Available online at www.sciencedirect.com

ScienceDirect

Can beggars be choosers? Male mate choice in a fiddler crab

KATRINA L. READING & PATRICIA R. Y. BACKWELL

School of Botany and Zoology, Australian National University

In most species the operational sex ratio is male biased, so females can be choosy when selecting a mate. Male choosiness, however, may also be beneficial, especially in species where female quality is variable, male mating investment is high and there is a high probability of attracting additional females. We investigated male choosiness in the fiddler crab *Uca mjoebergi*. Clutch size was positively correlated with female size. Since male mating investment is high (prolonged mate guarding), males would therefore benefit by mating with large females. Males were capable of discriminating between large and small females, and under both natural and experimental conditions they preferentially courted larger females. They did not, however, forego mating opportunities with small females, probably because the operational sex ratio was highly male biased, which limited their opportunity for attracting a second mate. Thus male *U. mjoebergi* not only engaged in competition for matings, but also showed mate choice.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: female size; fiddler crab; male mate choice; mutual mate choice; *Uca mjoebergi*

In most species, sexual selection has been traditionally thought to involve male–male competition and female choice (Darwin 1871; Bateman 1948; Trivers 1972), although the sex roles are sometimes reversed (Berglund et al. 1986). It is becoming increasingly clear, however, that the notion of one sex being discriminating and the other being competitive is overly simplistic. As a consequence, male mate choice in species where females show strong mating preferences and/or there is intense male–male competition has been found in a wide range of taxa, from insects to mammals (Sargent et al. 1986; Olsson 1993; Verrell 1995; Goshima et al. 1996; Jones et al. 2001; Craig et al. 2002). Male mate choice is predicted in species where female quality is variable, male mating investment is high and/or there is a good chance of attracting alternative females (Kokko & Johnstone 2002).

Males will benefit from being discriminating when females vary in their quality as mates. In many taxa, females vary considerably in adult body size (Bisazza et al. 1989; Bondurianky 2001). In some species this translates into variation in clutch size, with larger females producing more eggs (Murai et al. 1987; Côte & Hunte 1989). Males can, therefore, increase their fitness by mating with larger

females (Manning 1975; Gwynne 1981; Sargent et al. 1986; Verrell 1995).

Male choosiness may also be predicted when the current mating investment limits a male's ability to invest in future matings (Verrell 1995; Bondurianky 2001). Lengthy courtship, mate guarding, sperm depletion, predator attraction and physical injury can all directly (Trivers 1972; Koga et al. 1993; Jennions & Backwell 1998; Roberts & Uetz 2005) or indirectly (Stuart-Fox & Whiting 2005) limit a male's future reproductive success. If these costs are high, selection should favour the allocation of mating effort towards those females capable of providing maximum reproductive gains.

For males to benefit from being choosy, the risk of not attracting an alternative female must outweigh the benefits of mating with highly fecund females. The likelihood of attracting an alternative female depends on the operational sex ratio (OSR), specifically the number of receptive females to competing males (Emlen & Oring 1977). In species where males can achieve fast rates of reproduction through investing little in offspring production, the OSR will be biased towards an excess of males (Parker & Simmons 1996; Cunningham & Birkhead 1998). As a consequence, males should not necessarily forego mating opportunities with low-quality females (Olsson 1993; Verrell 1995). The optimum level of male choosiness is likely to be a function of the OSR (Owens & Thompson 1994).

Correspondence: K. Reading, School of Botany and Zoology, Faculty of Science, Canberra, A.C.T. 0200, Australia (email: katrina.reading@gmail.com).

Fiddler crabs (genus *Uca*) are a classic example of a group in which males compete for access to mates and females are often highly selective in their choice of males (Backwell & Passmore 1996; Jennions & Backwell 1996; Backwell et al. 1998; Backwell & Jennions 2004; deRivera 2005). It has generally been assumed that males are indiscriminate in their choice of mates. However, these crabs have two of the three predictors of male choosiness described above. Growth is indeterminate which results in a wide range of adult body sizes, and therefore the potential for highly variable female fecundity (Sebens 1987). Furthermore, there is a last-male sperm precedence which often causes males to invest in prolonged mate guarding following copulation (Goshima et al. 1996). This opportunity cost prevents a male from remating in a given reproductive cycle and may therefore represent a relatively high mating investment by males (L. T. Reaney & P. R. Y. Backwell, unpublished data). The OSRs of fiddler crab populations, on the other hand, are highly male biased (Nobbs & McGuinness 1999), which strongly limits a male's potential benefit from being choosy. In this study, we investigated whether a trade-off between the costs and benefits of choosiness selects for male choice of larger females in the fiddler crab *Uca mjoebergi*. We examined this experimentally and tested the idea under natural mate-searching conditions, a context seldom examined in male mate choice studies.

Uca mjoebergi is a small (5.4–15.0 mm) fiddler crab found in large mixed-sex colonies on intertidal mudflats across northwestern Australia (von Hagen & Jones 1989). Each individual defends its own territory comprising a burrow and a small (20-cm diameter) surrounding area of mudflat that is used for feeding and courtship in males. The mating system is characterized by female choice and male–male competition. Reproduction is synchronous and confined to several days either side of neap tide (L. T. Reaney & P. R. Y. Backwell, unpublished data). When females are ready to mate, they leave their territories and wander through the population. Males have a single enlarged claw that they wave at females in a courtship display. Females visit several males before selecting a mate and are known to select males on the basis of body and claw size, wave rate and burrow quality (L. T. Reaney & P. R. Y. Backwell, unpublished data). Mating can occur both on the sediment surface and underground, in the male's burrow (L. T. Reaney & P. R. Y. Backwell, unpublished data). In surface mating, a resident female is courted by a male neighbour or wandering burrowless male. The pair copulate for several minutes at the entrance to the female's burrow before separating. In underground mating, the pair remains inside the burrow until the female extrudes a clutch of fertilized eggs, 1–9 days after mating (L. T. Reaney & P. R. Y. Backwell, unpublished data). Once the clutch is extruded, the female remains underground for approximately 2 weeks while the embryos develop, whereas the male leaves the burrow and wanders away to fight for a new territory. This 1–9-day mate-guarding period prevents the female from remating, which will ensure paternity in a species with last-male sperm precedence (Olsson 1993; Goshima et al. 1996; Preston et al. 2005). Since females extrude their eggs roughly simultaneously (to have them ready for release during the following spring tide), by the time mate-guarding males have emerged from their burrows, the mating activity has ended for that reproductive cycle (L. T. Reaney & P. R. Y. Backwell, unpublished data). Males will not have the option of remating. This relatively high investment in the present mating may encourage males to be selective in their choice of females.

We examined the ability of males to discriminate between females and determined whether they use this ability under natural conditions. We tested the following predictions: (1) larger females are more valuable mates since they produce larger clutches of eggs; (2) males can discriminate between females based on their body size; and (3) males preferentially court larger females and/or reject smaller females. We also determined the potential of attracting a second female (a possible cost of rejecting a mate) by examining the OSR.

METHODS

We conducted the study in the mangroves of East Point Reserve, Darwin, Australia from September 2005 to January 2006. Observations were made 2 h before and 2 h after low tide, during periods of peak mating activity several days either side of neap tide. We used carapace width as a measure of crab size in our analyses. All summary statistics are presented as mean ± SE unless otherwise indicated.

Female Fecundity

We determined the clutch size of 33 females. We followed mate-searching females until they mated. Surface-mated females were collected immediately after they separated from their mate. When females mated underground, a plastic container (11 cm in diameter; 6 cm high) was placed over the burrow entrance and anchored to the substrate with metal stakes (10 cm long). During the 1–9-day mate-guarding period the containers were regularly checked for the male, which abandons his burrow when the female extrudes her eggs. When the male was present in the container, the gravid female was dug out from inside the burrow. Any wandering burrowless females found to be gravid were also collected. Gravid females were taken to the laboratory where we measured their carapace width, and housed them individually in small plastic containers (9 × 7 cm and 5 cm high) with an undefined volume of sea water (changed daily) and a rock platform until they released their larvae. The larvae were suspended in a total of 60 ml of sea water and stirred thoroughly while a 2-ml subsample was removed. The larvae in the subsample were counted on a dissecting microscope and used to estimate the total clutch size. We checked the repeatability of the larval counts by taking three measures from 23 of the clutches.

Male Discrimination Ability: Female Size

We conducted two types of discrimination trials, simultaneous and sequential. In both trials, a territory-holding adult male was randomly selected and visually isolated

from the population with a circular 4-cm-high opaque shield (40 cm in diameter). The male was then presented with two females, either simultaneously ($N = 25$) or sequentially ($N = 20$). The females were tethered, with cotton thread glued to the carapace and fastened to a nail placed in the mud, 15 cm from the male's burrow entrance. In simultaneous trials, the females were randomly positioned 180° apart. Following a settling period of roughly 1–2 min the male would emerge from his burrow. If he did not emerge during this time we abandoned the trial. Immediately after the male first emerged from his burrow, we videorecorded his behaviour using a camera (Sony TRV16E) on a tripod directly overhead. Filming ceased after 5 min. Each male was presented with a large and a small female (in a random order in sequential trials). Females were considered large if they fell in the top third of the female population size distribution, and small if they fell in the lowest third (T. Detto, unpublished data: range in carapace width of female population 6.5–11 mm, $N = 183$; 'large' ≥ 9.5 mm; 'small' ≤ 8.0 mm). For the sequential trials, a 10-min interval followed the original 5-min trial, after which the male was presented with the alternative large/small female. Each female was used in one trial only. Male carapace width was measured on completion of the experiment. From the video, we calculated and pooled the time the male spent courting and surface mating with a female and counted the waves given to each of the females. When courting a female, the male turns to face her and waves directly at her. Males would also approach females and use their walking legs to probe their abdomens, and/or mount them from the rear, and feed from their carapaces during courtship. We also measured the total (cumulative) time that females spent moving during the simultaneous trials.

Natural Courtship and Female Rejections

We videorecorded naturally wandering females ($N = 46$) as they moved through the population visiting potential mates. For each female, we filmed the full courtship sequence by a single male, from the initiation to cessation of waving. We then captured and measured the male and female. From the video, we timed the duration of the interaction, calculated the time a male spent courting and surface mating with the female, and counted the waves given to the female.

While watching females searching for mates, we documented every case of male rejection observed. A rejection was noted when a female approached a waving male and, during the final stages of courtship, the male refused the female entry into his burrow. Standing over his burrow entrance, the male faced perpendicular to the female and, with his claw extended at 90° out to his side, often hit her. After the female moved away we marked the burrow of the rejecting male with a small flag. To determine whether the female was sexually receptive and searching for a mate, we watched her behaviour after her rejection. It is relatively easy to track a mate-searching female since she is continually surrounded by avidly waving males. We considered the female to be 'receptive' if she continued to visit

courting males and eventually selected a male with whom she mated. Mate-searching females almost always end their search by selecting and mating with a male (L. T. Reaney & P. R. Y. Backwell, unpublished data). Females that continued to sample but did not go on to mate or females that immediately went in search of empty burrows were recorded as 'nonreceptive'. We also documented the behaviour of the rejecting male, noting whether he waved at the next wandering female encountered. Both male and female were captured and measured after the observations were complete.

Operational Sex Ratio

We determined the OSR in three ways. First, we counted the males and females present on the surface during a 10-min observation period for 30 randomly selected plots (1 m^2). In the same plots, we also counted the waving males and mate-searching females that were in the plot at any time during a 10-min observation period. Finally, we marked the burrows of 35 randomly selected males and observed each for a 30-min period during which we counted the females that approached (walked towards) and visited (entered the burrow) each male.

RESULTS

Female Fecundity

Clutch size was positively correlated with female body size (Pearson correlation: $r_{31} = 0.59$, $P < 0.001$; Fig. 1). The larval counts were highly repeatable (one-way ANOVA: $F_{22,46} = 14.7$, $P < 0.001$).

Male Discrimination Ability: Female Size

When presented simultaneously with a large and a small female, males spent more time courting and surface mating with the larger female (large: $\overline{X} \pm \mathrm{SD} = 107.78 \pm 18.20$ s;
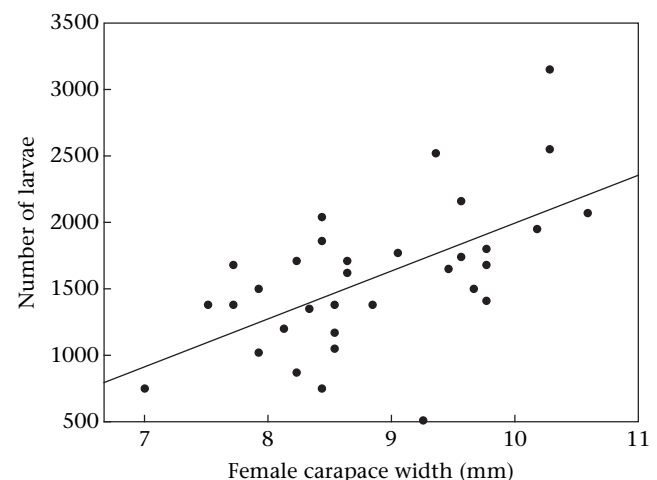
Figure 1. Relation between a female's carapace width (mm) and the number of larvae she produces.

small: 38.37 ± 12.81 s; Wilcoxon signed-ranks test: $Z = -2.30$, $N = 25$, $P < 0.05$). They also directed more waves to the large female (large: 19.64 ± 3.36 per 5 min; small: 8.72 ± 2.89 per 5 min; $Z = -2.21$, $N = 25$, $P < 0.05$). This difference was not due to differing levels of activity between small and large females (paired t test: $t_{24} = -0.737$, $P = 0.468$).

Male preference for large females was weaker in the sequential preference trials. When we examined the male response to the first female presented (either large or small), we found no difference in the time males spent courting and surface mating (student's t test: $t_{18} = -0.89$, $P = 0.39$) or the number of waves given ($t_{18} = -0.42$, $P = 0.68$). When presented sequentially with a large and a small female (in a random order), males could potentially alter their courtship effort in the second presentation depending on their experience during the first presentation. We found that males presented first with a large female spent significantly more time courting and surface mating (paired t test: $t_9 = -4.31$, $P < 0.01$) and gave her significantly more waves ($t_9 = -2.98$, $P < 0.05$) than the subsequent small female (Fig. 2). Males, however, did not intensify their courtship of large females when they were presented after a small female. There was no difference in the time spent courting and surface mating ($t_9 = -0.07$, $P = 0.94$) or the number of waves given ($t_9 = 0.52$, $P = 0.61$) to large and small females (Fig. 2).

Natural Courtship and Female Rejections

Males did not spend more time courting and surface mating with larger females (Pearson correlation: $r_{28} = 0.14$, $P = 0.45$), nor did they give larger females more waves ($r_{28} = 0.30$, $P = 0.11$). However, to control for the duration of the interaction, we divided the total number of waves by the total duration of the interaction to give an average wave rate. There was a significant positive correlation between average wave rate and female carapace width (partial correlation: $r = 0.54$, $N = 30$, $P < 0.001$; Fig. 3).

Males rarely rejected approaching females. We documented only 16 rejections out of hundreds of visits observed over seven breeding cycles (3.5 months). In all 16 cases, the male proceeded to court other wandering females. The rejected females, however, never went on to mate with another male, but all occupied empty burrows, dug new burrows or evicted a resident to take-over its burrow. Males thus appeared to reject only nonreceptive females.

Operational Sex Ratio

There were 10.7 surface-active males to each surface-active female in the plots ($N = 30$ plots). This differs significantly from a 1:1 ratio (Fisher's exact test: $P < 0.05$). The OSR was even more male biased when measured in terms of sexually receptive crabs: there were, on average, 45.0 waving males for each mate-searching female ($N = 30$ plots). Furthermore, during the 30-min observation periods, none of the 35 males were approached or visited by a mate-searching female.
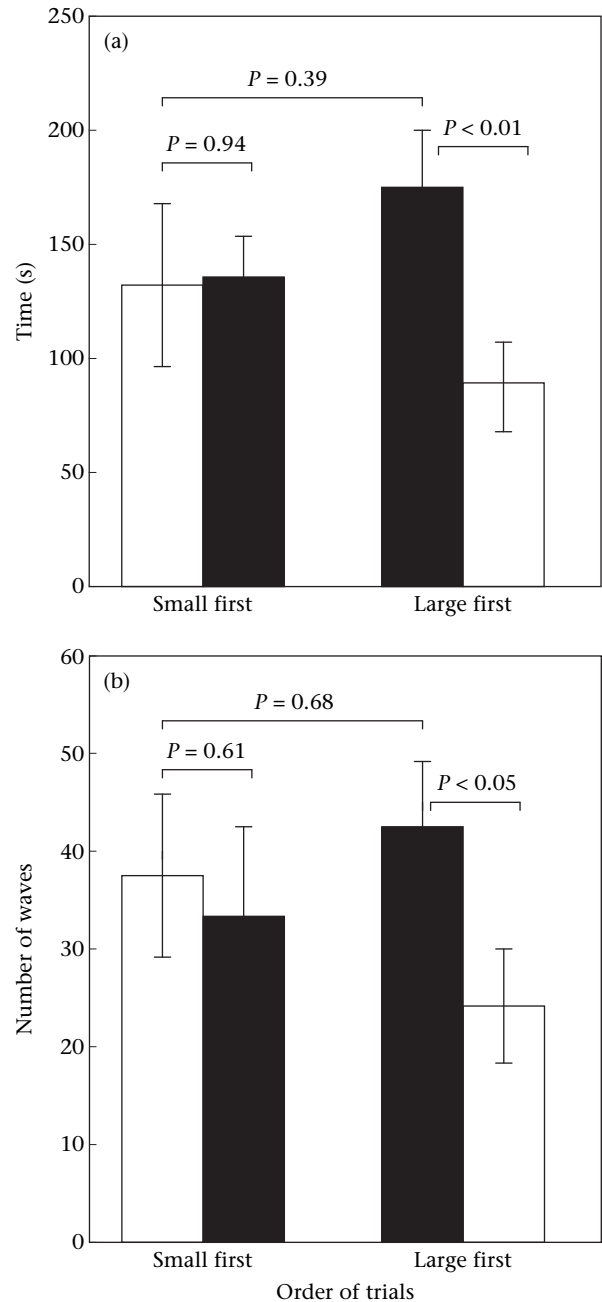
Figure 2. Mean $\pm$ SE (a) time spent courting and (b) number of waves given during sequential courtship trials. Trial order is shown on the X axis. ■: Males' responses to large females; □: males' responses to small females.

DISCUSSION

Female body size correlated positively with fecundity in *U. mjoebergi*, as in other fiddler crab species (e.g. *Uca rapax*: Greenspan 1980; *Uca lactea*: Murai et al. 1987; *Uca tetragonon*: Goshima et al. 1996). Larger females produced more eggs per clutch, probably because they had more body resources to maintain a pregnancy (Jorgenson et al. 1993; Saether & Heim 1993) or possessed a greater internal volume for amassing eggs (Bondiuriansky & Brooks 1998). This variation in female quality means that males can
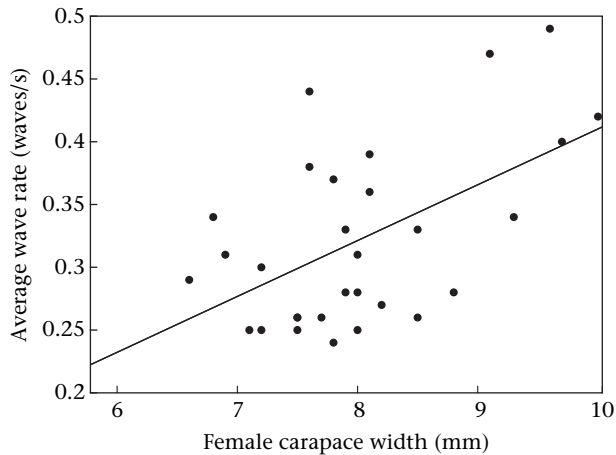
Figure 3. Relation between female carapace width (mm) and average wave rate. (Note that two points coincide at $X = 7.5$, $Y = 0.26$.)

increase their fitness by selectively mating with large females. To do this, males must be capable of distinguishing between large and small females. In simultaneous preference trials we showed that males can differentiate between females of different size and that they spent more time courting the larger female in the pair. They also directed more waves at the larger female. These differences in male behaviour are unlikely to be caused by differences in the visibility of the females since both were tethered close to the male and would have been clearly visible to him as he emerged from his burrow (Land & Layne 1995). In fact, males of this species are able to recognize their neighbours at distances greater than those used here (Backwell & Jennions 2004).

Under natural conditions, however, males would seldom encounter two mate-searching females simultaneously. In our second set of experimental trials, we presented males with a more natural sequential choice of large and small females. Examining only the first trial for each male, we showed that the male preference for large females was weak. This effect has previously been shown in mollies, *Poecilia latipinna* (MacLaren & Rowland 2006) and sticklebacks, *Gasterosteus aculeatus* (Rowland 1982) and is thought to demonstrate the importance of local density and the context of potential mate encounters in mate choice. Bakker & Milinski (1991) also showed that responsiveness to potential mates can be influenced by the order in which they are encountered. In our study we found that, when a male courted a large female first, he decreased his courtship effort (less time and fewer waves) when subsequently presented with a small female. When he courted a small female first, he did not adjust his courtship effort for the subsequent large female, indicating that the decrease was not due to depleted energy reserves. The strength of male mate choice under natural conditions may therefore be influenced by previous encounters with mate-searching females and is probably not a simple invariant preference.

Our documentation of naturally courting males indicates that males did not spend more time courting larger females. When we controlled for the duration of the courtship interaction, however, we found that males

waved more to larger females. This effect is unlikely to be caused by differences in female responsiveness since there was no relation between female size and the duration of courtship. Thus, males appear to be investing more effort in courting larger females. Bonduriansky (2001) argued that the effort a male expends in courting a specific potential mate is an accurate reflection of mate preference, since males experiencing a male-biased OSR must compete for access to females and may lose mating opportunities to more 'eager' courting males. Males never rejected mate-searching females, regardless of their size. In fact, the size distribution of mated females is very similar to that of the female population as a whole (L. T. Reaney & P. R. Y. Backwell, unpublished data). While males may preferentially court large females, they will not forego a mating opportunity with a small female. This is not surprising since the highly male-biased OSR means that males are unlikely to attract a second female after rejecting the first. By accepting all females available to them, but intensifying courtship towards larger more fecund females, males may be matching the cost of courtship to the potential benefits gained (Real 1991; Itzkowitz et al. 1998).

Male mate choice makes adaptive sense when female quality is variable and both male mating investment and the probability of encountering additional females are high (Kokko & Johnstone 2002). We have shown that males would benefit from mating with larger females because of their increased fecundity. In this species, male mating investment is high because of prolonged mate guarding, which prevents males from remating within a reproductive cycle. Both of these factors suggest that males should selectively court and mate with larger females. The extremely low encounter rate with females, however, appears to temper male choosiness. Although they preferentially court large females, males do not avoid mating opportunities with females of lower reproductive value. The high reproductive investment and/or the potential benefits of mate quality variance may have selected for male mate choice in this species, despite the bias in OSR towards an excess of males. Thus, male *U. mjoebergi* not only engage in competition for matings but also show mate choice. These findings contribute to a growing body of evidence which suggests that the notion of one sex being discriminating and the other competitive is overly simplistic.

References

Backwell, P. R. Y. & Jennions, M. D. 2004. Coalition among male fiddler crabs. *Nature*, **430**, 417.

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. 1998. Synchronized courtship in fiddler crabs. *Nature*, **391**, 31–32.

Bakker, T. C. M. & Milinski, M. 1991. Sequential female choice and the previous male effect in sticklebacks. *Behavioral Ecology and Sociobiology*, **29**, 205–210.

Bateman, A. J. 1948. Intra-sexual selection in *Drosophila*. *Heredity*, **2**, 349–368.

Berglund, A., Rosenqvist, G. & Svensson, I. 1986. Reversed sex roles and parental energy investment in zygotes of two pipefish (Syngnathidae) species. *Marine Ecology, Progress Series*, **29**, 209–215.

Bisazza, A., Marconato, A. & Marin, G. 1989. Male mate preference in the mosquitofish *Gambusia holbrooki*. *Ethology*, **83**, 335–343.

Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biological Reviews*, **76**, 305–339.

Bonduriansky, R. & Brooks, R. J. 1998. Male antler flies (*Protopiophila litigate*; Diptera: Piophilidae) are more selective than females in mate choice. *Canadian Journal of Zoology*, **76**, 1277–1285.

Côte, I. M. & Hunte, W. 1989. Male and female mate choice in the redlip blenny: why bigger is better. *Animal Behaviour*, **38**, 78–88.

Craig, A. S., Herman, L. M. & Pack, A. 2002. Male mate choice and male–male competition coexist in the humpback whale (*Megaptera novaeangliae*). *Canadian Journal of Zoology*, **80**, 745–755.

Cunningham, E. J. A. & Birkhead, T. R. 1998. Sex roles and sexual selection. *Animal Behaviour*, **56**, 1311–1321.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. 2nd edn. London: J. Murray.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.

Goshima, S., Koga, T. & Murai, M. 1996. Mate acceptance and guarding by male fiddler crabs *Uca tetragonon* (Herbst). *Journal of Experimental Marine Biology and Ecology*, **196**, 131–143.

Greenspan, B. N. 1980. Male size and reproductive success in the communal courtship system of the fiddler crab *Uca rapax*. *Animal Behaviour*, **28**, 387–392.

Gwynne, D. T. 1981. Sexual difference theory: mormon crickets show role reversal in mate-choice. *Science*, **213**, 779–780.

von Hagen, H. O. & Jones, D. S. 1989. The fiddler crabs (Ocypodidae: *Uca*) of Darwin, Northern Territory, Australia. *The Beagle*, **6**, 55–68.

Itzkowitz, M., Draud, M. J., Barnes, J. L. & Haley, M. 1998. Does it matter that male beaugregory damselfish have a mate preference? *Behavioral Ecology and Sociobiology*, **42**, 149–155.

Jennions, M. D. & Backwell, P. R. Y. 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biological Journal of the Linnean Society*, **57**, 293–306.

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.

Jones, K. M., Monaghan, P. & Nager, R. G. 2001. Male mate choice and female fecundity in zebra finches. *Animal Behaviour*, **62**, 1021–1026.

Jorgenson, J. T., Festa-Bianchet, M., Lucherini, M. & Wishart, W. D. 1993. Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. *Canadian Journal of Zoology*, **71**, 2509–2517.

Koga, T., Henmi, Y. & Murai, M. 1993. Sperm competition and the assurance of underground copulation in the sand-bubbler crab *Scopimera globosa* (Brachyura: Ocypodidae). *Journal of Crustacean Biology*, **13**, 134–137.

Kokko, H. & Johnstone, R. A. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 319–330.

Land, M. & Layne, J. 1995. The visual control of behaviour in fiddler crabs I. Resolution, thresholds and the role of the horizon. *Journal of Comparative Physiology*, **177**, 81–90.

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.

Manning, J. T. 1975. Male discrimination and investment in *Asellus aquaticus* (L) and *A. meridianus racovitsza* (Crustacea: Isopoda). *Behaviour*, **55**, 1–14.

Murai, M., Goshima, S. & Henmi, Y. 1987. Analysis of the mating system of the fiddler crab, *Uca lactea*. *Animal Behaviour*, **35**, 1334–1342.

Nobbs, M. & McGuinness, K. A. 1999. Developing methods for quantifying the apparent abundance of fiddler crabs (Ocypodidae: *Uca*) in mangrove habitats. *Australian Journal of Ecology*, **24**, 43–49.

Olsson, M. 1993. Male preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*). *Behavioral Ecology and Sociobiology*, **32**, 337–341.

Owens, I. P. F. & Thompson, D. B. A. 1994. Sex differences, sex ratios and sex roles. *Proceedings of the Royal Society of London, Series B*, **258**, 93–99.

Parker, G. A. & Simmons, L. W. 1996. Parental investment and the control of sexual selection: predicting the direction of sexual competition. *Proceedings of the Royal Society of London, Series B*, **263**, 315–321.

Preston, B. T., Stevenson, I. R., Pemberton, J. M., Coltman, D. W. & Wilson, K. 2005. Male mate choice influences female promiscuity in Soay sheep. *Proceedings of the Royal Society of London, Series B*, **272**, 365–373.

Real, L. A. 1991. Search theory and mate choice. II. Mutual interaction, assortative mating, and equilibrium variation in male and female fitness. *American Naturalist*, **138**, 901–917.

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.

Roberts, J. A. & Uetz, G. W. 2005. Information content of female chemical signals in the wolf spider, *Schizocosa ocreata*: male discrimination of reproductive state and receptivity. *Animal Behaviour*, **70**, 217–223.

Rowland, W. J. 1982. Mate choice by male sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, **30**, 1093–1098.

Saether, B. & Heim, M. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. *Journal of Animal Ecology*, **62**, 482–489.

Sargent, R. C., Gross, M. R. & van den Berghe, E. P. 1986. Male mate choice in fishes. *Animal Behaviour*, **34**, 545–550.

Sebens, K. P. 1987. The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics*, **18**, 371–407.

Stuart-Fox, D. M. & Whiting, M. J. 2005. Male dwarf chameleons assess risk of courting large, aggressive females. *Biology Letters*, **1**, 231–234.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man 1871–1971* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine Press.

Verrell, P. A. 1995. Males choose larger females as mates in the salamander *Desmognathus santeetlah*. *Ethology*, **99**, 162–171.