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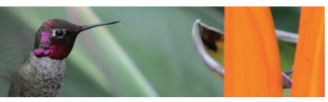

Even Weak Males Help Their Neighbours: Defence Coalitions in a Fiddler Crab

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Abstract

Large male fiddler crabs sometimes help smaller neighbours to defend their territories against intruders. These coalitions occur when the helper is likely to defeat the intruder (helper larger than intruder) *and* the neighbour is likely to lose his territory without help (intruder larger than neighbour). Previous studies of coalitions have excluded males with regenerated claws. Such claws are weaker weapons that make the bearer competitively inferior. Here, we show that male *Uca annulipes* with regenerated claws are as likely as males with original claws to help their neighbours in territory defence, even though, as weaker males they potentially pay greater costs, being more likely to lose their undefended burrow. We suggest that males with regenerated claws gain greater benefits from retaining a current, small neighbour and that, as in non-coalition fights, the regenerated claw acts as a visual bluff in the early stages of combat. Furthermore, we show that intruders with regenerated or original claws are equally likely to be attacked by a 'helping' neighbour. This bolsters the argument that males cannot visually differentiate between original and regenerated claws.

Introduction

Territorial animals need to defend their territory from intruders that try to steal it. In species where males differ greatly in size, hence strength, smaller males are at a disadvantage: How do they fight off larger rivals and keep their territories? In four species (a pipit and three fiddler crabs; Elfstrom 1997; Backwell & Jennions 2004; Booksmythe et al. 2010; Detto et al. 2010; Milner et al. 2010), small males gain help from larger neighbours in repelling intruders. In all cases, helping has been explained as by-product mutualism: the immediate cost of helping to retain a small, familiar neighbour is less than that of renegotiating territory boundaries with a larger replacement neighbour (Krebs 1982; Getty 1987).

Helping is costly. Fighting is dangerous, energetically expensive and, furthermore, helpers leave their own territories to fight the intruder on a neighbour's territory, thereby leaving their own territories temporarily undefended (Crane 1975; Backwell et al. 2000; Hemmi & Zeil 2003). Although costly, helping is effective as it increases the likelihood that small residents retain their territories. In unassisted fights in the fiddler crab *Uca annulipes*, residents lost their territories in 31% of the cases when they were attacked by an intruder, but only 10% of cases when assisted by a neighbour (Detto et al. 2010).

In fiddler crabs, there is a clear size relationship between the males involved in assisted fights: helper > intruder > assisted neighbour (Detto et al. 2010). This pattern is thought to arise because of the judicial use of help: males assist when their neighbour is most likely to lose his territory (i.e. the intruder is larger than the neighbour) and when they are most likely to defeat the intruder (i.e. the helper is larger than the intruder).

Coalition formation in fiddler crabs is particularly interesting because there is a potentially confounding effect of deceptive signalling. In all fiddler crabs, males that lose their large claw (during fights, predation attempts or faulty moults) regenerate a new claw that is eventually the same length as the original claw (Yamaguchi 1973). In some species, including all three that form defence coalitions (*U. mjoebergi, U. elegans* and *U. annulipes*), the regenerated claw is very different in structure to the original. It is much lighter than an original claw, with a thinner exoskeleton, a smaller pincer-closing muscle, and lacks teeth on the inner surfaces of the pincers (Backwell et al. 2000; Lailvaux et al. 2009; Fig. 1). Regenerated claws are inferior weapons (Lailvaux et al. 2009; McLain et al. 2010) and effectively bluff fighting ability to deter potential opponents during the early stages of a contest (Backwell et al. 2000).

All previous studies on coalition formation in fiddler crabs have excluded males with regenerated claws as a confounding source of variation (Backwell & Jennions 2004; Booksmythe et al. 2010; Detto et al. 2010; Milner et al. 2010). Claw regeneration might have an effect on coalition formation because it alters the costs and benefits of helping. If helping occurs when the helper is most likely to defeat the intruder, then males with regenerated claws should be less likely to assist their neighbours because they are competitively inferior. Conversely, males with regenerated claws might have more to gain from helping a small neighbour because they are also more likely to lose fights over territory boundaries with a new, larger replacement neighbour. It is unknown whether these possible changes in costs and benefits for potential helpers cancel out. In addition, males are most likely to assist when a small neighbour is at greatest risk of losing his territory to an intruder. If the intruder has a regenerated claw, and the potential helper can detect this, then he should be less likely to assist.

Fig. 1: An original (top) and regenerated (bottom) *Uca annulipes* claw.

Here, we test whether: (1) males with regenerated claws are as likely as original-clawed males to help their neighbours and (2) helping is equally likely to occur when the intruder has a regenerated rather than original claw. We use the fiddler crab *U. annulipes*, a territorial crab that lives in dense, mixed sex colonies. Territories, which consist of a central burrow and surrounding surface area, are essential for an individual's survival and reproductive success. The central burrow is a refuge from predators and the high tide, a site for mating and incubation, and a source of water during low tides (Backwell & Passmore 1996). The surface area surrounding the burrow is used for feeding and courting. Territories are vigorously defended against wandering crabs and intrusion by neighbours. The indeterminate growth of fiddler crabs results in a wide range of body sizes. Because fighting success is largely determined by size, neighbours can differ vastly in their defence abilities so that coalitions are common (Detto et al. 2010).

Methods

We studied *U. annulipes* in the Chukwani Mangroves, Zanzibar (6°13′21″S, 39°12′14″E), from Sept.–Oct. 2010. We experimentally tested whether claw regeneration affects the likelihood of coalition formation. We simulated an attack by an unknown male on a resident and observed whether his neighbour assisted him in defending his territory. To do this, we caught a territory-holding male (>2 m away from the focal resident) and tethered him to a nail with a 2 cm length of cotton thread glued to his carapace. We then located a pair of males who were nearest neighbours of the appropriate relative sizes: potential helper > tethered intruder > resident. The tethered intruder was placed 5 cm from the focal resident, on the opposite side of his burrow to the potential helper so that he did not pose a direct threat to the neighbour's territory. We observed the crabs until they were all surface active and the resident and tethered intruder had started to interact.

We then recorded whether the neighbouring male approached and fought (minimum of claw touching) the tethered intruder within 5 mins. We used each trio of individuals in a single trial. All males were released at the end of each trial, and their burrows were marked to avoid reuse.

We ran 20 trials in each of three treatments. In the first treatment, all three males had original claws. In the second treatment, the tethered intruder had a regenerated claw, and the other two males had original claws. In the third treatment, the neighbouring male (potential helper) had a regenerated claw, and the other two males had original claws. All statistical tests were performed using SPSS software (Ver. 19.0 SPSS, Chicago, IL, USA) with $\alpha = 0.05$.

Results

The sizes of each type of male did not differ between the three treatments (ANOVA: tethered intruders: $F_{2,57} = 1.43$, $p = 0.25$; mean claw length = 2.28 cm; potential helpers: $F_{2,57} = 1.45$, $p = 0.24$; mean claw length = 2.50 cm; resident males: $F_{2,57} = 0.99$, $p = 0.38$; mean claw length = 1.44 cm). The size difference (claw length) between the three males within a trial also did not differ (potential helper – tethered intruder: $F_{2,57} = 1.30$, $p = 0.28$; tethered intruder – focal resident: $F_{2,57} = 0.01$, $p = 0.99$). Given the consistent size differences among treatments, we could then test for an effect of claw regeneration on the likelihood of coalition formation.

When all males had original claws, nine of the 20 neighbours helped the resident male to fight the tethered intruder (45%). When the tethered intruder had a regenerated claw, eight of the 20 neighbours assisted in the fight (40%). When the neighbour (potential helper) had a regenerated claw, in ten of 20 cases, they assisted in the fight (50%). There was clearly no effect of claw type on helping behaviour (likelihood ratio test: $G = 0.41$; $df = 2$, $p = 0.82$).

Discussion

Intruding males with regenerated claws were as likely to be attacked by a 'helping' neighbour as those with original claws. Regenerated claws are weaker weapons so intruders with regenerated claws posed less of a threat to a small resident. If helpers assist when their neighbours are most likely to lose a fight (see Backwell & Jennions 2004; Detto et al. 2010), we would expect the rate of helping to be lower when the intruder has a regenerated claw because these weaker males are less likely to evict a resident territory owner. It is possible that males with a regenerated claw, despite being weaker competitors, still pose a serious threat to a smaller resident. A more likely explanation, however, is that the 'potentially helpful' neighbour cannot differentiate between regenerated and original claws. This has been suggested in previous work on *U. annulipes*: territory-seeking males do not disproportionately target males with regenerated claws when fighting for a new burrow, even though these males are weaker and easier to beat (Backwell et al. 2000).

We also found that males with regenerated claws were as likely as original-clawed males to help their neighbours in territory defence. While males might be unable to visually differentiate between original and regenerated claws (Backwell et al. 2000; Reaney et al. 2007), it is unlikely that males with regenerated claws are themselves unaware of their lower fighting ability. Previous work shows that they are more likely (than original-clawed males) to lose their territories in fights and that, when they need to obtain a new territory, they avoid fights and seek out empty territories (Backwell et al. 2000). As males with regenerated claws tend to avoid fights, why do they still assist smaller neighbours to repel intruders? Helping is costly because the helper leaves his own territory and fights in the centre of his neighbour's territory. This leaves his own burrow unguarded and open to potential occupation by another territory-seeking male. Regenerated clawed males face greater costs than original-clawed males because, if their territory is invaded while helping, they are less capable of winning it back and are also less likely to win a fight for a new territory (see Backwell et al. 2000).

So why are males with regenerated claws as likely as original-clawed males to assist their neighbours despite the greater risks? One plausible explanation is that there are greater rewards. It could be more important for a regenerated male to retain a small male as a neighbour because he has more to lose if he has to renegotiate territory boundaries with a replacement neighbour. The new, larger neighbour will require more feeding and courting space, and a weaker regenerated claw male might be less able to avoid conceding some of his territory. It may therefore be more important for a regenerated claw male to retain his current neighbour. The greater costs of helping might balance by the higher gains from retaining a small, familiar neighbour. An alternative explanation is that the strength of the helping male is not critical to defending a neighbour's territory.

Facing two rivals is clearly more challenging for an intruder than facing a single opponent, even if one of them is weaker than expected for his claw size. Furthermore, as our data suggest, intruders are probably incapable of differentiating between original and regenerated claws so, as in non-coalition fights, the regenerated claw might act as a deceptive signal during the early stages of aggressive encounters (Backwell et al. 2000).

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