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Interspecific assistance: fiddler crabs help heterospecific neighbours in territory defence

Isobel Booksmythe*, 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 (isobel.booksmythe@anu.edu.au).

Theory predicts that territory owners will help established neighbours to repel intruders, when doing so is less costly than renegotiating boundaries with successful usurpers of neighbouring territories. Here, we show for the first time, to our knowledge, cooperative territory defence between heterospecific male neighbours in the fiddler crabs *Uca elegans* and *Uca mjoebergi*. We show experimentally that resident *U. elegans* were equally likely to help a smaller *U. mjoebergi* or *U. elegans* neighbour during simulated intrusions by intermediate sized *U. elegans* males (50% of cases for both). Helping was, however, significantly less likely to occur when the intruder was a *U. mjoebergi* male (only 15% of cases).

Keywords: cooperative defence; interspecific; neighbour; territory; *Uca*

1. INTRODUCTION

Territory owners can be extremely aggressive towards intruders but show reduced aggression towards neighbours once territory boundaries are established (Jaeger 1981). This ‘dear enemy’ relationship between neighbours creates stable neighbourhoods that benefit all residents (Getty 1987). Whenever an intruder usurps a territory, all neighbouring residents must fight the new neighbour to re-establish territory boundaries (Krebs 1982). Renegotiation costs can be so great that it is better to help established neighbours defend their territories against intruders than risk their replacement (Getty 1987; Mesterton-Gibbons & Sherratt 2009). These costs are likely to be exacerbated because successful intruders are often larger and stronger than the residents they evict (Getty 1987). Examples of this kind of cooperative territory defence come from rock pipits, *Anthus petrosus* (Elfström 1997) and two species of fiddler crab, *Uca mjoebergi* (Backwell & Jennions 2004) and *Uca annulipes* (Detto *et al.* 2010; Milner *et al.* 2010), in all of which male residents will leave their own territories to repel intruders on neighbours’ territories. This benefits the defended neighbour. In both fiddler crabs, neighbour-assisted fights were significantly less likely to result in eviction than those without neighbour intervention (Backwell & Jennions 2004; Detto *et al.* 2010).

As helpers face costs of fighting and risk losing their own temporarily undefended territories, the

circumstances under which it is worth helping a neighbour might be limited. Retaining smaller neighbours should confer the greatest benefits to a resident, as neighbours are close rivals in many competitive situations. Larger individuals often have an advantage in physical combat (e.g. Jennions & Backwell 1996; Taylor & Jackson 2003) and mate choice (see Andersson 1994); so having smaller neighbours can increase success in territorial disputes, and mate attraction. A size advantage during fights can have direct implications for whether helping occurs during an intrusion event (Mesterton-Gibbons & Sherratt 2009). The ability to predict the outcome of fights between neighbours and intruders, based on their relative sizes, allows residents to restrict their helping behaviour to those fights that a neighbour is likely to lose. Furthermore, if residents can predict their own ability to repel an intruder, they should help only when they are likely to succeed. Judicious helping behaviour has been shown in fiddler crabs, where the relative size of neighbours and intruders strongly influences the likelihood that helping occurs. Helping is most likely when the potential helper is larger than the intruder and the intruder is larger than the targeted neighbour (Detto *et al.* 2010).

But what if established neighbours are heterospecific? Sympatric species with similar resource use often hold mutually exclusive territories (e.g. Genner *et al.* 1999; Tynkkynen *et al.* 2006). Territories can be interspersed so that residents have conspecific or heterospecific neighbours, or both. Species differences mean that costs imposed probably differ when neighbours are heterospecifics rather than conspecifics. For instance, if heterospecific neighbours do not develop ‘dear enemy’ relationships, the cost of repeated boundary disputes could remove the incentive to help heterospecific neighbours in territory defence. Additionally, residents might not help if they are unable to recognize a heterospecific neighbour, or identify potential threats to that neighbour’s ongoing residency, particularly from heterospecific intruders. There could, however, also be benefits to having heterospecific neighbours. For example, they do not compete for mates (although heterospecifics can interfere with reproduction in other ways, Gröning & Hochkirch 2008). If heterospecific neighbours are recognized, and there are benefits of stability in mixed-species neighbourhoods, cooperative territory defence between heterospecific neighbours might be expected whenever the cost of defending an established heterospecific neighbour is less than the cost of renegotiating territory boundaries with a new neighbour. Here, we use fiddler crabs to investigate whether residents help heterospecific neighbours defend a territory against conspecific and/or heterospecific intruders.

2. MATERIAL AND METHODS

We investigated the occurrence of cooperative territory defence between males of two sympatric species of fiddler crab, *Uca elegans* and *U. mjoebergi*, at East Point Reserve, Darwin, Australia. In both species, each individual holds a territory containing a central burrow, which is a refuge from predators and tidal inundation. Like all fiddler crabs, males of both species have one greatly enlarged claw that is used as a weapon. Territories are defended against wandering individuals that have abandoned or been evicted from their own territories. Such interactions are known to occur between

U. mjoebergi and *U. elegans* individuals, as we have observed interspecific fights resulting in evictions (I. Bookmythe 2009, unpublished data). *Uca mjoebergi* individuals are smaller, on average, than *U. elegans* individuals (mean \pm s.e. claw length, *U. mjoebergi*: 17.79 ± 0.124 mm, $n = 704$ (Morrell *et al.* 2005); *U. elegans*: 21.70 ± 0.309 mm, $n = 116$ (this study); $t_{818} = 11.841$, $p < 0.001$).

First, we determined whether *U. elegans* residents help smaller conspecific neighbours against conspecific intruders. Twenty pairs of *U. elegans* neighbours were located. For each pair, a third *U. elegans* individual was caught from elsewhere in the population and tethered 3 cm from the smaller neighbour's burrow entrance to simulate an intrusion. The intruder chosen was always intermediate in size between the neighbours, as helping is most likely to occur when potential helper $>$ intruder $>$ neighbour (Detto *et al.* 2010). Helping was scored as occurring if the larger neighbour approached and fought the tethered intruder within the first 5 min after the neighbours emerged from their burrows. Aggression between the intruder and the smaller neighbour was not a criterion as one response to intruders is to retreat into the burrow, which in our trials resulted in no contact with the intruder. To tether intruders, a 1–2 cm length of cotton thread was glued to the carapace of the crab and tied to a nail pressed into the sediment. Intruders were placed on the distant side of the smaller neighbour's burrow entrance to ensure that the response of the larger neighbour was not owing to immediate, direct defence of his own territory. After each trial, the crabs were caught and measured (claw length and carapace width) using dial calipers (± 0.1 mm).

Second, we tested whether *U. elegans* residents are as likely to help smaller heterospecific neighbours against conspecific and/or heterospecific intruders. Using the same experimental protocol as above, 40 *U. elegans* residents with smaller *U. mjoebergi* neighbours were located and an intermediate-sized intruder of either *U. elegans* ($n = 20$) or *U. mjoebergi* ($n = 20$) was tethered next to the *U. mjoebergi* resident's burrow entrance.

We used a Fisher's exact test to investigate whether the species identity of the intruder or smaller neighbour affects the likelihood of helping. We used *t*-tests to compare the relative size of helpers and intruders across treatments. Carapace width and claw length are strongly correlated (*U. mjoebergi*: $r_{52} = 0.895$, $p < 0.001$, $n = 53$; *U. elegans*: $r_{115} = 0.905$, $p < 0.001$, $n = 116$), so we only present the results of analyses for claw length (carapace width gave almost identical results). Data are presented as mean \pm s.d.

3. RESULTS

Large *U. elegans* residents helped a smaller *U. elegans* neighbour repel *U. elegans* intruders in 10 of 20 trials. Cooperative defence of heterospecific neighbours also occurred: in 10 of 20 trials, large *U. elegans* residents helped a smaller *U. mjoebergi* neighbour repel a *U. elegans* intruder. The likelihood of helping, however, differed depending on the species identity of the intruder. Large *U. elegans* residents helped their smaller *U. mjoebergi* neighbours repel *U. mjoebergi* intruders in only three of 20 trials. Resident *U. elegans* were therefore more likely to defend *U. mjoebergi* neighbours against *U. elegans* intruders than *U. mjoebergi* intruders (Fisher's exact test, $p = 0.041$), while they were equally likely to help conspecific and heterospecific neighbours against *U. elegans* intruders.

Uca mjoebergi intruders were smaller than *U. elegans* intruders in heterospecific neighbour trials (18.56 ± 2.05 versus 20.42 ± 2.91 mm; $t_{38} = 2.334$, $p = 0.025$). However, *U. elegans* residents used in trials with *U. mjoebergi* intruders were smaller than those used in trials with *U. elegans* intruders (20.91 ± 2.43 versus 23.99 ± 3.05 mm; $t_{35} = 3.35$, $p = 0.002$). This meant that the relative size of helpers and intruders (helper/intruder claw length), which is the best biological predictor of fight outcome and initiation (Jennions & Backwell 1996; Morrell *et al.* 2005), did not differ between treatments (*U. mjoebergi* intruder:

1.15 ± 0.10 , *U. elegans* intruder: 1.18 ± 0.13 ; $t_{35} = 0.842$, $p = 0.406$). Controlling for relative size, the effect of treatment type remained significant (logistic regression: Wald's $\chi^2 = 6.09$, d.f. = 2, $p = 0.048$). There was no interaction between relative claw size and treatment (Wald's $\chi^2 = 1.8$, d.f. = 2, $p = 0.407$), so it was removed from the final model. In fact, because of the experimental design restricting variation in relative size (i.e. always greater than 1), it too had no significant effect on whether helping occurred (Wald's $\chi^2 = 0$, d.f. = 1, $p = 0.985$).

4. DISCUSSION

Our study is the first, to our knowledge, to show cooperative territory defence between heterospecific neighbours. *Uca elegans* residents left their own territories to attack intruders on the territories of neighbouring heterospecifics. Helping between heterospecific neighbours was as likely as helping between conspecific neighbours when the intruder was the same species as the larger resident, occurring in 50 per cent of trials. When, however, the intruder was heterospecific to the potential helper, helping occurred in only 15 per cent of trials. There are several plausible reasons why *U. elegans* residents are less likely to help a *U. mjoebergi* neighbour repel a *U. mjoebergi* intruder. First, *U. elegans* residents might not recognize individual *U. mjoebergi* and therefore not know which male in a fighting pair is their neighbour. Second, *U. elegans* residents might be less responsive to *U. mjoebergi* intruders because social interactions with heterospecifics are less frequent than interactions with conspecifics. These explanations are both based on proximate constraints. Third, a major adaptive benefit of having heterospecific neighbours could be reduced mate competition, making it more advantageous to prevent conspecific than heterospecific intruders from usurping neighbouring territories.

A large variety of mutualistic interspecific relationships have been described in the literature, ranging from plant–pollinator associations to within-cell symbionts. While cooperative territory defence between heterospecifics is a unique finding, it is consistent with explanations for other mutually beneficial interspecific interactions. For example, bird species that form mixed flocks (or are otherwise spatially associated) often benefit from the alarm calls of heterospecifics (Magrath *et al.* 2007, 2009). Costs to the caller should not differ whether receivers are only conspecifics, or include heterospecific individuals. There might even be additional benefits of associating with heterospecifics, such as an increased ability of the group to perceive predators owing to interspecific differences in sensory abilities (Burger 1984; Semeniuk & Dill 2006), or reduced competition for resources or mates. While one species will often gain greater benefits than the other from an interspecific association, asymmetrically beneficial associations can be maintained as long as neither participant suffers a net cost.

Similar territorial behaviour and territory use in *U. elegans* and *U. mjoebergi*, and the relatively stable nature of neighbourhoods in this system are likely to

be important in accounting for our finding that *U. elegans* residents help both smaller heterospecific and conspecific neighbours to repel intruders. We predict that *U. mjoebergi* residents will also defend smaller heterospecific neighbours against intermediate-sized intruders. We were unable to test this in the current study, however, as the species size difference meant that *U. mjoebergi* residents with smaller *U. elegans* neighbours were very uncommon in the study population. However, our current results indicate that the benefits of defending an established neighbour do not appear to depend on a neighbour's species identity.

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