



## Investigating the 'dear enemy' phenomenon in the territory defence of the fiddler crab, *Uca mjoebergi*

Isobel Booksmythe\*, Michael D. Jennions, Patricia R.Y. Backwell

Division of Evolution, Ecology & Genetics, Research School of Biology, The Australian National University

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Territory owners often respond with greater aggression to strangers than to neighbouring individuals, a phenomenon known as the 'dear enemy' effect. As strangers are usually 'floating' individuals seeking to acquire a territory they pose a relatively greater threat to a resident than do neighbours, who are already territory owners. This explains why residents are less aggressive towards neighbours but not how they distinguish neighbours from strangers: do residents recognize their neighbours or respond to differences in the behaviour of neighbours and strangers? Using measures of fighting intensity we investigated the dear enemy effect in a fiddler crab, *Uca mjoebergi*. We then experimentally manipulated the residency status of pairs of neighbours to distinguish between mechanisms enabling the dear enemy response. Fights between resident and nonterritory-owning individuals were longer and more escalated than fights between neighbouring residents, whether the nonterritory-owner was familiar (a former neighbour) or unfamiliar to the resident. Our results are consistent with the 'relative threat' hypothesis to explain the dear enemy effect, and support the suggestion that residents use cues in the behaviour of an intruder to determine the level of threat posed and distinguish between neighbours and strangers. However, we note that the observed patterns can occur even if residents do not differentiate between intruder types, and simply respond appropriately to the aggressiveness and persistence of an intruder.

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In studies of territoriality, the 'dear enemy' effect describes the phenomenon whereby residents are less aggressive towards neighbouring territory owners than towards strangers (non-neighbours). The dear enemy effect is widely observed in territorial species, and has been shown to occur in a range of mammals (e.g. Rosell & Bjorkoyli 2002; delBarco-Trillo et al. 2009), birds (e.g. Hyman 2005; Hardouin et al. 2006; Briefer et al. 2008), reptiles and amphibians (e.g. Jaeger 1981; Husak & Fox 2003), fish (e.g. Leiser 2003; Frostman & Sherman 2004) and invertebrates (e.g. Langen et al. 2000; Pratt & McLain 2006). The hypotheses proposed to explain the dear enemy phenomenon can be grouped into (1) those based on the difference in familiarity a resident has with neighbours and strangers; and (2) those based on the difference in threat posed by intruders of each type (Temeles 1994).

Familiarity hypotheses suggest that individuals with previous experience of fighting each other are more likely to assess their chance of winning correctly earlier in a fight, making prolonged, escalated fighting unnecessary (Ydenberg et al. 1988, 1989; Getty 1989). Alternatively, 'relative threat' hypotheses propose that

a resident has much more to lose to a stranger than to a neighbour. Strangers are usually nonterritory-owning individuals ('floaters') that fight to evict a resident, and as such they pose a greater threat than neighbouring territory owners, who take only small areas of territory, or steal resources such as food or mates (Jaeger 1981; Getty 1987). A review of empirical studies on a range of vertebrate and invertebrate species broadly rejected explanations based on familiarity in favour of those based on relative threat (Temeles 1994). This conclusion was supported by studies of species in which, contrary to the dear enemy effect, territory residents were more aggressive to neighbours than to strangers. In these cases, losing to a neighbour imposed higher costs on a resident than losing to a stranger (Temeles 1990). One such example comes from a study of red-winged blackbirds, *Agelaius phoeniceus*, where neighbours posed a greater threat of cuckoldry than non-neighbours; consequently residents responded more aggressively to simulated intrusions by neighbouring than by non-neighbouring individuals (Olendorf et al. 2004).

Relative threat hypotheses require a mechanism by which residents can differentiate between neighbours and strangers or, more specifically, between more and less threatening intruders. In many cases, familiarity with an individual is likely to be a contributing indicator of the level of threat to the resident (i.e. neighbours are familiar and pose a small threat). Trials run in territorially

\* Correspondence: I. Booksmythe, Building 116, Daley Road, Acton, ACT 2602, Australia.

E-mail address: [isobel.booksmythe@anu.edu.au](mailto:isobel.booksmythe@anu.edu.au) (I. Booksmythe).

neutral arenas have found that familiar individuals are less aggressive to one another than unfamiliar individuals (Jaeger 1981). However, familiarity alone is an imprecise way to estimate threat, as demonstrated by studies that show spatial and temporal flexibility in the dear enemy response (e.g. Briefer et al. 2008). For example, Husak & Fox (2003) found that collared lizards, *Crotaphytus collaris*, showed increased aggression towards familiar neighbours when they were detected approaching from the wrong direction than when they approached from their usual territory boundary. As lizards were less aggressive towards familiar neighbours than strangers in a neutral arena, the possibility that neighbours were simply not recognized in an unfamiliar context could be ruled out. Thus, lizards could recognize and respond to the potential increase in threat posed by a familiar individual in a new context. Judging the threat posed by an individual based on context requires that residents have the ability to recognize and remember individuals. However, other studies have suggested that differences in the typical behaviours of floating and territory-owning intruders may provide cues that a resident can use to differentiate the two intruder types without the need for individual recognition (Pratt & McLain 2006).

We investigated the occurrence of the dear enemy effect in an Australian fiddler crab, *Uca mjoebergi*, and devised an experimental test to distinguish between the proposed mechanisms by which residents differentiate between neighbours and strangers. We compared fights between neighbouring residents with fights between residents and strangers, to determine the extent to which the dear enemy effect occurs in *U. mjoebergi*. We then manipulated the threat posed to territory owners by familiar neighbouring individuals, by blocking a neighbour's access to his burrow and forcing him to find a new territory, thus increasing his motivation to evict the territory owner.

## METHODS

### *Study Species and Site*

We studied a population of *U. mjoebergi* in the East Point Reserve, Darwin, Australia, from September 2003 to January 2004, during November–December 2008 and September 2009. This species lives in dense, mixed-sex populations on intertidal mudflats where, year round, each individual defends a multipurpose territory consisting of a burrow and a small area (about 10–20 cm diameter) on the surface around the burrow entrance. The burrow is a necessary resource for every crab as a refuge from tidal inundation, desiccation and predation, and is also the site of mating and egg incubation. When on the mud surface, crabs feed largely within their territory boundaries, and males additionally use the territory as an arena for mate attraction, using their greatly enlarged major claw in a conspicuous waving display (Crane 1975). The major claw is also used as a weapon in aggressive interactions between males. A resident defends its territory against 'floaters', wandering individuals that have abandoned or been evicted from their own territories (Morrell et al. 2005). Residents also frequently and repeatedly engage in aggressive interactions with their neighbours when they encroach on the territory to feed (Backwell & Jennions 2004). The consequences of losing to a stranger are eviction from the territory and loss of all associated resources. In contrast, neighbour fights rarely result in eviction, and losing to a neighbour usually appears to entail reduced or lost access to a small area of territory, which may limit feeding opportunities (personal observation).

Aggressive territorial interactions between males consist of a number of distinctive components of varying intensity, from noncontact threats to highly escalated fights. We divided fight

components into four categories, in order of increasing intensity: 'touch/push', where a crab used the outer surface of its major claw to push at the claw of its rival, was the minimum contact constituting a fight; 'grapple', where crabs interlocked their major claws and pushed at each other; 'flick', where a grappling crab used its major claw to lift and flip its rival; and 'digging out', where one crab retreated into the burrow, followed by the other who removed sand, widening the burrow entrance. The sound of claws rubbing together during digging out indicated that pushing or grappling contact probably continued in this stage, but as this was not observable little detail was obtained about the behaviour of the first crab to enter the burrow. Usually this is the resident; however, sometimes an intruder manages to enter the burrow ahead of the resident who then takes up the digging role. While fights that included a digging stage were more often won by the digging crab (binomial test: 35/45,  $P < 0.001$ ) digging did not guarantee a win.

### *Dear Enemy in U. mjoebergi*

We documented naturally occurring fights between floaters and residents ( $N = 145$ ), as well as fights between neighbouring territory holders ( $N = 78$ ). To document resident–floater fights, we scanned the mudflat until we found a male floater. We observed him until he fought with a resident male, and recorded the level of fight escalation (whether crabs grappled, flicked or dug out their rivals), the identity of the winner (the male who occupied the territory after the fight) and the duration (s) of the fight (from first to last contact). We then captured both males and measured their carapace widths and major claw lengths ( $\pm 0.1$  mm) using dial callipers. To avoid potential confounding effects, we used only brachychealous (original-clawed) males in our observations, as a regenerated claw compromises a male's fighting ability (Lailvaux et al. 2009). The large size of the study population ( $37 \pm 17$  crabs/m<sup>2</sup> over an area of about 2500 m<sup>2</sup>, P. Backwell, L. Reaney & R. Slatyer, unpublished data) allowed us to move to different areas between observations, to avoid recording fights involving previously observed individuals.

To document neighbour fights, we scanned the mudflats until we saw a pair of neighbouring males fighting. We then watched these males in the hope that they would fight again. This approach was necessary because of the difficulty in locating fights between neighbours from their onset. Once the neighbours fought, we documented this in the same way as for a resident–floater fight. In most fights between neighbours, however, it is not possible to determine a winner since both males return to their own burrows and there is no obvious change in the behaviour of either male; potential changes to the space use of each male are difficult to quantify and their interpretation is somewhat subjective. Evictions rarely occur in these fights. Fights were considered to have ended when rivals broke physical contact and moved away from each other or resumed other activities such as feeding.

### *Experimental Manipulation of Neighbour Status*

To determine whether fights with familiar individuals are affected by the threat they pose, we experimentally altered the residency status of males after they had fought with a neighbour. We located fights between male neighbours as above, and recorded the duration and level of escalation of their next fight (hereon the 'pre-eviction fight'). The entrance to the burrow of one of the males was then plugged with a dowel rod, evicting the owner, but creating as little disturbance as possible so the evicted crab remained on or within a few centimetres of his territory. The evicted crab was observed for about 5 min as he began to search for a new burrow. If the evicted crab refought the focal neighbour

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