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Safe sex: male–female coalitions and pre-copulatory mate-guarding in a fiddler crab

Richard N. C. Milner*, Michael D. Jennions and Patricia R. Y. Backwell

Evolution, Ecology and Genetics, Research School of Biology, The Australian National University, Canberra 0200, Australia
*Author for correspondence (richard.milner@anu.edu.au).

In fiddler crabs both males and females defend territories that are essential for survival. Given pronounced sexual dimorphism in weaponry, how do weaponless females defend their territory from well-armed males? Using observational data and two simple experiments, we test whether male *Uca annulipes* protect their female neighbours from conspecific intruders. We show that males defend their female neighbours against male but not female intruders. We also show that females sometimes mate with their immediate neighbours. Male defence of female neighbours appears to represent both pre-copulatory mate-guarding and a territorial coalition. Males who ensure that their neighbour remains female could benefit through increased opportunity for future reproductive success and lower boundary maintenance costs.

Keywords: coalitions; female protection; Fiddler crabs; mate-guarding; mating benefits; surface-mating

1. INTRODUCTION

In many animal species males bear weapons such as horns, tusks or claws that are used in territorial defence or fighting for access to females (Emlen 2008). In contrast, females are often weaponless, even in species where both sexes hold territories (Kiltie 1985). Males who have lost their territories should benefit from challenging weaponless female residents rather than fighting well-armed males. How then, do females maintain their territories? One explanation is that females gain protection from their male neighbours through neighbour coalitions and/or mate-guarding (where females exchange sex for protection).

Neighbour coalitions can occur in territorial species if it is less costly to help a neighbour defend its territory against intruders than re-negotiate boundaries with a new, potentially stronger individual (Getty 1987; Mesterton-Gibbons & Sherratt 2009). Such by-product mutualisms have only been convincingly reported in three species: rock pipits (*Arthrus petrosus*; Elfstrom 1997) and fiddler crabs (*Uca mjoebergi* and *U. annulipes*; Backwell & Jennions 2004; Detto *et al.* in preparation). In each case, males left their territories to help familiar male neighbours fight off intruders. The authors argued that the costs of helping were

outweighed by the benefit of not having to re-establish territory boundaries with new, stronger neighbours (e.g. in *U. annulipes* and *U. mjoebergi* males more often help when the intruder is larger than the neighbour). As males are often physically dominant over females, boundary maintenance should be less costly for males with a female neighbour. Nevertheless, helping can also be extremely costly. In fiddler crabs, fights can result in injury, claw loss and death (Milner *et al.* in press), and males who leave their territory to help a neighbour run the risk of having their own unattended burrow usurped.

Males might also protect females in exchange for mating opportunities. Trading sex for material benefits is known from several taxa. For example, female red-winged blackbirds (*Agelaius phoeniceus*) that mate with an extra-pair male are subsequently allowed to forage on his territory (Gray 1997). In the Adeline penguin (*Pygoscelis adeliae*) females exchange copulations for highly sought-after stones used for nest building (Hunter & Davis 1998). Furthermore, in pigeons, females trade copulations for protection. Females initiate frequent copulations to keep their male partner close, thereby avoiding harassment from other males (Lovell-Mansbridge & Birkhead 1998).

2. FIDDLER CRABS

Fiddler crabs display pronounced sexual dimorphism. Females have two small feeding claws while males have one feeding claw and one greatly enlarged major claw (up to 50% of total body weight) that is used during courtship and as a weapon during antagonistic interactions (Crane 1975). They live in dense, mixed sex colonies and both sexes defend territories that contain a burrow. Burrows are vital as shelter from tidal inundation, predation and desiccation (Koga *et al.* 2001). They are also used during reproduction as the site of mating and incubation, with females in some species choosing mates based on male burrow quality (e.g. *U. annulipes*; Backwell & Passmore 1996).

Recent work on territory defence and acquisition in *U. annulipes* has shown that males and females are equally successful at gaining and holding a territory, despite the strong competition for burrows between weaponless females and well-armed males (Milner *et al.* in preparation). Females rarely evict resident crabs and instead tend to search for empty burrows, while males usually fight and evict a resident male or female. This study raised an important question: why do burrow-searching males not always evict female residents? Fights between males can be extremely costly, and it would seem that a well-armed burrow-searching male should target female-owned territories. We proposed three non-mutually exclusive explanations for these results. (i) Female burrows could be of poorer quality than male burrows as females generally acquire abandoned, empty burrows. Males might therefore avoid evicting females because burrow quality is a criterion for female mate choice. (ii) Males might assist in the defence of neighbouring females' territories (as they do for males) to escape re-negotiation costs with a new resident. (iii) Neighbouring males might defend female residents to increase their potential future mating opportunities (Milner *et al.* in preparation).

In fiddler crabs, mating can occur underground in the male's burrow, or on the surface outside the female's burrow. In some species only surface- or burrow-mating occurs (Crane 1975). In other species both mating behaviours occur (Koga *et al.* 1998). Burrow matings require females to leave their burrow and wander through the population in search of a mate. Wandering females are highly vulnerable to predation, as they do not have a burrow to retreat into (Koga *et al.* 1998). When surface-mating, a male approaches a resident female and the pair copulate at the entrance of her burrow (Yamaguchi 2001). Although copulating on the surface is probably more risky than inside a burrow, the overall risk is likely to be lower than that arising from mate-searching prior to burrow-mating (Koga *et al.* 1998).

Uca annulipes is known to both surface and burrow mate, and previous work has shown that males form defence coalitions with male neighbours (P. R. Y. Backwell 1992, unpublished data; Detto *et al.* in preparation). Our study was designed to determine whether: (i) males form similar defence coalitions with female neighbours; (ii) there is evidence of females exchanging sex, with their nearest male neighbour, for protection. We predicted that males would protect their female neighbours, both to avoid re-negotiating territory boundaries with a new male neighbour and to increase their reproductive success through future surface-mating opportunities.

3. MATERIAL AND METHODS

(a) Does surface-mating occur only between females and their nearest neighbouring males?

We observed surface matings ($n = 52$) in a population of *U. annulipes* in Durban Harbour, South Africa from November to December. We noted whether or not mating crabs were immediate neighbours that shared a territory boundary.

(b) Do male residents help defend their female neighbours' territories from intruding males?

To determine whether male residents protect female neighbours from intruding males, we tethered (superglued a 1 cm length of cotton thread to the crab's carapace and attached it to a nail pushed into the sediment) and placed a male at the entrance of a female's burrow to simulate an intrusion. To avoid confusing male defence of his own territory with female protection, the intruder male was always placed on the side of the female's burrow furthest from the focal male's burrow. The intruder male (major claw length: 20.7 ± 4.2 mm; $n = 20$) was always smaller than the male neighbour (25.1 ± 5.3 mm; $n = 20$). This increased the likelihood of a male neighbour response, as he was more likely to defeat the intruder (Backwell & Jennions 2004). The focal male neighbour was always the closest neighbour to the focal female. Female protection was scored if the male neighbour approached and fought with the intruder male within 5 min of re-emerging from his burrow.

(c) Do male residents help in territorial defence if the intruder is a female?

To determine whether male residents protect female neighbours from intruding females, we repeated the previous experiment but replaced the tethered male with a tethered female (female intruder). Half of the female intruders (carapace width: 14 ± 0.9 mm; $n = 10$) used were larger than the focal female (11.7 ± 1.5 mm; $n = 10$) and half were smaller (12.1 ± 1.1 mm; $n = 10$) than the focal female (13.1 ± 0.8 mm; $n = 10$). This allowed us to test whether there was any relative female size effect present. All female intruders were smaller than the focal male.

Both protection experiments were carried out on tidal mudflats on Inhaca Island, Mozambique from October to November.

4. RESULTS

(a) Does surface-mating occur only between females and their nearest neighbouring males?

In 44 of the 52 surface matings we observed (85%), the mated male was a neighbour who shared a territory border with the resident female. In the remaining 15 per cent, the mated male was a stranger: either a burrowless male or a non-neighbouring resident.

(b) Do male residents help their female neighbours defend their territories from intruding males and female?

In 20 of 21 experimental trials (95%), the male neighbour approached and fought off the tethered intruding male. This required that the male left his own territory unprotected while he fought the intruder on the female's territory. In only 3 of 20 trials (15%) did the neighbouring male approach and fight off the tethered intruding female.

There was a significant relationship between the sex of the intruder and whether or not a male protected his female neighbour (Fisher's exact test: $n = 41$, $p < 0.001$). Unlike the case in male–male coalitions (see Backwell & Jennions 2004), whether the intruding female was smaller or larger than the neighbouring female did not significantly affect the likelihood that the male helped (0/10 versus 3/10; Fisher's exact test: $n = 20$, $p = 0.211$; Power $\approx 65\%$ to detect the effect of $h = 1.05$ noted by Backwell & Jennions 2004; Methods in Cohen 1988).

5. DISCUSSION

We have shown that male *U. annulipes* protect their female neighbours from intruding males but not intruding females; and that females that surface mate mainly do so with their immediate neighbours. We suggest that males: (i) form defensive coalitions with their female neighbours against intruding males; and (ii) protect their female neighbours in exchange for future mating benefits. These results support those of Backwell & Jennions (2004), who showed that males protect their male neighbours from intruders that are smaller than themselves but larger than their neighbour to avoid re-negotiating territory boundaries with a new, stronger individual. We argue that males are protecting their female neighbours for a similar reason, but, in addition, do so to increase their opportunity for surface-matings.

Males protected their female neighbours in 95 per cent of instances where the intruder was male and only 15 per cent of instances where the intruder was female. This suggests that males either do not care who their neighbour is, as long as they are female, or that they are unable to individually distinguish females. While we did not test whether *U. annulipes* recognize their neighbours, individual recognition based on carapace coloration occurs in other fiddler crabs (Detto *et al.* 2006). Regardless, by ensuring that their neighbour is female, males will benefit through increased opportunity for future reproductive success as well as reduced boundary maintenance costs (i.e. it is less costly to maintain a territory boundary with a female than a male).

While it is possible guarding is post- rather than pre-copulatory, we believe that this is highly unlikely. Our results imply that males do not care whether one female replaces another as a neighbour. If guarding occurs post-copulation one might expect a male to guard a female regardless of the intruder's sex. As this does not occur, we suggest that the available evidence is more consistent with pre-copulatory guarding.

Our results can partly explain why burrow-seeking males do not always target burrow-owning females. Although females are apparently defenceless, Milner *et al.* (in preparation) showed that they are as capable as males at holding territories. Here we show that females might hold their territory by gaining protection from their male neighbour. Therefore, burrow-searching males might have to contend with fighting a male regardless of whether they attempt to usurp a female's or a male's burrow.

To the best of our knowledge we have provided the first experimental evidence for pre-copulatory mate-guarding in fiddler crabs and for defence coalitions between territorial males and female neighbours. This might explain why weaponless females and well-armed males are similarly capable of retaining a territory (Milner *et al.* in preparation). More generally, we have exposed some important links between coalition formation, the evolution of surface-mating and pre-copulatory mate-guarding in fiddler crabs that can now be explored more thoroughly.

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