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

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ARTICLE INFO

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

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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 (± 0.1 mm) using dial callipers. To avoid potential confounding effects, we used only brachychelous (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 ± 17 crabs/ m^2 over an area of about 2500 m^2, 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

('posteviction fight') the fight duration and level of escalation were recorded, resulting in paired fights between the same, familiar rivals. As the evicted crab often did not refight the focal neighbour the sample size we were able to obtain was relatively small ($N = 17$ paired fights). However, the resulting low statistical power means that significant results reflect strong effects (see Results). Both crabs were then caught and their claw size and carapace width were recorded. To control for the possibility that refights between the same individuals show a predictable change in duration or intensity, we also recorded the duration and level of escalation of two consecutive fights between neighbour pairs without performing the manipulation ($N = 15$ paired fights).

Statistical Analysis

Carapace width and major claw length are highly correlated ($r_{442} = 0.89$, $P < 0.001$) and both measures of male size gave the same results in our analyses. Here we only present results using claw length. Fight durations were log transformed to meet assumptions of normality. Means and 95% confidence intervals we present below are back-transformed from the log values. All tests are two tailed with $\alpha = 0.05$. We used t tests to compare mean fight durations; likelihood ratio tests were used to compare fight escalation. The nonparametric Wilcoxon signed-ranks test was used where normality could not be achieved through transformation, to test for changes in fight duration across pairs.

RESULTS

Dear Enemy in U. mjoebergi

After the removal of one clear outlier (a resident–floater fight lasting over 15 min), fights between residents and floaters (16.06 s, 95% confidence interval, CI: 12.41–20.78, $N = 144$) were significantly longer than fights between neighbours (10.72 s, 95% CI: 8.21–13.99, $N = 78$; $t_{197} = 2.165$, $P = 0.03$, unequal variances). Fights between residents and floaters were no more likely than neighbour fights to escalate to grappling (78/144 versus 36/78; $G_1 = 1.301$, $P = 0.25$) or flicking (11/144 versus 6/78; $G_1 = 0.000$, $P = 0.99$). However, resident–floater fights were significantly more likely to escalate to digging out the burrow entrance than neighbour fights (44/144 versus 14/78; $G_1 = 4.342$, $P = 0.04$). Across all fights, those that escalated to digging were significantly longer (60.93 s, 95% CI: 46–79.16, $N = 58$) than those without digging (8.27 s, 95% CI: 6.86–9.96, $N = 164$; $t_{220} = 11.296$, $P < 0.001$). When we excluded fights that escalated to digging, there was no difference in the duration of neighbour fights (8.77 s, 95% CI: 6.56–11.74, $N = 64$) and resident–floater fights (7.96 s, 95% CI: 6.22–10.18, $N = 100$; $t_{162} = 0.05$, $P = 0.62$).

Fighting was size-assortative (competitor sizes were correlated) for both resident–floater fights ($r_{142} = 0.48$, $P < 0.001$) and neighbour fights ($r_{76} = 0.57$, $P < 0.001$). To investigate any effects of competitor size on fight duration, we ran a general linear model with adjusted sum of squares, including smaller rival's claw length, larger rival's claw length, fight type, and the interactions between fight type and smaller rival's claw length and fight type and larger rival's claw length. There was a significant interaction between fight type and larger rival's claw length, which indicated that the effect of claw length on fight duration differed between fight types (Table 1). This prompted us to look separately at each type of fight. The duration of neighbour fights was positively related to the smaller rival's claw length ($B = 0.05$, $F_{1,75} = 3.97$, $P = 0.05$); there was a negative relationship with the larger rival's claw length, but this was nonsignificant ($B = -0.04$, $F_{1,75} = 3.122$, $P = 0.08$). The duration of resident–floater fights was not related to either the

Table 1
Effects of rivals' claw lengths on fight duration

	F	df	P
Fight type	1.299	1, 216	0.26
Smaller rival's claw length	1.552	1, 216	0.21
Larger rival's claw length	0.019	1, 216	0.89
Fight type*smaller rival's claw length	1.856	1, 216	0.18
Fight type*larger rival's claw length	4.171	1, 216	0.04

smaller or larger rival's claw length (smaller: $F_{1,141} = 0.008$, $P = 0.93$; larger: $F_{1,141} = 1.797$, $P = 0.18$). However, residency asymmetries often exert a strong influence on fight outcomes, interacting with the effects of size asymmetries (Turner 1994; Jennions & Backwell 1996). In our data set, residency was as good as claw size as a predictor of winning, as both the resident and the larger-clawed individual of a pair won a significant majority of fights (in both cases: 104/144; binomial test: $P < 0.001$). To investigate any effects of residency status on fight duration we ran the model again using floater and resident claw length instead of larger and smaller claw length. There was a positive relationship between duration and the floater's claw length ($B = 0.12$, $F_{1,141} = 55.86$, $P < 0.001$) and a negative relationship with the resident's claw length ($B = -0.07$, $F_{1,141} = 24.951$, $P < 0.001$). Fights were longest when between a large floater and small resident. This was still the case when the model was run again, excluding fights that escalated to digging (floater claw: $B = 0.096$, $F_{1,97} = 32.47$, $P < 0.001$; resident claw: $B = -0.037$, $F_{1,97} = 4.79$, $P = 0.03$).

Experimental Manipulation of Neighbour Status

There was a strong correlation between the claw sizes of rivals in the 'evicted neighbour' experiment ($r_{15} = 0.73$, $P = 0.001$). The durations of pre- and posteviction fights were not correlated ($r_{15} = 0.29$, $P = 0.26$). Posteviction fights were significantly longer (Wilcoxon signed-ranks test: $Z = -3.051$, $P = 0.002$; Fig. 1) and more likely to escalate to digging (10/17 versus 0/17; $G_1 = 18.159$, $P < 0.001$) than pre-eviction (i.e. neighbour) fights. Posteviction and pre-eviction fights did not differ in their likelihood of escalating to grappling (9/17 versus 5/17; $G_1 = 1.964$, $P = 0.16$). No flicks occurred in any fight in this experiment.

To compare the durations of posteviction and natural resident–floater fights, we used the parameter estimates from the model for the
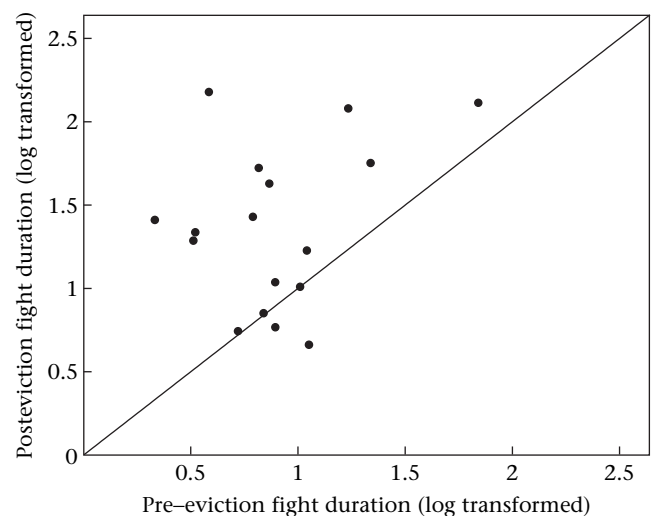

Figure 1. Relationship between the duration of pre- and posteviction fights between neighbouring residents. The line is $Y = X$.

duration of resident–floater fights to predict posteviction fight duration. The equation used was $Y = 0.299403 - (0.069266 \times \text{resident claw length}) + (0.117953 \times \text{evicted neighbour claw length})$. There was no significant difference in the observed and predicted fight durations (paired t test: $t_{16} = -0.496$, $P = 0.63$). This suggests that familiarity did not decrease fight duration.

Our control for refights showed there was no difference in duration between first and second fights of neighbouring pairs when the manipulation was not applied (Wilcoxon signed-ranks test: $Z = 0.227$, $P = 0.82$). First and second fights did not differ in the likelihood of escalating to grappling (6/15 versus 8/15; $G_1 = 0.537$, $P = 0.46$). No digging or flicks occurred in either first or second fights.

DISCUSSION

In *U. mjoebergi*, fights between neighbours were shorter than fights between residents and floaters, and were less likely to involve digging. Digging is a fight component of very high intensity and entails high time and energy costs. Resident–floater fights are therefore longer and more escalated than neighbour fights, a pattern consistent with the dear enemy effect. When we evicted one of a pair of neighbouring residents, making a neighbour into a floater familiar to the resident it then fought, fights between pairs of rivals were longer and more likely to involve digging after one rival had been evicted than when both were neighbouring territory owners. This result provides support for relative threat as the mechanism behind the dear enemy effect in *U. mjoebergi*, as it indicates that a resident is able to respond to the increased threat posed by a familiar individual under new circumstances (in this case, a newly evicted former neighbour).

The effect of claw length on fight duration was different for the smaller and larger rival and between neighbour and resident–floater fights. In neighbour fights, duration increased with the smaller rival's claw length. In resident–floater fights, fight duration increased with increasing claw length of the floater, and with decreasing claw length of the resident. In combination, these results suggest that the rival that is at a greater disadvantage from competitive asymmetries, such as size or residency (Fayed et al. 2008), has the greater influence over the duration of the fight. This is consistent with the predictions of theoretical models of fighting (e.g. sequential assessment, Enquist & Leimar 1983; cumulative assessment, Payne 1998), which expect duration to be strongly influenced by the weaker rival's fighting ability (reviewed in Arnott & Elwood 2009). The different effects seen in the two fight types result from the different importance of asymmetries in such factors as fighting ability, costs, payoffs and the motivation of rivals in each type of fight.

Neighbours and floaters fight residents for different resources: neighbours attempt to increase their access to a small amount of territory area, while floaters seek to evict the resident and claim the entire territory. A floater poses the greater threat to a resident, not only because losing to a floater (eviction) is more costly than losing to a neighbour, but because a floater is more motivated than a neighbour to persist in fighting because of the greater value of the resource at stake. Following our experimental manipulation, durations of posteviction fights between former neighbours were not significantly different to what would be expected for natural resident–floater fights between the individuals observed. Despite having fought previously as neighbours, rivals did not appear to possess information on their relative fighting abilities. First, there was no correlation between the duration of pre- and posteviction fights. Second, familiarity between individuals did not mediate any reduction in fight intensity when the context of the fight changed. We suggest that the difference in motivation of floaters and neighbours means that previous experience of fighting a neighbour

will not allow a resident to predict the fighting ability of that individual when his residency status changes (i.e. he is evicted). Instead, it appears that an increase in the motivation to fight of the former neighbour, which, after eviction, must win a new territory, presents an increased threat that is treated by the resident as equal to that posed by an unfamiliar floater.

It has been suggested that residents use the behaviour of an intruder (e.g. using a higher intensity action to initiate a fight) as a cue to differentiate floaters from neighbours (Pratt & McLain 2006). Our 'evicted neighbour' experiment provides some support for this hypothesis as our manipulation controlled for the effects of contextual cues such as the intruder's direction of approach, as well as familiarity. However, we make the further suggestion that recognizing a difference between floaters and neighbours is unnecessary if the persistence of the intruder determines the intensity of the fight. Our study used measures of fight intensity to compare the aggressive response of residents to intruders of different types. However, we did not record information on which rival initiated a fight, as it is hard to judge the instigator in most cases. While residents are more aggressive in more escalated fights, this may simply be a response to the level of aggression or persistence shown by the intruder.

If, strictly defined, the dear enemy effect describes a resident's aggressive response to different stimuli, it is possible that some studies report the dear enemy effect where it does not occur. In our study, fights between neighbours were shorter and less escalated than fights between residents and intruders, but this does not necessarily indicate a dear enemy effect. When measures of fight intensity, such as duration or escalation, are used to indicate the level of aggression with which a resident responds to an intruder, it is important to ensure that fight intensity is controlled by the resident, or at least that the extent to which the resident determines fight intensity can be distinguished from the effect of the intruder. This problem is not encountered in experimental designs that explicitly elicit threatening behaviour from focal individuals. For example, experiments in songbirds that broadcast calls of familiar and unfamiliar conspecifics within a resident's territory successfully isolate the aggressive response of the resident. Observational studies measuring such variables as the number of attacks on or chases of different intruder types also avoid the confusion of resident and intruder effects. Similarly, designs in which physical contact between rivals is prevented, such as the use of transparent barriers, should enable largely independent measurement of each rival's aggression. While a shortcoming of our study is that we could not separate resident and intruder effects, the results of our manipulation are valuable as a demonstration of the importance of relative threat over familiarity in determining fight duration and intensity.

In summary, *U. mjoebergi* residents fight floaters in high-stakes contests that are longer and more escalated than fights between neighbouring residents. This pattern remains whether the floater is familiar or unfamiliar to the resident, indicating that familiarity does not affect the intensity of fights under new circumstances. Fight intensity can be explained by the level of threat posed by intruders in each type of fight, which differs as a result of motivation and resource value differences between floaters and neighbours. However, the observed patterns can occur without residents being able to differentiate between intruder types, if residents simply adjust their fighting effort appropriately to the aggressiveness and persistence of an intruder.

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