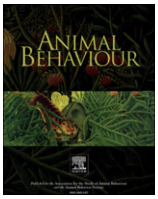
Animal Behaviour 81 (2011) 775–778

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



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.

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 *Calyopteryx 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).

0003-3472/$38.00 © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2011.01.009

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/m^2; 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.