choice, suggest that females of most fiddler crab species are likely to be equally discriminatory. Thus *U. mjoebergi* males are unlikely to attract heterospecific females successfully. This limits the costs imposed to time and energy wasted courting heterospecifics (i.e. excludes actual mating costs). Second, in our study population *U. mjoebergi* females greatly outnumber those of other species and are the females most commonly encountered by courting males. The chance of courting a heterospecific, even when courting indiscriminately, is therefore fairly low. This is, however, not the case in marginal habitat where heterospecific females are more common. Third, males encounter receptive females sequentially and the operational sex ratio is highly male biased (Reading & Backwell 2007). This means that the availability of females is low. Rejection of a suitable conspecific mate is therefore likely to be far more costly than an acceptance error when courting an undesirable mate (i.e. *U. signata* females).

Arguably, a no-choice arena test, in which the same male was presented with a female of each species sequentially, would provide a better comparison to the simultaneous choice experiment than the sequential design we used. A no-choice test would have allowed the use of the same measures of male preference as in the simultaneous

choice experiment, and to control factors such as distance to the female. However, as females in the sequential experiment could be anywhere from 0 to 20 cm from a male, and females in the simultaneous experiment were tethered 10 cm away (the midpoint of that distance range), it is unlikely that differences in female distance account for the contrasting results of the two experiments. The simultaneous choice experiment revealed a male preference that was not detected in the sequential choice experiment, which closely mimicked a natural mate encounter scenario. Although the designs of our two experiments are not directly comparable, together they provide a more accurate picture of male mate discrimination in *U. mjoebergi* than either experiment could yield individually.

Acknowledgments

We thank Richard Milner and the crab lab for assistance and the Australian Research Council for funding (to P.R.Y.B.).

References

- Barry, K. L. & Kokko, H. 2010. Male mate choice: why sequential choice can make its evolution difficult. *Animal Behaviour*, **80**, 163–169.
- Booksmythe, I., Milner, R. N. C., Jennions, M. D. & Backwell, P. R. Y. 2010. How do weaponless male fiddler crabs avoid aggression? *Behavioral Ecology and Sociobiology*, **64**, 485–491.
- Crane, J. 1975. *Fiddler Crabs of the World*. Princeton, New Jersey: Princeton University Press.
- Detto, T., Backwell, P. R. Y., Hemmi, J. M. & Zeil, J. 2006. Visually mediated species and neighbour recognition in fiddler crabs (*Uca mjoebergi* and *Uca capricornis*). *Proceedings of the Royal Society B*, **273**, 1661–1666.
- Gröning, J. & Hochkirch, A. 2008. Reproductive interference between animal species. *Quarterly Review of Biology*, **83**, 257–282.
- Hårdling, R., Gosden, T. & Aguilee, R. 2008. Male mating constraints affect mutual mate choice: prudent male courting and sperm-limited females. *American Naturalist*, **172**, 259–271.
- Jennions, M. D. & Kokko, H. 2010. Sexual selection. In: *Evolutionary Behavioral Ecology* (Ed. by D. F. Westneat & C. W. Fox), pp. 343–364. Oxford: Oxford University Press.
- Kokko, H. & Ots, I. 2006. When not to avoid inbreeding. *Evolution*, **60**, 467–475.
- Kozak, G. M., Reisland, M. & Boughmann, J. W. 2009. Sex differences in mate recognition and conspecific preference in species with mutual mate choice. *Evolution*, **63**, 353–365.
- MacLaren, R. D. & Rowland, W. J. 2006. Differences in female preference for male body size in *Poecilia latipinna* using simultaneous versus sequential stimulus presentation designs. *Behaviour*, **143**, 273–292.
- Matsumasa, M. & Murai, M. 2005. Changes in blood glucose and lactate levels of male fiddler crabs: effects of aggression and claw waving. *Animal Behaviour*, **69**, 569–577.
- Peterson, M. A., Honchak, B. M., Locke, S. E., Beeman, T. E., Mendoza, J., Green, J., Buckingham, K. J., White, M. A. & Monsen, K. J. 2005. Relative abundance and the species-specific reinforcement of male mating preference in the *Chrysochus* (Coleoptera: Chrysomelidae) hybrid zone. *Evolution*, **59**, 2639–2655.
- Reading, K. L. & Backwell, P. R. Y. 2007. Can beggars be choosers? Male mate choice in a fiddler crab. *Animal Behaviour*, **74**, 867–872.
- 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.
- Rowland, W. J. 1982. Mate choice by male sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, **30**, 1093–1098.
- Saetre, G.-P., Kral, M. & Bures, S. 1997. Differential species recognition abilities of males and females in a flycatcher hybrid zone. *Journal of Avian Biology*, **28**, 259–263.
- Shettleworth, S. J. 1998. *Cognition, Evolution, and Behavior*. Oxford: Oxford University Press.
- Svensson, E. I., Karlsson, K., Friberg, M. & Eroukhanoff, F. 2007. Gender differences in species recognition and the evolution of asymmetric sexual isolation. *Current Biology*, **17**, 1943–1947.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine.
- Wirtz, P. 1999. Mother species–father species: unidirectional hybridization in animals with female choice. *Animal Behaviour*, **58**, 1–12.