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Eavesdropping in crabs: an agency for lady detection

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Although conspicuous courtship displays are an effective way of attracting the attention of receptive females, they could provide valuable information to rival males on the location of these females. In fiddler crabs, males that see a receptive female wave their single, greatly enlarged claw in a highly conspicuous courtship display. We test whether other males use this courtship display to alert them to the presence of receptive females that they cannot directly see. We show that male fiddler crabs (*Uca mjoebergi*) eavesdrop on the courtship displays of nearby males to detect mate-searching females. This allows males to begin waving before a female becomes visible. Furthermore, males appear to adjust their waving according to the information available: eavesdropping males wave 12 times faster than non-courting males but only 1.7 times slower than males in full visual contact with the female.

1. INTRODUCTION

Animal communication generally occurs within a complex social environment (McGregor 2005) with both target and non-target receivers (McGregor & Peake 2000). The use of signal information by non-target receivers is termed 'eavesdropping' (Peake 2005). By eavesdropping, individuals are able to effectively acquire information that might benefit them. To date, most studies concerning eavesdropping have focussed on male–male aggressive interactions in either a territorial or mate choice context. For example, in green swordtails (*Xiphophorus helleri*), males that observed contests between two other males were less likely to initiate a contest with the observed winner (Earley & Dugatkin 2002). Similarly, in fighting fish (*Betta splendens*), females that eavesdropped on aggressive interactions between males subsequently spent more time with the winner of the encounter (Doutrelant & McGregor 2000). Far fewer studies have investigated the importance of eavesdropping in the context of mate attraction. One such example comes from the Australian bushcricket (*Elephantodeta nobilis*), where females give response calls to male advertisement calls, forming calling duets. In this case, unattractive males are attracted to these duets and occasionally successfully intercept the receptive female (Bailey & Field 2000). Similarly, in the Broadley's painted reed frog (*Hyperolius marmoratus*

broadleyi*), males will increase their own call rate in response to the increased call effort of males that have detected a female (Grafe 2005).

Male reproductive success is usually limited by female availability and the difficulty and time associated with locating a mate (Alcock 2005). Males should therefore be finely attuned to any cues or signals that provide information on the location of potential mates, including cues from rival males' courtship displays (Roberts *et al.* 2006). In fiddler crabs, males attract mate-searching females by waving their one greatly enlarged claw in a highly conspicuous display. Receptive females approach males based on wave rate, wave leadership and claw size (Reaney & Backwell 2009; Milner *et al.* 2010). The fact that males produce a conspicuous waving display once a receptive female is detected suggests that other males could potentially use this information to alert them to the presence of a mate-searching female. That is, males could use other males as 'female detectors', reducing the time taken to locate potential mates and effectively increasing the distance at which they detect, and therefore respond to, receptive females. Ultimately, this should increase a male's probability of successfully attracting a mate. In this study we aim to determine whether male fiddler crabs (*Uca mjoebergi*) eavesdrop on the courtship displays of nearby males to detect mate-searching females.

2. MATERIAL AND METHODS

We studied *U. mjoebergi* on mudflats in East Point Reserve, Darwin, Australia from September to November 2009. *U. mjoebergi* is a small fiddler crab (carapace width less than 20 mm) that inhabits intertidal mudflats across northern Australia. They occur in dense, mixed sex colonies (37 ± 17 crabs m^{-2}; R. Slatyer, L. T. Reaney & P. R. Y. Backwell, unpublished data) and both sexes defend individual territories that are centred on a burrow (Reaney & Backwell 2007a). During the mating period, receptive females leave their territories and wander through the population in search of prospective mates. They visit several males (2.2 ± 1.6 males) and can travel metres (50.2 ± 73.4 cm) while mate-searching (Reaney & Backwell 2007b). Once a female selects a male, she enters his burrow and the pair mate. Following copulation and oviposition, the male abandons the burrow, while the female remains to incubate the eggs.

We conducted an experiment with a repeated-measures design with four treatments that manipulated the social environment of a focal male. We then measured his wave rate under each treatment. For the first treatment, we located a naturally occurring group of courting males and removed any wandering females within 50 cm of the group. A group of males consisted of at least four neighbouring males that were all waving at the same female at the time of initial sighting. We then randomly designated a focal male from the group and, after a 3 min waiting period, measured his wave rate. This was measured by counting the number of waves produced over a 30 s period.

For the second treatment, we placed a small piece of plywood (2.5×4.5 cm) vertically into the mud approximately 13 cm in front of the focal male. This prevented the male from seeing the area directly behind the barrier. After a 3 min waiting period, we again measured the number of waves the male produced in a 30 s period. This is unlikely to have increased male wariness as wave rate actually increased slightly (see §3).

For the third treatment, we collected a mate-searching female from another area of the population and tethered her on a short leash immediately behind the plywood visual barrier. She was not visible to the focal male, even if he moved to the edge of his territory. To tether her, we glued her carapace to a short (1–2 cm) length of cotton thread that was tied to a nail pushed into the mud. While the focal male could not see the tethered female, the vertical partition was placed so that all the other males in the group could see the female. After a 3 min waiting period, we again measured the number of waves given by the focal male in a 30 s period.

For the fourth treatment, we removed the plywood barrier from treatment 3, making the tethered female visible to the focal male, waited for 3 min and again measured the number of waves produced by the focal male in a 30 s period. In this treatment, the tethered female was clearly visible to the focal male and to all the other males in the group.

We tested 50 different groups of males. The same male was designated the focal male for all four treatments. We tested for an overall treatment effect using Friedman's test.

We then used Wilcoxon signed-rank tests to compare wave rate between pairs of treatments. All tests were two-tailed with a Bonferroni correction to account for multiple testing so that $\alpha_{critical} = 0.05/6 = 0.0083$. Data are presented as medians and upper and lower quartiles.

(a) Carry over and order effects

It was important to wait 3 min between successive treatments to minimize potential 'carry over' effects where male wave rate continues to be directly affected by the previous treatment. Any such effects should lead to an increase in wave rate when a male is stimulated to wave in the preceding treatment (e.g. when he sees a female). When designing our study we realized that 'carry over' effects were more likely to affect our results if we first presented the treatment predicted to be most stimulating (female visible). For this reason, we always presented the treatments in the same order: no female; visual barrier; visual barrier with female behind it; visible female. This does, however, mean that we have potentially introduced a confounding order effect (the order of the trials affects the results). On biological grounds, we argue that it is very unlikely that males increase their wave rates in subsequent treatments as a direct response to the preceding treatments, or because there is a general increase in wave rate with the time of day. There is an indirect way to test this. If a general temporal effect influenced our results, then we would expect it to be unidirectional: the wave rate should increase or decrease with each subsequent treatment. We did not find this: the wave rate stayed the same or dropped between the first and second treatments, and then increased substantially between the second and third, and increased less strongly between the third and fourth treatments (see §3).

3. RESULTS

The wave rate differed among the four treatments (Friedman's test, $\chi^2 = 140.4$, d.f. = 3, $p < 0.00001$). The median wave rate of the focal male in the first treatment (no female, no barrier) was one wave per minute (upper to lower quartile: 0–4). In the second treatment, when the barrier was added, the focal male's wave rate was 0 waves per minute (0–4). In the third treatment, when a female was placed behind the barrier and was therefore not visible to the focal male but clearly visible to the rest of the courting group, the focal male's wave rate was 12 waves min^{-1} (10–14; $n = 50$). In the final treatment, when the female was visible to the focal male, his wave rate was 20 waves min^{-1} (16–28; all $n = 50$). Individual male wave rates are shown in figure 1. There was a significant difference between all pair-wise comparisons of wave rate (all $p < 0.001$, $Z = 6.17$ except treatment 3 versus 4, where $p < 0.001$, $Z = 5.90$), except for a non-significant difference between the wave rate in treatments 1 and 2, once multiple testing was taken into account ($p = 0.026$, $Z = 2.23$).

4. DISCUSSION

We have presented strong evidence that male fiddler crabs (*U. mjoebergi*) eavesdrop on the courtship displays of nearby males to detect mate-searching females. Furthermore, we found that males adjust their response according to the source of the information received. Directly seeing a female led to a
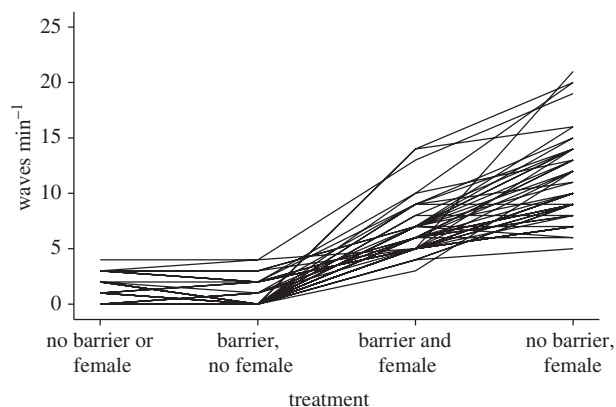
Figure 1. Individual male wave rate across four treatments.

higher wave rate than when inferring her presence from the behaviour of surrounding males.

Taking into account multiple testing, and our caveat about order effects, there was no difference in the wave rate of a male when a barrier was added (treatment 1 versus 2), so the barrier itself did not affect male wave rate. The small decrease of 1 wave min^{-1} in the focal males' wave rates between the initial and subsequent measurement (i.e. when all females had been removed from the area versus approximately 5 min later when the barrier was in place) is probably attributable to a small carry over effect. That is, males in the first treatment most likely waved at a slightly higher rate because they had more recently seen a mate-searching female. However, when a male could not directly see a female (because of the presence of the barrier) but could see neighbouring males courting, he waved significantly faster than when there were no females present (treatment 3 versus 2). In addition, once the barrier was removed so that the female was directly visible to the focal male, his wave rate again increased significantly (treatment 4 versus 3).

Owing to the importance of waving for mate attraction in fiddler crabs, detecting receptive females as early as possible is likely to be of great importance in determining male success at mate attraction. Through eavesdropping, males are effectively increasing the distance at which they can detect receptive females, thereby increasing their conspicuousness and consequently elevating their likelihood of being sampled by a mate-searching female. While it might seem maladaptive for a male to wave before seeing a female, if this means that the female cannot see him, the greater conspicuousness of males owing to their enlarged claw means there is a probably an asymmetry in the distance at which females and males detect each other.

The use of socially acquired information has been shown in at least one other context in fiddler crabs. In *U. pugilator*, fiddler crabs retreat into their burrows when they detect their neighbours fleeing, even if they are unable to see the stimulus that induced their neighbours' responses (Wong *et al.* 2005). Furthermore, in *U. tangeri* it has been suggested that males might use other males as female detectors (Pope 2005), but this data remains unpublished.

While the use of rival males' signals as a cue to detect receptive females is likely to be a widespread

phenomenon, very few studies have investigated this possibility (*but see* Bailey & Field 2000; Grafe 2005; Roberts *et al.* 2006). Here, we provide a rare example of males eavesdropping on rival males' courtship displays to detect receptive females. To the best of our knowledge this is the first such evidence from a visual communication system.

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