



More signalling for earlier mating: conspicuous male claw waving in the fiddler crab, *Uca perplexa*

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The male courtship display of the fiddler crab *Uca perplexa* is a conspicuous claw waving that is directed at females to attract them to their burrows for mating. Like most other fiddler crabs, this species has an approximately biweekly reproductive cycle with mating spread over about 10 days. However, most mating takes place in the 3 days immediately preceding new and full moons. We examined the relation between the time males spend waving to females and the time they subsequently spend underground in their burrow, guarding their mates until they ovulate and then fertilizing their eggs. Early in the mating period, males courted females for about 3–5 s before the female entered their burrows, and males guarded these females for 3–5 days. During the 3 days of peak mating activity, courting time decreased significantly to about 2 s and guarding time decreased to about 1 day. This pattern cannot be explained by females preferring extended waving periods, decreased female choosiness towards the end of the mating period or variation in male waving over the mating period. We conclude that males of this species modulate their investment in courtship according to changing levels of female responsiveness to courtship.

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Many species have evolved large conspicuous courtship signals. For example, the courtship displays of birds of paradise (Frith & Beehler 1998), the sexual display of peacocks (Petrie et al. 1991) and lyrebirds (Lill 1979) and the claw-waving displays of fiddler crabs (Crane 1975) are conspicuous and energy consuming (Dawkins 1993). Over small timescales, however, one would expect males to modulate their investment in courtship according to changing conditions. For example, courtship signals in the guppy, *Poecilia reticulata*, change with social conditions (the presence of a second male is sufficient to increase display frequency, Farr & Herrnkind 1974) and ecological conditions (e.g. in the presence of a predator, Magurran & Seghers 1990). Courtship behaviour may also be affected by other variables. For example, the increasing risk of suboptimal mating caused by temporal constraints reduces female choosiness over the brief period of mating activity in fiddler crabs (Backwell & Passmore 1996); males may mate with less receptive females when

the sex ratio is more male biased in isopods and gammarid amphipods (Jormalainen 1998); and levels of sexual conflict between males and females may increase courtship behaviour (Parker 1979). When females are more choosy, less responsive or unwilling to mate, males are likely to use their signals more frequently, at higher intensity and/or for longer periods.

We investigated the effect of a change in female responsiveness, which could be related to her sexual receptivity, on the time males spend signalling to females. Individuals of the fiddler crab *Uca perplexa* live in burrows in mixed-sex colonies on intertidal mudflats; each individual has its own burrow. Each day during the 10-day mating period, which occurs every 2 weeks from April to August, males produce a courtship display in which the single enlarged claw is repetitively waved to attract females (Nakasone & Murai 1998). Wandering females move through the population of displaying males, while males compete to attract females to their burrows. Females respond to some of the displaying males by approaching them. When a male is approached, he starts high-intensity waving in which he unflexes his large claw and raises and lowers it several times. Along with the waving of the large claw, the male also raises and lowers his small claw as well as one or two of his walking legs. The male descends into his burrow when the female is at a mean

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distance \pm SE of 8.9 ± 0.45 cm from it (Nakasone & Murai 1998). The female then does one of three things: (1) she passes by the male, in which case she continues to wander through the population of displaying males; alternatively, (2) she continues to approach the male, touches his burrow entrance with a few walking legs, then moves on; or (3) she responds to the male by approaching his burrow, touching its entrance with her walking legs and then descending into it and remaining there with the male. In this case, the male emerges to plug the burrow entrance and mating occurs underground soon afterwards (Nakasone & Murai 1998). The pair spends 1–5 days underground until the female ovulates. This is the 'guarding period'. By preventing the female from having access to other males during this time, males increase their chances of fertilizing the ovulated eggs (Koga et al. 1993). Immediately after the female has ovulated, the male leaves the burrow. The female remains in the burrow, incubating her eggs for 14–15 days and rarely emerges to feed or engage in surface activities (Nakasone & Murai 1998).

The single large claw of the male fiddler crab has evolved for signalling and is probably involved in sexual selection. It is waved rhythmically in the air at females, suggesting that claw waving is a conspicuous stimulus to females. We examined the time that males spend waving at females at different times of the mating period. Early in the mating period, males will encounter females with relatively unripe ovaries. These females should be reluctant to mate because early mating means long guarding durations and therefore decreased feeding time before the long incubation period. We therefore predicted that the signalling period should be longest at this time. Later in the mating period, females do not benefit by delaying mating and we predicted that a relatively short signalling period would then suffice to attract a female to mate.

METHODS

We studied *U. perplexa* on an intertidal mudflat on the Okukubi River, Okinawa, Japan. Observations were made from June to August 1997, 1999 and 2000. We studied males with a carapace width (CW) of 15–17 mm and females with a CW of 9–15 mm. These fell within the size range of mated males and females previously reported (mated male CW: $\bar{X} \pm \text{SE} = 15.15 \pm 0.33$ mm, range 11.8–18.6 mm; mated female CW: 12.34 ± 0.27 mm, range 9.7–15.0 mm; Nakasone & Murai 1998).

We followed wandering females as they moved through the population and approached males. For each female, we documented the time each male spent waving to her. The measurement started when the male unflexed his large claw before giving the first wave, and ended when he flexed his claw shortly before entering his burrow. We selected for analysis the first male that the female visited (by touching his burrow). This male was called the focal male. We then continued to follow the female until she selected and mated with a male. We eliminated those cases in which the female did not select a mate within the first hour of observation or occupied an empty burrow. Occasionally, males would stop waving and flex their

claws when the female temporarily stopped moving, began feeding or entered a neighbouring burrow but they would resume waving once the female continued to move. We did not use these as focal males.

When the female selected a male and entered his burrow to mate with him, we covered the burrow entrance with a mesh cage (10 cm diameter, 5 cm high, fixed to the sediment surface) so that we could capture the male when he left the burrow after the female ovulated. By observing when the male left the burrow, we could calculate the mate-guarding period between mating and ovulation. We measured mate-guarding periods to allow us to judge the reproductive state of females' ovaries: those with ripe ovaries should ovulate shortly after mating, whereas those with relatively unripe ovaries should require more time to ovulate.

We supplemented the data set ($N = 54$ matings) with an additional 27 matings that we observed when we observed the duration of waving (1997, 1999, 2000). For these additional matings, we did not record the time spent waving but did have measurements for guarding periods. We used the combined data set ($N = 81$ matings) to examine the relation between mating date and mate-guarding duration. We also calculated when mating occurred relative to the full or new moon ($N = 81$ matings). For the data set in which we had male waving periods ($N = 54$ matings), we examined the relation between the mate-guarding duration classified as 1, 2 or 3+ days and how long the focal male spent waving to the female.

After examining the above data, we found that further information was needed. If females were more likely to use multiple-choice cues to choose males earlier than later in the mating cycle, this could potentially explain differences in the waving period durations over the mating cycle. First, we determined whether females selectively visited males that waved for longer periods. To do this, we followed a further 66 mate-searching females using the methods described above. We measured the waving period duration for males that the females visited (i.e. touched their burrows) and for those that the females did not visit (passed without touching the burrow entrance); both types of male entered their burrows (i.e. responded to the female as if they were going to be visited) before the female touched the burrow or passed by. For each wandering female we collected data on multiple visits and nonvisits (one to five males in each category). We calculated two averages for each female: the waving period duration of visited and nonvisited males. We compared these averages over the 66 females to determine whether visited males were those that had waved for longer during early, middle and late periods of the mating cycle. Second, females should be choosier earlier in the mating cycle. When each female approached vigorously waving males and then one of these males entered his burrow, we observed this male and noted whether he was visited or not by the focal female (i.e. whether the female touched his burrow or not). Using only those females that approached a sufficient number of males (a minimum of five was needed to calculate a proportion accurately), we calculated the proportion of males visited by each female (i.e. number of males visited/number of males approached; $N = 71$ females). We defined an approach as one resulting in the

male entering his burrow. We compared the proportion of visits for early, middle and late periods of the mating cycle to determine whether females were less likely to visit males earlier than later in the mating cycle. The mate-searching females that we followed mated within the first hour of observation; hence, it is unlikely that we followed any female more than once in a 10-day mating cycle.

To see whether the time each male spent waving was related to the phase of moon, we followed nonreceptive wandering females that passed males without touching their burrows and eventually occupied empty ones. We measured the duration of waving directed at these females by the males they passed. For each wandering female, we collected data on multiple nonvisits (one to five males). We covered the entrance of burrows occupied by wandering females, using the methods described above, and excluded cases where the female ovulated within 5 days. Female crabs near ovulation readily lay unfertilized eggs (Yamaguchi 1998). Those that did not ovulate within 5 days were not in reproductive condition (Murai et al. 1987). By measuring waving towards females that were not pre-ovigerous in the current tidal cycle, we were able to exclude the effect of variation in response threshold among receptive females on the duration of waving.

Data on guarding duration were not normally distributed and could not be transformed to fit a normal distribution. We therefore used standard nonparametric tests. The data on male waving periods (in 1997, 1999 and 2000) were transformed ($1/x$) since this improved normality and eliminated heterogeneity of variances (Kolmogorov-Smirnov test: $c^2 = 0.926$, $P > 0.999$; Bartlett's test: $F = 1.739$, $P = 0.175$). Arcsine-transformed variables on proportion of males visited by the female were distributed normally and had equal variances (Kolmogorov-Smirnov test: $c^2 = 1.803$, $P = 0.812$; Bartlett's test: $F = 1.101$, $P = 0.332$). All statistics are two tailed and means are given \pm SE.

RESULTS

Matings occurred around the new and full moons, ranging from 6 days before the new/full moon to 3 days after the new/full moon (1.296 ± 0.189 days before new/full moon; Fig. 1). Ovulation was also concentrated around the new or full moon (1 day before to 4 days after the new/full moon, 0.765 ± 0.128 days after the new/full moon; Fig. 1). Matings occurred over a 10-day period, whereas ovulation was concentrated over 6 days.

The earlier a male mated, the longer the guarding duration (Spearman rank correlation: $r_s = -0.726$, $Z = 6.493$, $N = 81$, $P < 0.0001$; Fig. 2). Males that attracted females later in the mating period guarded them for less time.

Males waved for longer periods to females that required longer guarding durations (ANOVA: $F_{1,51} = 5.283$, $N = 54$, $P = 0.008$; Fig. 3). Males spent significantly more time waving at females that took 3 or more days to ovulate than they did to females that took either 1 day (Fisher's protected least-significant difference, PLSD: $P = 0.01$) or 2 days (Fisher's PLSD: $P = 0.05$).

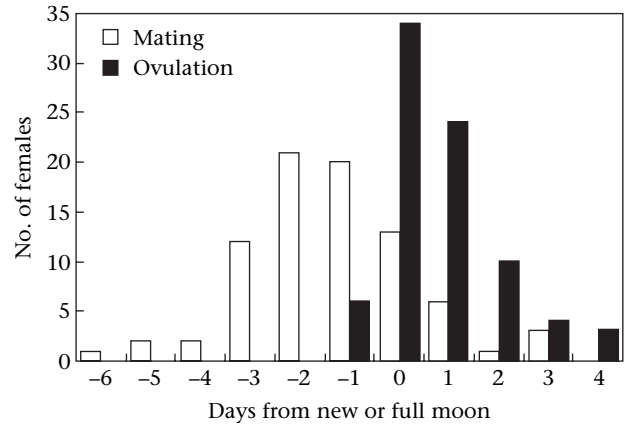


Figure 1. Number of females that mated or ovulated in relation to the new or full moon.

Females did not selectively visit males that waved for longer periods. In fact, males waved for longer periods at females that did not visit them. This was true during the early, middle and late parts of the mating cycle, although the difference was significant only during the middle and late parts of the cycle (early: 3–6 days before the new/full moon: 4.046 ± 0.261 s, 3.672 ± 0.213 s; paired t test: $t_{16} = 1.123$, $P = 0.278$; middle: 1–2 days before the new/full moon: 2.490 ± 0.239 s, 2.004 ± 0.137 s; $t_{21} = 2.179$, $P = 0.041$; late: 0–3 days after the new/full moon: 2.199 ± 0.167 s, 1.567 ± 0.094 s; $t_{26} = 3.404$, $P = 0.002$).

Females were not more choosy earlier in the mating period. The proportion of males visited by each female was not different between the early, middle and late parts of the mating cycle (early: 3–6 days before new/full moon: 0.679 ± 0.044 , $N = 16$; middle: 1–2 days before new/full moon: 0.619 ± 0.027 , $N = 26$; late: 0–3 days after new/full moon: 0.650 ± 0.026 , $N = 29$; $F_{2,68} = 0.767$, $P = 0.468$).

There was no significant relation between the time spent waving and the number of days (–6 to +4) before and after full/new moon (Spearman rank correlation: $r_s = -0.118$,

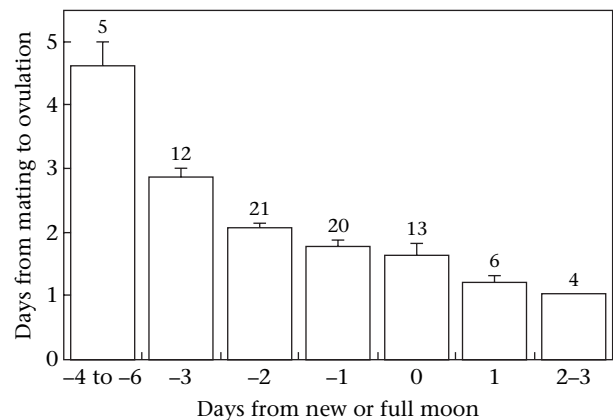


Figure 2. Days ($\bar{X} \pm$ SE) from mating to ovulation for females that mated, in relation to the new or full moon. Number of females is given above the bars.

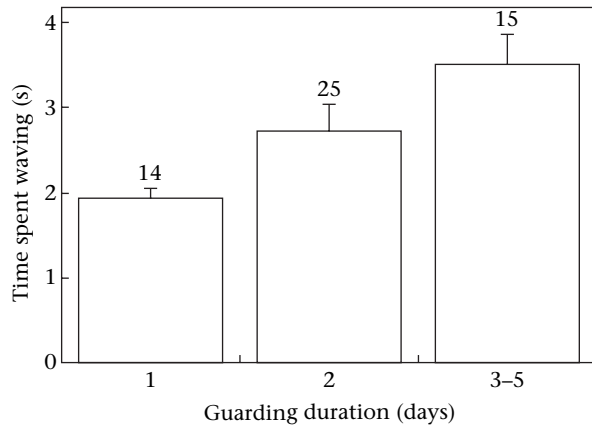


Figure 3. Time ($\bar{X} \pm \text{SE}$) that males spent waving to females that needed a 1-, 2-, or 3–5-day guarding period. Number of females is given above the bars.

$N = 86$, $P = 0.276$). The duration was thus not related to the phase of moon.

DISCUSSION

Males attracted females for mating over a relatively long period of 10 days, and they guarded these females until ovulation, which occurred 1–5 days later. Females that selected a male and mated with him early in the mating period were also those that required the longest guarding periods. This resulted in ovulation being concentrated over a narrower period than mating (6 versus 10 days). Christy (1978) similarly reported a significant reduction in variance between the temporal distributions of mating in *Uca pugilator* and larval release 2 weeks later. We also found that males spent more time waving to females that required longer guarding durations.

During the *U. perplexa* annual breeding season, there are two peaks of mating activity, one at the end of May and the other in mid-July. In the population studied here, 50% or less of the females are ovigerous during these peaks (Nakasone & Okadome 1981). The operational sex ratio is therefore highly male biased, even at the peaks of female mating activity. Within the 2-week tidal cycle, the number of gravid females (those ready for mating) decreases as the number of already mated females increases over the cycle. When there is an excess of males, some remain unmated. If a male is unlikely to attract a second mate and his current mate is likely to mate again if abandoned, then it may be best for males to mate whenever the opportunity arises and guard until the female ovulates.

Male spider crabs *Inachus phalangium* also guard females between mating and spawning (Diesel 1986). Guarding costs males time that they could spend in searching for new mates. To minimize their costs, relatively larger males chased guarding males away from their females, mated with these females and took over the guarding. This behaviour decreased the male's guarding time (Diesel 1986). Intruding males only occasionally disrupt guarding in *U. perplexa*. This is because, unlike the spider crabs which guard their females on the sea floor, guarding in

U. perplexa occurs underground, in the male's plugged burrow. Intruders rarely succeed in taking over a female from a guarding male (Nakasone & Murai 1998). Since mate-guarding success is high, it would be advantageous for a male to attract a female early in the tidal cycle and to guard her until she ovulates.

An important function of courtship displays is to induce females to mate (Tinbergen 1953; Vinnedge & Verrell 1998). We found that females are slower to respond to a male at the beginning of the mating cycle and faster to respond to them at the end of the cycle. Females did not selectively visit males that waved for longer periods. This suggests that females took longer to respond to a waving male earlier in the mating cycle, but the length of waving did not affect the decision to visit a particular male. This distinction was also made by Maklakov et al. (2003) in discriminating between sexual arousal and quality signalling in the courtship behaviour of the spider *Stegodyphus lineatus*.

Our study on *U. perplexa* provided no evidence that females are choosier at the beginning and less choosy at the end of the mating cycle. However, in *U. annulipes*, Backwell & Passmore (1996) found that choosiness declined over the brief period of mating activity in each semilunar cycle. *Uca* females time larval release to coincide with the following nocturnal spring tide (Morgan & Christy 1995) and must therefore leave sufficient time for embryonic development after mating. Backwell & Passmore (1996) suggested that, at the start of the mating period (when time constraints are minimal), females are probably more selective. However, this is true only because the species they studied had a fixed guarding period and the constraint was in the time remaining for embryonic development. In *U. perplexa*, the guarding duration is not constant, but declines over the mating period. It is unlikely that these early-mating females are 'more' choosy than later-mating females, because earlier-mating females are 'less' constrained by time.

Males spent more time stimulating females with less well-developed ovaries (less responsive females) to enter their burrows to mate, whereas females with more developed ovaries were more responsive and required less stimulation by waving males. Although males benefit by attracting females at any stage of ovary development, they pay a cost in missed days for feeding when they attract females that require long guarding periods. Neither males nor females leave the burrow during the guarding period, and, since they eat microorganisms and detritus on the sediment surface (Dye & Lasiak 1986), they are unable to feed during this time. Loss of feeding time is especially important to females since they will not feed during the following 2 weeks of incubation and will have to compensate for the lost nutritive reserves after larval release.

To induce reluctant females to mate early, males need to spend long periods waving to them. Females need little stimulation to mate towards the end of the mating period, and males subsequently need to spend little time waving at these females to induce their response. This study is the first to show that males spend more time stimulating females to mate when the female is less responsive to male courtship, because sexual selection favours males wanting to mate.

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