



Elevated predation risk changes mating behaviour and courtship in a fiddler crab

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The fiddler crab, *Uca beebei*, lives in individually defended burrows, in mixed-sex colonies on intertidal mud flats. Avian predation is common, especially of crabs unable to escape into burrows. Mating pairs form in two ways. Females either mate on the surface at their burrow entrance ('surface mating') or leave their own burrow and sequentially enter and leave ('sample') courting males' burrows, before staying in one to mate underground ('burrow mating'). We tested whether perceived predation risk affects the relative frequency of these mating modes. We first observed mating under natural levels of predation during one biweekly, semi-lunar cycle. We then experimentally increased the perceived predation risk by attracting grackles (*Quiscalus mexicanus*) to each half of the study site in two successive biweekly cycles. In each experimental cycle, crabs were significantly less likely to mate on the side with more birds. Moreover, on the side with elevated predation risk, the number of females leaving burrows to sample was greatly reduced relative to the number of females that surface-mated. Males waved less and built fewer mud pillars, which attract females, when birds were present. We discuss several plausible proximate explanations for these results and the effect of changes in predation regime on sexual selection.

Keywords: fiddler crabs; female choice; mating tactics; predation; sexual selection; *Uca*

1. INTRODUCTION

There is growing awareness of the variability in female mating behaviour (Jennions & Petrie 1997). This can take the form of variation in the propensity to sample mates (Backwell & Passmore 1996), criteria for mate acceptance (Johnstone *et al.* 1996), resistance to forced copulation attempts (Arnqvist 1992), the propensity to mate-choice copy (Dugatkin & Godin 1993), or the frequency of deployment of different sampling tactics (Gibson & Langen 1996). Sometimes discrete mating categories are defined based on male type or mating location. For example, ornithologists distinguish between within-pair copulations with breeding partners and extra-pair copulations with neighbours (Birkhead & Møller 1992). For species that lek, distinctions are drawn between lek matings and matings with territorial males or satellite males away from the lek (Gosling & Petrie 1990; Lanctot *et al.* 1997).

Fiddler crabs (genus *Uca*) provide good opportunities to examine causes of variation in female mating behaviour because there are two kinds of matings: underground, burrow mating and surface mating. In a few species, only burrow mating occurs (e.g. *U. pugilator* (Christy 1983)); in others, only surface mating is reported (e.g. *U. vocans vomeris* (Salmon 1984, 1987)). In several species, however, both mating types occur (e.g. *U. lactea*, *U. tetragonon* (Murai *et al.* 1987, 1995); *U. beebei* (Christy 1987); *U. annulipes*, *U. urvillei* (P. R. Y. Backwell, unpublished

data)). In these species, males defend burrows and court females from the entrance by waving their major claw. Females enter the male's burrow to mate, then remain there for oviposition, incubation and larval release ('burrow mating'). Females that burrow mate must first leave their own burrow and wander on the surface. While wandering, they sequentially enter and leave the burrows of several males ('sampling') before remaining in the chosen male's burrow (Christy & Schober 1994; Backwell & Passmore 1996). Surface mating occurs when a female is approached by a male neighbour or a wandering, burrowless male. The pair copulate on the surface, typically at the entrance to the female's burrow.

Predation risk is greater for a wandering, sampling female than one who stays at her burrow, because fiddler crabs evade predators by retreating into burrows (Crane 1975). Although the act of copulation may be more risky when performed on the surface, this risk is probably far smaller than that the total risk arising from mate searching prior to burrow mating. Wandering females sometimes fail to locate a burrow when frightened by a predator and are therefore prone to being eaten. In contrast, surface-copulating pairs break-up rapidly when a predator approaches and quickly retreat into their respective burrows (personal observations). Females should therefore be sensitive to predation risk and less inclined to leave their burrow when predation risk is unacceptably high.

Here, we experimentally test whether a greater perceived risk of avian predation affects the extent to which female *U. beebei* engaged in burrow and surface

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mating. More specifically, we test whether the relative frequency of burrow mating decreases when there is a greater perceived predation risk. We also test whether elevated predator presence reduces male courtship. We discuss our results in terms of proximate causes of the observed changes in mating behaviour and then consider their wider implications for sexual selection on each sex.

2. METHODS

(a) *Natural history of U. beebei*

Uca beebei lives in mixed-sex colonies on intertidal mud flats (Crane 1975), at an approximately 1:1 sex ratio (T. Koga, unpublished data). Both sexes defend burrows and emerge to surface feed during diurnal low tides. Females engage in both surface and burrow matings. There are no obvious differences between female burrows, sampled males' burrows and male burrows in which females mate, suggesting female choice is not based on burrow quality (Christy & Schober 1994). When a female enters a burrow to mate, the male seals the entrance with a mud plug. He then remains with the female for 1.5 h to 3 d. The female remains for another 12–14 d until larval release. Males wave their major claw to attract females. They also build mud pillars about 15 mm high at their burrow entrance (Christy 1988a). Receptive, wandering females are more likely to initially enter burrows with pillars (Christy 1988b). Food supplementation experiments indicate that pillar building is influenced by male body condition (Backwell *et al.* 1995). Pillars are built anew each day because they are destroyed by the incoming tide.

The study site was on the west bank of the Pacific entrance of the Panama Canal (Christy 1988a). *Uca beebei* occurs in an almost monospecific colony on the central elevated section of the mudflat. Here, the great-tailed grackle, *Quiscalus mexicanus*, is a common and persistent avian predator of *U. beebei*.

(b) *Experimental design*

We observed behaviour for three successive, biweekly, semi-lunar cycles. Daily for days 1–9 of each cycle at 2 h before low tide we divided the mudflat in half by erecting a 50 cm high, 10 m long, cloth fence. Crabs on one side of the fence were unable to see birds or crabs on the opposite side. We used string to delimit six permanent rectangular plots (3.5 m × 2.7 m) on each side of the fence. For the first cycle we obtained baseline data on crab behaviour on each side of the fence. For the second cycle, we attracted birds to the six plots on side A of the mudflat. A small handful of moistened dog food pellets were placed on plastic plates skewered on wooden pegs inserted into the sediment. The plates' rims prevented crabs gaining access to food. Each plot on side A had a plate on each corner. Empty plates were identically positioned on side B. For the third cycle, we reversed the treatment and attracted birds to side B. To allow the grackles sufficient time to become accustomed to the food source, we added food from day 1 of each cycle. Food addition was halted on day 10. The food attracted a large number of grackles (see § 3). Occasionally a bird landed on the side without food. The observer on that side immediately chased off such birds using light, blunt darts from a blowpipe.

Behavioural observations were made from day 4 to day 9 of each cycle. We monitored animals through binoculars at a sufficient distance (>5 m) to avoid disturbing either the crabs or the birds. On day 4, one observer monitored two plots on side A, and another observer two plots on side B. These plots were in mirror positions with respect to the fence. On day 5, the two

observers switched sides and monitored the same two plots their colleague had observed the previous day. On days 6 and 7 and 8 and 9, respectively, two new plots per side were observed. After 6 d, all 12 plots had been monitored twice, once by each observer.

The daily protocol for behavioural data collection was as follows: from 1.5 h before low tide to 1.5 h after low tide, we recorded behaviour during six, sequential 30 min sessions with a standardized protocol. For the first 5 min, each observer counted the total number of birds landing on their side of the fence. In the next 5 min, the observers slowly scanned each plot twice and counted the number of males waving per plot. For the remaining 20 min, each observer continuously monitored each of their two plots and counted the number of surface matings and wandering, 'sampling' females per plot. Sampling females were those who fully entered and then left the burrows of one or more males. Females with immature ovaries sometimes wander on the surface while seeking a new burrow, but do not fully enter males' burrows. Ninety minutes after low tide, we removed the cloth fence and counted the number of open and plugged burrows with pillars in all 12 plots. At this time a plugged burrow indicates a burrow mating. Only burrows with pillars can be used, as pillarless burrows could belong to females.

(c) *Statistical analyses*

For each crab behavioural variable, each plot provided one data point per cycle. For 'males waving' this was the total number counted from 24 scan samples; for 'sampling females' and 'surface copulations' it was the total number seen during 12 samples of 20 min each; for 'pillars built' it was the total number built over 6 d. There was no pseudoreplication for these variables. The number of birds present per side, however, was calculated by tallying up the total number of birds seen each day ($n=6$ counts) and then treating the total per side per day as independent data points ($n=6$ days).

To determine whether food addition affected behaviour we performed two separate analyses using different, but overlapping, data sets. First, we compared data from the first baseline cycle with data from the cycle when the side in question had food added (side A in cycle 2, side B in cycle 3) in two-way Model III ANOVAs with 'side' as a random factor and 'food' as a fixed factor (present/absent). This analysis cannot exclude the possibility that a temporal trend rather than the food treatment is responsible for differences between cycles. In a second analysis, we then compared data between sides within the same cycle. We only used data from cycles 2 and 3 in two-way Model II ANOVAs with 'side' and 'cycle' as random factors. If food had an effect, the interaction term should be significant, because food was added to side A in cycle 2 and to side B in cycle 3. We confirmed graphically that significant interactions arose because the direction of the response changed between cycles. In all analyses, the ratio of the number of females sampling to surface mating was arcsin-transformed. Separate univariate analyses were performed for each behavioural variable.

To investigate temporal trends within cycles we used ANCOVA, with cycle as a factor and day as the covariate. The total number of surface copulations, sampling females and pillars built per day were treated as independent points ($n=6$ days per cycle). If the interaction term was non-significant it was excluded from the final model. To test whether female mating behaviour changed depending on the time to or from low tide, we performed a two-way ANOVA, with time-period and cycle as factors. We first totalled the number of surface copulations

Table 1. Summary statistics for the two sides over the three cycles

(Data expressed as mean \pm s.e.)

variable	cycle 1 ('control')		cycle 2		cycle 3	
	side A	side B	side A+food	side B	side A	side B+food
birds per day (sum of six counts per day) ($n=6$ days)	7.3 \pm 0.8	4.8 \pm 0.8	39.0 \pm 12.6	2.0 \pm 0.4	1.8 \pm 0.6	88.5 \pm 14.3
pillars (sum of 6 days) ($n=6$ plots)	36.3 \pm 4.1	70.5 \pm 9.2	0.5 \pm 0.3	7.8 \pm 2.3	23.3 \pm 3.5	4.3 \pm 1.1
males waving (sum of 24 counts) ($n=6$ plots)	703 \pm 85	727 \pm 54	314 \pm 48	392 \pm 49	770 \pm 126	314 \pm 58
sampling females (sum of 12 20-min samples) ($n=6$ plots)	2.5 \pm 0.8	2.8 \pm 0.7	0.2 \pm 0.2	1.5 \pm 0.6	7.2 \pm 1.0	0.2 \pm 0.2
surface copulations (sum of 12 20-min samples) ($n=6$ plots)	7.3 \pm 0.9	11.5 \pm 1.3	4.3 \pm 0.3	10.5 \pm 1.1	10.8 \pm 1.4	3.8 \pm 1.0
ratio of sampling females to surface copulations	0.37 \pm 0.15	0.28 \pm 0.09	0.06 \pm 0.06	0.15 \pm 0.06	0.75 \pm 0.17	0.03 \pm 0.02

and sampling females per plot for each of the six, 20-min time-periods for the 2 d that a plot was observed during each cycle ($n=216$; 12 plots \times 6 time-periods \times 3 cycles). However, as the addition of food had a strong negative effect on female mating (see §3), we then repeated the analysis excluding side A from cycle 2 and side B from cycle 3 ($n=144$). Unless otherwise stated all tests are two-tailed, the significance level was set at 0.05, and results are presented as mean \pm standard error. Data were analysed using SYSTAT 5.0, following Wilkinson *et al.* (1996) and Zar (1984).

3. RESULTS

(a) The baseline cycle

Grackles were present on the mudflat each day. The mean number naturally present on side B was slightly less than on side A (Mann–Whitney U -test, $p=0.07$). There were more pillars built on side B than side A (Mann–Whitney U -test, $p=0.004$), but no difference in the number of males waving. There were more surface matings on side B (Mann–Whitney U -test, $p=0.03$), but no difference in the number of wandering, sampling females (Mann–Whitney U -test, $p>0.20$) (all tests, $n=6$, 6; table 1).

(b) Comparing the baseline and food addition cycles

When comparing data from the baseline cycle with the cycle of food addition, there was a significant increase in the number of birds after food addition (food: $F_{1,20}=36.67$, $p<0.001$) for both sides A and B. The birds fed from the plates of food and repeatedly flew or walked in and out of plots. They seldom chased crabs, but the crabs were affected by their presence and retreated into their burrows whenever a bird was nearby. There were significant decreases in the numbers of males waving (food: $F_{1,20}=40.81$, $p<0.001$), pillars built (food:

$F_{1,20}=101.81$, $p<0.001$), the numbers of sampling females (food: $F_{1,20}=18.75$, $p<0.001$) and the numbers of surface copulations (food: $F_{1,20}=30.21$, $p<0.001$) when more birds were present. The presence of birds therefore reduced the total mating rate. More importantly, the ratio of females seeking burrow matings to those engaging in surface copulations was lower when more birds were present (food: $F_{1,20}=9.46$, $p=0.006$) (table 1). In the baseline cycle, 32 females sampled, but only two sampled when birds were attracted to a side. In contrast, there were 113 surface copulations during the baseline cycle, and 49 when birds were attracted. There was therefore a decrease in the relative frequency of burrow mating. Of the burrows with pillars, too few were built when birds were present to determine directly whether burrow matings were less common. Twelve out of 641 were plugged during the baseline cycle, and zero out of 29 when food was added.

The above analyses are slightly complicated because the interaction between side and food was significant for the number of pillars built ($F_{1,20}=9.00$, $p=0.007$), and for the number of surface copulations ($F_{1,20}=5.78$, $p=0.026$). In neither case, however, was this due to the trend going in opposite directions for sides A and B. Rather, it was due to a far stronger effect for side B. This may be due to the fact that the interaction was also significant for the number of birds ($F_{1,20}=7.46$, $p=0.013$) with many more birds being attracted during cycle 3 than cycle 2 (table 1). This occurred because the birds became more familiar with the food source over the course of the study.

(c) Comparing sides within the food addition cycles

The addition of food to a side significantly increased the number of birds relative to the side without food (interaction: $F_{1,20}=42.26$, $p<0.001$). There was a significant decrease in the number of males waving (interaction:

$F_{1,20}=11.93$, $p=0.003$), pillars built (interaction: $F_{1,20}=36.18$, $p<0.001$), number of sampling females (interaction: $F_{1,20}=52.08$, $p<0.001$) and number of surface copulations (interaction: $F_{1,20}=39.85$, $p<0.001$) on the side where birds were attracted. Again, the ratio of sampling, burrow-mating females to surface copulations was lower when birds were attracted (interaction: $F_{1,20}=42.26$, $p<0.001$). In total, only two females wandered when birds were attracted, whereas 52 wandered on the opposite side of the mudflat. In contrast, surface copulations only decreased from 128 on the sides without food to 49 on the sides where birds were attracted. There was therefore a change in the relative occurrence of the two mating behaviours when birds were attracted to a side. Of the burrows with pillars, four out of 187 were plugged on the sides without food, and zero out of 29 on the side with food.

(d) *Temporal trends*

There was an increase in the number of pillars built over days 4–9 (days: $F_{1,12}=12.72$, $p=0.004$), although this trend varied among cycles (interaction: $F_{2,12}=5.64$, $p=0.019$). There was no directional trend for the number of surface copulations per day (days: $F_{1,14}=0.44$, $p=0.517$) or sampling females per day (days: $F_{1,14}=2.19$, $p=0.161$).

We divided the day into six observation periods (30 min each) centred around low tide. There was no significant variation in the number of surface copulations or sampling females per time-period, whether data from plots on the side with food were included or excluded (surface copulations: $F_{5,208}=0.36$, $p=0.877$ and $F_{5,136}=0.34$, $p=0.886$, respectively; sampling females: $F_{5,208}=0.86$, $p=0.511$ and $F_{5,136}=1.07$, $p=0.381$, respectively).

4. DISCUSSION

Food addition clearly increased the number of potential avian predators and its effects can be attributed directly to the presence of birds. We therefore treat 'food present' and 'greater presence of birds' or 'higher predation risk' as synonymous. To briefly summarize, elevated predation risk resulted in fewer males waving and building pillars. Females were less likely to engage in either burrow or surface matings, but the effect was far stronger for burrow matings.

(a) *Male behaviour*

The reduction in courtship waving was mainly due to males spending more time in their burrows after being startled by birds. Pillar building occurs over 20–60 min, but only involves collection of 8–12 loads of sediment which take about 6–7 s to collect and pile up (Christy 1988*b*, unpublished data). Even though time on the surface was reduced, it still seems likely that there was enough time for males to build pillars (but see explanation 3 below). Despite this, far fewer males than expected built pillars. There are three possible proximate explanations.

1. Previous work shows pillar building is associated with male body condition. Males provided with additional food are more likely to build pillars (Backwell *et al.* 1995). The decreased time males were able to spend

feeding may have indirectly led to fewer males being in sufficiently good body condition to build pillars.

2. When more birds are present, females are unlikely to wander and sample. Pillars benefit males because they increase the likelihood that a sampling female enters a male's burrow. Males may therefore halt pillar building when their own assessment of predator intensity indicates that a pillar will confer little benefit. Alternatively, pillar building may be directly stimulated by the presence of wandering females. Suppression of wandering by females may therefore have led to males failing to build pillars.
3. If predator disturbance was sufficiently frequent, it may have caused males to fail to collect sediment on the way out of the burrow or to deposit it on the way back.

(b) *Female behaviour*

When more birds were present, fewer females copulated on the surface. It is unlikely that the presence of grackles directly prevented females from surface copulating. On several occasions, we observed a pair form on the surface only to break up a few moments later when a bird landed nearby. Subsequently, the female and male, having re-emerged from their respective burrows, always managed to successfully complete the copulation. There are at least three proximate explanations for the reduction in surface copulations.

1. Some females may choose not to engage in surface mating owing to the increased risk of predation. They may be more resistant to a male's attempts to initiate copulation.
2. Fewer males may have tried to initiate surface copulations because of the increased predation risk.
3. Disturbance by predators may have reduced the number of interactions between males and females. This could have led to fewer males successfully initiating surface copulation attempts, or to a greater likelihood that the male and female were disturbed before the necessary courtship signals had been exchanged.

Females were far less likely to wander and burrow mate when grackles were present. Only one female/side wandered when birds were attracted by food, whereas 21 females/side wandered on the sides to which birds were not preferentially attracted. There are two non-mutually exclusive explanations for this reduction. First, fewer females may have been expelled from their burrows owing to the general reduction in the level of interaction between crabs. Second, females, even when faced with agonistic threats from other individuals, may be less willing to leave their burrows when birds are present.

It is unclear whether females that wander and sample burrows voluntarily vacate their own burrows, or are forced out following aggressive interactions with males (Zucker 1977; Christy & Schober 1994). In *U. lactea*, for example, aggressive interactions with males, often following female refusal of surface courtship attempts, lead to females vacating their burrows (Murai *et al.* 1987; Goshima & Murai 1988). If these females have mature ovaries, they begin to wander and sample, and eventually end up mating in a male's burrow. Indeed, in *U. beebei*, females sometimes leave their burrows following agonistic

interactions with other crabs. Females involved in a high number of agonistic interactions are more likely to leave their burrows (T. Koga, unpublished data). There may, however, be other mechanisms that initiate female wandering. In several fiddlers, sampling females are only seen in high numbers for a few days in each cycle (e.g. *Uca annulipes* (Backwell & Passmore 1996); *Uca pugilator* (Christy 1978)). These periods of peak sampling activity seem to coincide with the point in the cycle when females must mate if there is to be sufficient time for subsequent embryonic development before larval release at the next nocturnal spring tide. This pattern suggests that females are more ready to relinquish, or even voluntarily abandon, their burrows when they are ready to mate.

(c) *Predation and sexual selection*

Regardless of proximate causes, the marked shift away from burrow mating when predators are present has predictable consequences. First, there may be weaker selection on male size. Although there is no difference in size between sampled and mated males (Christy & Schober 1994), the average burrow-mated male is probably larger than the average surface-mated male (e.g. *Uca annulipes* (P. R. Y. Backwell, unpublished data); *Uca beebei* (T. Koga *et al.*, unpublished data)). In general, studies in other taxa show that predator presence reduces large-male mating advantages (Houde 1997). Second, there is reduced selection for male traits such as pillars and courtship waving, which increase attractiveness to wandering females (see also Reynolds 1993; Godin 1995). Third, there is greater selection on males due to sperm competition. Last-male sperm precedence is common in Ocypodid crabs (Diesel 1991; Koga *et al.* 1993) and there will be stronger selection on males for mechanisms that prevent female remating (e.g. mating plugs), or increase sperm precedence should females remate (e.g. greater sperm production). In contrast, when a female burrow mates, the male guards her until fertilization occurs, giving him high confidence of paternity.

Several studies show that female mate choice and mating preferences change in response to predation risk (Jennions & Petrie 1997). Here we have shown that predators can also change the location where matings occur. Similarly, female Ugandan Kob antelope are less willing to mate in areas where the threat of predation from lions is high owing to vegetation structure (Deutsch & Weeks 1992). There is wide interspecific variation in the proportion of surface and burrow matings across the genus *Uca* (from 100% surface to 100% burrow mating). Our study suggests that elevated predation risk may be one factor that biases some species towards mainly surface mating.

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