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Original Article

Know thine enemy's neighbor: neighbor size affects floaters' choice of whom to fight

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It can be less costly to help a neighbor repel an intruder than to renegotiate boundaries with a new and potentially stronger individual. Male fiddler crabs will help a smaller neighbor fight off an intruder when the intruder is intermediate in size relative to the 2 neighbors. Fights involving neighbor coalitions are costly for an intruder because he rarely wins when a larger neighbor intervenes. It might therefore be expected that territory-seeking males will avoid fighting residents that have large neighbors. We found a strong effect of the neighbor's size on whether or not a territory-seeking male initiated a fight with a resident male. Although territorial coalitions in the fiddler crab *Uca mjoebergi* are relatively uncommon, the potential for them to occur appears to impose strong selection on the fighting decisions of territory-seeking males. *Key words:* coalitions, fiddler crabs, fight choice, territoriality, *Uca mjoebergi.* *[Behav Ecol 22:947–950 (2011)]*

INTRODUCTION

Fight outcome is largely determined by differences in the resource-holding potential (RHP) of opponents (Parker 1974). As fights are often costly due to greater energetic demands, lost time, and the risk of injury, those individuals that can accurately assess the RHP of an opponent before participating in a contest should be at a selective advantage (Maynard Smith and Parker 1976). However, there are factors other than RHP that can also contribute to contest outcome, such as the relative value of the contested resource to each opponent (Krebs 1982), body condition (Fitzstephens and Getty 2000), age (Kemp 2003), energy reserves (Marden and Waage 1990), fighting experience (Hsu and Wolf 2001), and territorial coalitions (Detto et al. 2010).

In some territorial species, residents are less aggressive toward neighbors than toward strangers who are nonterritorial "floaters" ("dear enemy" effect). In most cases, this occurs because neighbors are familiar and/or pose less of a threat (i.e., they are only temporarily intruding onto the focal individual's territory) compared with unknown, territorial intruders who could potentially challenge the resident for his territory (Temeles 1994). This creates a stable community due to the benefit of reduced conflict that accrues to all residents. This can, in some cases, lead to residents helping their neighbors defend their territory against intruders (Booksmythe et al. 2010). By retaining an existing neighbor, a resident removes the cost of having to renegotiate boundaries with a new neighbor. Furthermore, because a new neighbor has evicted the former neighbor, it is, on average, likely to be a relatively stronger individual. This increases the likelihood that the new neighbor will reduce the size of the resident's territory (Getty 1987; Mesterton-Gibbons and Sherratt 2009). Coalitions that arise due to this type of by-product mutualism have been reported in 4 species: rock pipits (*Arthus petrosus*) and 3 fiddler crabs (*Uca mjoebergi*, *U. annulipes*, and *U. elegans*) (Elfstrom 1997; Backwell and Jennions 2004; Booksmythe et al. 2010; Detto et al. 2010; Milner, Jennions, et al. 2010). In each case, males have been seen to leave their own territory to help familiar male or female neighbors repel intruders (i.e., territory-less floaters). In fiddler crab species, male–male coalitions mainly occurred when the ally was larger than the intruder who, in turn, was larger than the assisted male (Backwell and Jennions 2004; Detto et al. 2010). Males appear to make judicious size-based decisions as to when they should help, which suggests that they can determine the size of an intruder relative to themselves and their neighbor. We now have a relatively good understanding of the circumstances under which coalitions are formed in fiddler crabs (Detto et al. 2010), but we know nothing of the broader selective pressures imposed by their potential formation. For example, does the formation of defensive coalitions influence which individuals a territory-seeking male challenges?

In fiddler crabs, territory-seeking males frequently bypass and avoid many resident males prior to initiating a fight (Milner, Booksmythe, et al. 2010). Fight outcome in fiddler crabs is largely determined by claw size (Morrell et al. 2005). In order to counteract an ownership advantage (Fayed et al. 2008), territory-seeking males tend to choose rivals that are slightly smaller than themselves (Jennions and Backwell 1996). This can account for males avoiding larger residents when searching for a territory, but it does not explain why they pass and avoid numerous males of a seemingly "contestable" size. Why are these males avoided? Fighting in fiddler crabs is costly and can result in wasted time, claw loss, injury, and even death (Milner, Detto, et al. 2010). The costs imposed on an intruding male are likely to be exaggerated during coalition fights. This suggests that selection should favor males that reduce the risk of these potentially costly interactions. More importantly, if a resident assists his neighbor, the intruder has a much lower likelihood of winning a fight (Milner, Detto, et al. 2010).

Here, we investigate whether the occurrence of defensive coalitions in the fiddler crab *U. mjoebergi* influences a territory-seeking male's choice of opponent. Specifically,

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do territory-seeking males take into account the size of neighboring males before they initiate a fight with a resident?

MATERIALS AND METHODS

The study was conducted at East point reserve, Darwin, Australia from September to December 2009.

Study system

Uca mjoebergi is a small fiddler crab (carapace width < 20 mm) that inhabits intertidal mudflats in northern Australia. They occur in dense mixed sex colonies (37 ± 17 crabs m−2; Slatyer R, Reaney LT, Backwell PRY, unpublished data; inter-burrow distance between neighboring males: 11.84 ± 3.49 cm; see RESULTS), and both sexes defend a territory centered on a burrow (Reaney and Backwell 2007). Territories are uniformly distributed. Burrows are a vital resource as they are used as a site of reproduction, as well as shelter from tidal inundation, predation, and desiccation (Smith and Miller 1973; Backwell and Passmore 1996; Koga et al. 2001). The small area of sediment surrounding the burrow is the source of food (organic matter deposited on the sediment each high tide; Crane 1975). The species shows pronounced sexual dimorphisms. Males have one small feeding claw and one greatly enlarged ("major") claw (up to 50% of total body weight; 14.97 ± 4.29 mm; see RESULTS). Females lack a major claw and instead have 2 small feeding claws (Crane 1975). The enlarged claw is used both for mate attraction and fighting. Fights occur over territories and either involve boundary disputes between 2 resident neighbors or a territory-seeking male (hereafter, floater) trying to evict a resident.

Do floaters take into account the size of their opponent's nearest neighbor?

To determine whether a floater takes into account the size of the neighbor when deciding whether or not to challenge a resident for his territory, we monitored the fighting decisions of males in the field. We captured males and then measured their major claw length (±0.1 mm), after which they were individually released (≥2 m from initial capture point so that they no longer had a burrow). We then followed them until they had fought with 2 resident males. We did not record a focal male's first fight to ensure that he had recovered from any short-term effects associated with his capture (e.g., scared responses). Focal males that won a burrow on their first fight were excluded from the analysis. A fight was classified as any interaction where 2 males touched major claws. After the second fight, the challenged resident male and his nearest neighbor were captured and measured ($N = 50$ pairs of males). To provide a "control," we then located the nearest male of equivalent size (<1 mm) to the fought resident. The control male and his nearest neighbor were then captured and measured. Neither the control male nor his nearest neighbor were ever the challenged resident or the challenged resident's neighbor. The distance between the burrows of the challenged resident and his nearest neighbor and between the control resident and his nearest neighbor were also measured. We used paired *t*-tests to compare the claw size of the different sets of males.

An experimental test: do floaters avoid fighting males with large neighbors?

To determine whether floaters avoid fighting males with large neighbors, we conducted a choice experiment in situ. A focal male was given a choice between 2 pairs of males ($N = 30$). Pair

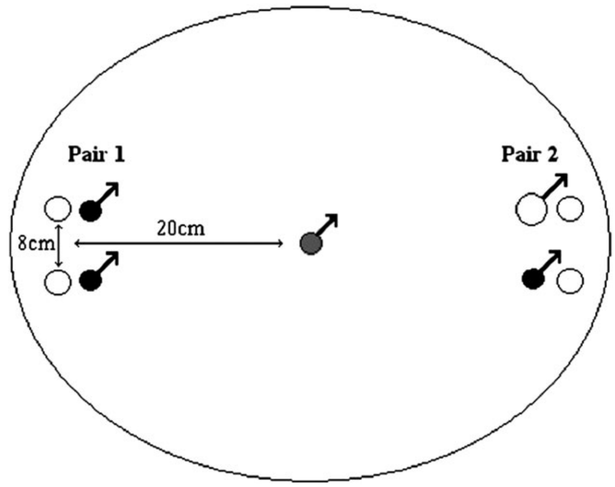

Figure 1
Fight choice arena for experiment testing whether territory-seeking males avoid contesting males with large neighbors. [♂]: Focal/floater male; [♂]: large male resident; [♂]: size matched male residents; and [○]: resident male burrow.

1 consisted of 2 size-matched males (<1 mm) that were 1–2 mm smaller than the focal male. Pair 2 consisted of a male that was also 1–2 mm smaller than the focal male, and a male that was 2–6 mm larger than the focal male. Males in each pair were tethered (2 cm piece of cotton glued to the carapace and attached to a nail inserted into the sediment) and placed 8 cm apart and each 3 cm in front of their own artificial burrow. The 2 pairs were on opposite sides of a test arena equidistant from the focal male release point (20 cm away) (Figure 1). A barrier was placed around the arena to prevent other males entering and/or the focal male leaving the arena. A positive choice was scored if the focal male moved in a direct line toward and then fought with 1 of the 4 tethered males ($N = 20$). A trial was discarded if the male ran immediately after being released or did not initiate a fight within 3 min ($N = 10$). A new set of males was used in each trial. To determine whether the focal male avoided fighting a male with a neighbor larger than himself, we conducted a chi-square goodness-of-fit test. We were only interested in cases where a male chose a similar sized opponent. In such cases, the null hypothesis is that the ratio of approaches to Pair 1 to Pair 2 should be 2:1.

Summary statistics are presented as mean ± standard deviation. All tests are 2 tailed with $\alpha = 0.05$.

RESULTS

Do floaters take into account the size of their opponent's nearest neighbor?

The mean size of the floater males was 15.55 ± 3.16 mm ($n = 50$). These males were of average size and did not differ significantly from the population mean of 14.97 ± 4.29 mm ($n = 222$) (Independent sample *t*-test, unequal variances: $t_{94.55} = 1.098$, $P = 0.275$). In agreement with earlier studies, we found that floaters generally fought males that were slightly smaller than themselves (resident: 13.26 ± 3.44 mm) (Paired *t*-test: $t_{49} = 4.721$, $P < 0.001$) (Figure 2).

The opponent's nearest neighbor was, on average, significantly smaller than the floater (neighbor: 13.49 ± 3.59 mm $t_{49} = 4.721$, $P < 0.001$). The size difference between the floater and his opponent's nearest neighbor was not simply a by-product of the floater's choice of a smaller opponent

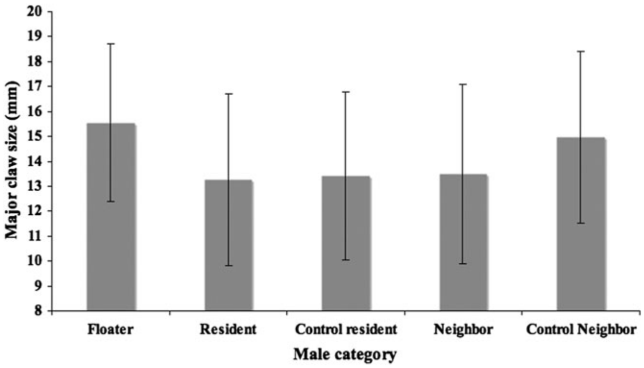

Figure 2
Major claw size (millimeter) of the intruding floater male, resident male fought, control male resident, fought male resident's neighbor, and control male resident neighbor.

combined with smaller males clumping together. Although control and opponent males were closely size-matched, the nearest neighbors of control males were significantly larger than those of opponent males (control neighbor: 14.96 ± 3.44 mm; $t_{49} = 2.227$, $P = 0.031$). Consequently, the control male's nearest neighbor did not differ significantly in size from the floater ($t_{49} = 0.982$, $P = 0.331$) (Figure 2).

The inter-burrow distance between the opponent and his nearest neighbor (11.39 ± 3.68 cm) did not significantly differ from that of the control resident and his nearest neighbor (11.84 ± 3.49 cm; $t_{48} = 0.601$, $P = 0.551$).

Do floaters avoid fighting males with large neighbors?

In 18 of 20 fights, the focal floater male fought a size-matched male slightly smaller than himself. In 17 of these 18 fights, the floater avoided fighting a male who had a larger neighbor. This is significantly more often than predicted by the null hypothesis ($\chi^2_1 = 6.25$, $P = 0.012$).

DISCUSSION

We have provided strong evidence that territory-seeking male *U. mjoebergi* choose whom to fight based partly on the size of the potential opponent's nearest neighbor. Floaters preferentially fought slightly smaller males, but both the observational study and experiment test show that they tend to avoid such males if their nearest neighbor was larger than themselves. Previous studies have shown that floaters usually target slightly smaller males, presumably to counter a well-documented ownership advantage (Jennions and Backwell 1996; Fayed et al. 2008). However, no study has shown that the size of neighbors influences which resident a floater will attack. Our results might help to explain why territorial coalitions are rarely seen in fiddler crabs: only 6.3% of fights between an intruder and floater resulted in a territorial coalition in *U. mjoebergi* (Backwell and Jennions 2004). Specifically, if floaters avoid males with larger neighbors, this decreases the likelihood that neighbors will form a territorial coalition to repel the floater. Our result might also account for the observation that floaters frequently avoid males of a seemingly suitable size (i.e., slightly smaller than the floater) when searching for a new territory.

It is clear floaters can reduce the costs associated with coalition fights by paying attention to the size of potential opponents' neighbors. In addition, however, floaters that target males with smaller neighbors are effectively determining their social environment and thereby altering the selection pressures that both they and residents experience (Oh and Badyaev 2010). In general, much emphasis has been placed on the benefits of associating with weaker and/or less attractive males. For example, it is beneficial for a male to have a small neighbor when establishing and maintaining territory boundaries because smaller males are less costly to fight (i.e., fights are shorter as smaller neighbors retreat sooner) (Pratt and McLain 2006). In addition, by preferentially associating with smaller or less attractive conspecifics, males can increase their perceived attractiveness to mate–searching females (Bateson and Healy 2005). Callander, Jennions, and Backwell (unpublished data) recently showed in *U. mjoebergi* that there was a mating cost to being surrounded by more attractive males and argued that by retaining (i.e., helping) smaller neighbors, males could potentially increase their relative attractiveness. Similar results have been reported in the house finch *Carpodacus mexicanus*, whereby some less attractive males increase their attractiveness by actively seeking out social groups composed of even less attractive males (Oh and Badyaev 2010).

Our study is a reminder that there can also be costs to associating with weaker males. In *U. mjoebergi*, floaters are less likely to attack residents with large neighbors (this study), and when they do the neighbor will often help the resident retain his territory (Backwell and Jennions 2004; Detto et al. 2010). Given the costs and benefits of larger neighbors, it is unclear what size neighbor will maximize a given male's fitness. Answering this question is beyond the scope of the current study. Nonetheless, our results provide strong evidence to suggest that even though the formation of territorial coalitions in *U. mjoebergi* is relatively uncommon, the potential for such coalitions imposes strong selective pressures on the fighting decisions of territory-seeking males as well as the helping decisions of residents. Ultimately, these selective pressures should affect the social structure of the population.

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