

Original Article

The effects of neighbor familiarity and size on cooperative defense of fiddler crab territories

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Cooperation between neighbors in territory defense is expected when the cost of helping a neighbor is less than that of establishing new boundaries with a successful usurper of a neighboring territory. Cooperation has been documented in 3 species of fiddler crab and is understood to depend strongly on the relative sizes of participants—large residents will help smaller neighbors repel intermediate-sized intruders. Simply meeting these criteria does not, however, guarantee that helping occurs, and additional factors are likely to affect the benefits of providing help. We tested whether the likelihood that a large resident would help his smaller neighbor was affected by neighbor familiarity or the relative size of the smaller neighbor, by replacing neighbors with smaller, larger, or size-matched individuals and then simulating intrusions onto their territories. The likelihood of helping did not differ between familiar and unfamiliar neighbors of the same size, but it decreased when the replacement resident differed in size from the original resident. These results suggest that although residents do not recognize their neighbors individually, size acts as a cue to neighbor identity. *Key words*: cooperative defense, familiarity, individual recognition, neighbor, size, territory, *Uca annulipes*. [*Behav Ecol*]

INTRODUCTION

Territorial animals vigorously defend their territories from intruders but often show little aggression toward their established neighbors (the “dear enemy” effect, Jaeger 1981). This leads to stable neighborhoods in which all residents benefit from the reduced costs of aggressive interactions with neighbors. Neighborhood stability can be mediated through a range of mechanisms from strict adherence to boundary lines, to established social dominance relationships between neighbors (Stamps and Krishnan 1994). Cooperation between neighbors in defense against conspecific intruders is predicted to be advantageous under such conditions (Getty 1987). Empirical examples are limited: cooperative territory defense has been shown in rock pipits (*Anthus petrosus*; Elfström 1997) and 3 species of fiddler crab (*Uca mjoebergi*; Backwell and Jennions 2004; *Uca annulipes*; Detto et al. 2010; Milner et al. 2010; *Uca elegans*; Booksmythe et al. 2010). In all 4 species, male residents will leave their own territories to repel intruders on neighbors’ territories. The benefits to the defended male are clear. For example, in fiddler crabs, unassisted residents are more likely to be evicted than residents whose neighbors intervene (Backwell and Jennions 2004; Detto et al. 2010). Less obvious is why helpers pay the costs of fighting intruders that do not pose a direct threat to them, thereby leaving their own territories temporarily undefended. Helping can, however, be understood in the context of the individual benefits of stable neighborhoods. When an intruder usurps a territory, all neighboring residents must fight the new, often larger and stronger, neighbor to reestablish territorial relationships (Krebs 1982). If the costs of renegotiation outweigh those of helping to repel an

intruder, it can be better to help existing neighbors defend their territories than to risk their replacement (Getty 1987; Mesterton-Gibbons and Sherratt 2009).

In fiddler crabs, the relative size of neighbors and intruders strongly affects 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 neighbor (Detto et al. 2010). Size is an advantage in fiddler crab fights (Jennions and Backwell 1996), and residents appear to use this information to predict their neighbors’ and their own chance of success in repelling intruders. This makes them more likely to provide help when their neighbor is likely to lose if unassisted (intruder > neighbor) and when they are likely to defeat the intruder (helper > intruder). The second condition is important as an intervening neighbor takes over the fight completely and the resident no longer participates. Finally, the size pattern means that, as smaller residents do not help their larger neighbors, reciprocity cannot explain the occurrence of helping in these crabs.

Although the size of neighbors and intruders is clearly important in determining whether helping benefits the helper, the observed rate of helping varies across studies of cooperative territory defense that have experimentally manipulated the relative sizes of participants. Detto et al. (2010) found that resident *U. annulipes* provided help in 80% of trials in which helper > intruder > neighbor, whereas resident *U. elegans* provided help in 50% of equivalent trials (Booksmythe et al. 2010). Additional factors such as population density, size distributions, or neighborhood stability might partly account for these differences in rates of helping. One potentially key factor is whether residents have been neighbors long enough to establish stable territorial relationships (i.e., “familiarity”), which occurs through aggressive interactions between neighbors. The benefits of providing help to new neighbors should be greatly reduced if access to territory remains to be negotiated. Accordingly, Detto et al. (2010) found that male *U. annulipes* that had been introduced into a new burrow,

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and therefore had unfamiliar neighbors, were less likely to provide help than “control” males who had been captured and replaced in their own burrow. Even so, retaining a small unfamiliar neighbor in favor of a larger unfamiliar intruder could still benefit a resident, as neighbors are rivals in many competitive situations. For example, having smaller neighbors could increase success in territorial disputes and is advantageous when competing to attract mates (Callander et al. 2011), as females prefer larger males (Backwell and Passmore 1996). The benefits of helping might therefore be expected to increase with decreasing neighbor size, even when neighbors are unfamiliar. This could result in an increase in the likelihood that a resident provides help as neighbor size decreases, a possibility that can be explored by manipulating the size of new neighbors.

One issue that arises when manipulating neighbor size is that size could also be an important cue in neighbor recognition (i.e., could affect assessment of familiarity). Individual recognition has been shown in one species of fiddler crab, *Uca capricornis*, in which males used unique color patterns on the carapace to recognize neighboring females (Detto et al. 2006). Currently, individual recognition has not been demonstrated in any fiddler crab species known to cooperate in territory defense. However, studies of fighting behavior indicate that *U. annulipes* can visually assess the size of other crabs and use this information when deciding, for example, whether to initiate a fight (Milner et al. 2011). It is therefore plausible that size might be used as an imperfect cue in neighbor recognition. It is also possible, however, that discriminatory helping behavior does not require individual recognition of neighbors. Residents could use simple rules-of-thumb to judge whether a neighbor is established and familiar or a recent arrival. For example, a potential rule for when to help could be based on the time since the last fight with a neighbor at a known location. The interval will be short when the neighbor is new because territorial incursions occur often, but long once neighbors are established.

We investigated the importance of neighbor familiarity to cooperative defense of fiddler crab territories, experimentally manipulating neighbor identity by replacing neighbors with unfamiliar smaller, larger, and size-matched individuals or retaining the familiar neighbor. We then investigated the effect of the relative size difference between neighbors on the likelihood that help was provided. By simulating intrusions onto the territories of replacement neighbors, we could compare the propensity of residents to help familiar versus unfamiliar neighbors and different size classes of unfamiliar neighbors.

MATERIALS AND METHODS

We studied the fiddler crab *U. annulipes* in Chukwani, Zanzibar. This species occurs in large populations on intertidal mudflats where each individual defends a burrow and a small (~15 cm diameter) area on the mudflat surface around the burrow entrance, hereafter referred to as the “territory.” The burrow is vital for shelter and breeding, and feeding takes place within the territory on the mudflat surface (Crane 1975). Residents defend their territories against wandering individuals that have abandoned or been evicted from their own territories and intrusions by neighbors. Territories do not have strictly delineated boundaries, and access to the area around the burrow is more likely dictated by dominance relationships between neighboring residents (Christy J, personal communication). Fiddler crabs are sexually dimorphic, with males having one greatly enlarged (“major”) claw that is used as a weapon in territorial conflict (Jennions and Backwell 1996). In *U. annulipes*, the recorded major claw size of displaying (sexually mature) males ranges from 9 to 39 mm (Crane 1975). All the crabs used in our experiments were male.

We located pairs of different-sized males that were neighbors with burrows <15 cm apart ($n = 100$ pairs). The smaller neighbor was caught and measured using dial calipers (± 0.1 mm major claw length). We then either placed the smaller neighbor back in his burrow (control, $n = 25$) or replaced him with a male that was 1) size matched within 0.5 mm ($X \pm$ standard deviation difference: 0.22 ± 0.16 mm or $1.7 \pm 1.4\%$, $n = 25$), 2) >1 mm smaller (3.2 ± 1.12 mm or $22.2 \pm 7.0\%$ smaller, $n = 25$), or 3) >1 mm larger (2.6 ± 1.27 mm or $21.8 \pm 10.9\%$ larger, $n = 25$). All replacement males were still smaller than the large resident. Replacement males were caught at their own burrows and measured before being placed in the new burrow, so they had the same handling as control males. The focal burrows were then observed until both the small (control or replacement) neighbor and the large resident were simultaneously active on the surface, and the large resident had an unobscured view of the small neighbor. Then, before any physical contact occurred between the 2 crabs, the observer moved to startle both of them into their burrows. Another male was then tethered (with a ~1 cm length of cotton thread glued to the carapace and tied to a nail pushed into the ground) beside the entrance to the small neighbor’s burrow to simulate an intruder (see Detto et al. 2010). Intruders were placed so they could just reach the burrow entrance with their legs but could not enter the burrow. This often led intruders to pull sand from around the burrow entrance, resembling an aggressive action of natural intruders who often remove sand to enlarge the burrow entrance of residents they attempt to evict. Tethered intruders were placed on the far side of the small neighbor’s burrow to avoid posing a direct threat to the large resident’s territory. Intruders (18.3 ± 2.5 mm, $n = 100$) were always intermediate in size between the large resident (22.9 ± 2.8 mm, $n = 100$) and the replacement small neighbor (12.8 ± 3.0 mm, $n = 100$), with a size difference of >1 mm. We then recorded whether the large resident fought with the tethered intruder within the first 5 min after both residents reemerged from their burrows, which we scored as helping. Tethering intruders meant we were only assessing the likelihood that a potential helper responded to the presence of an intruder and not the effectiveness of the help provided. A fight was defined by physical contact between the large resident’s major claw and the intruder. Aggression between the intruder and the smaller neighbor was not a criterion, as one response to an intruder is to retreat into the burrow, which in our trials resulted in no contact between the resident and the intruder. As our trials were performed in a natural population, occasionally a trial would be interrupted by a non-focal crab (such as another neighbor or a wandering individual) either directly interacting with or moving close enough to provoke a reaction from one of the focal trio. These few trials were terminated and are not included in our analysis.

We first separately examined the effects of neighbor familiarity and size on the likelihood that helping occurred. We used log-likelihood ratios (G) to compare control trials to trials with size-matched replacements (i.e., familiarity with no size effects) and smaller replacement trials with larger replacement trials (i.e., size with no familiarity effects). The results of these tests (see Results below) raised the possibility that residents in the smaller and larger replacement treatments used a change in neighbor size as a cue of neighbor familiarity. To investigate this, we then compared treatments with no change in neighbor size (pooled control and size-matched replacement trials) with treatments where the neighbor’s size changed (pooled smaller replacement and larger replacement trials). The 3 tests are orthogonal, so no correction for multiple testing was required. As a shorter distance between burrows can lead to increased interaction between neighbors (Pratt and McLain 2006), we used a logistic regression to test for an effect of

the distance between burrows on the likelihood that help was provided.

RESULTS

The likelihood that the large resident fought with the tethered intruder did not differ between the control and the size-matched replacement treatments (12/25 vs. 14/25; $G = 0.321$, degrees of freedom [df] = 1, $P = 0.571$), indicating neighbor familiarity had no effect when controlling for size (Figure 1). The likelihood that the large resident fought with the tethered intruder did not differ between the smaller replacement and the larger replacement treatments (7/25 vs. 8/25; $G = 0.095$, df = 1, $P = 0.758$), indicating no effect of the relative size of the smaller neighbor when controlling for familiarity (Figure 1). When we compared treatments with no change in neighbor size with treatments where the neighbor's size changed, however, we found that the large resident was significantly more likely to provide help when his neighbor remained the same size (26/50 vs. 15/50; $G = 5.051$, df = 1, $P = 0.025$) (Figure 1). The distance between burrows did not differ between treatments (Table 1); nor did it affect the likelihood that help occurred ($\chi^2_1 = 2.98$, $P = 0.084$, $n = 99$).

DISCUSSION

Resident male *U. annulipes* helped a smaller neighbor against an intermediate-sized intruder in nearly half of the control trials. Residents were as likely to help a size-matched replacement as they were to help a familiar neighbor. At first glance, this suggests that familiarity between neighbors is not a criterion for help. This is an unexpected finding given the theoretically predicted importance of neighbor establishment to cooperative territory defense (Getty 1987), as well as previous empirical work supporting this prediction (Detto et al. 2010).

One explanation is that although the future territorial cost (e.g., fights resulting from territorial incursions) imposed by established neighbors is expected to be lower than that of new neighbors (Getty 1987), this difference in cost is too small to affect the benefit of providing help. Alternatively, the motive for helping might simply be to retain smaller neighbors. If this is the case, our size manipulations suggest that residents only assess whether a neighbor is smaller than an intruder (who, in turn, is smaller than the resident) and do not give greater value to retaining relatively smaller neighbors. The benefits of helping a neighbor might be expected to be greater as neighbor size decreases, given the potential advantages of

smaller neighbors (e.g., Callander et al. 2011). However, we found no difference in the likelihood of helping between the smaller replacement and the larger replacement treatments. This suggests that the size of a smaller neighbor does not affect the net benefit of helping for the resident, at least over the range of size difference created by our treatments. However, if the net benefit of helping declines both as the size of a smaller neighbor increases and also as it decreases below a certain relative size, an optimal size difference between neighbors could drive the pattern observed here. It is difficult though to imagine what costs would increase (or benefits diminish) with decreasing size of a smaller neighbor. It is possible that crabs below a certain size threshold (e.g., before reaching sexual maturity) are not perceived as part of the territorial or social system by larger crabs; very small crabs are rarely seen interacting with crabs in the sexually mature size range (Booksmythe I, personal observation), and immature recruits do not incur a territorial response from adults in other crab species (Baeza et al. 2002). However, this would not necessarily predict a lower likelihood of helping by a resident because an intruder attacking an insignificantly small "neighbor" would appear to be annexing part of the large resident's own territory, thus provoking direct defense. Furthermore, we doubt this explains our experimental result as the small replacement males used were of reproductive size. Our interpretation, that the size of a smaller neighbor has little effect on a resident's decision to help, does not contradict previous studies that clearly demonstrate that the size ranking of participants is important in determining when help is provided (Backwell and Jennions 2004; Detto et al. 2010). Helping mainly occurs when the potential helper > intruder > neighbor, but our results indicate that given this condition holds, the finer-scale detail of the relative size of the neighbor and potential helper does not influence the decision to help. It is then unclear, however, what factor is the main determinant of whether to help (given helper > intruder > neighbor).

An alternative explanation for our results that is consistent with the strong existing support for the benefits of retaining established neighbors (Getty 1987; Detto et al. 2010) is that *U. annulipes* do not individually recognize neighbors. Instead they might judiciously help neighbors perceived to be established using indirect or contextual cues or simple rules-of-thumb. Individual recognition (recognition based on individually distinctive characteristics) is widespread across many different vertebrate and invertebrate taxa (review: Tibbetts and Dale 2007), including the fiddler crab *U. capricornis* (Detto et al. 2006). However, no evidence exists for individual recognition in *U. annulipes*, which lacks the distinctive

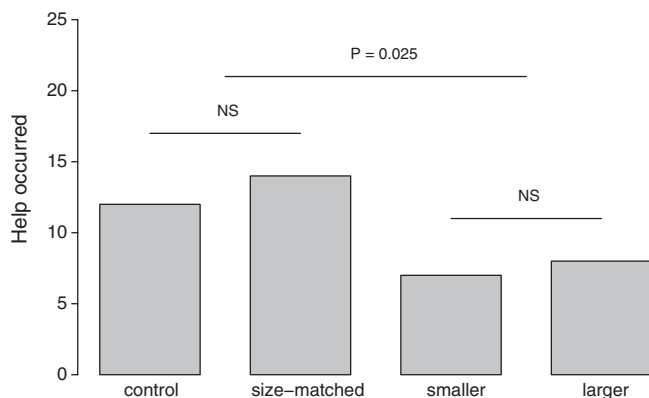


Figure 1
Number of trials in which the large resident fought the tethered intruder.

Table 1

Difference in distance between neighbor burrows in each treatment

| Treatment | Mean \pm SD burrow distance (cm) | Mann-Whitney U | P |
|--------------------------|------------------------------------|------------------|-------|
| Control | 8.14 \pm 3.03 | 307.5 | 0.922 |
| Size-matched replacement | 8.36 \pm 2.7 | | |
| Larger replacement | 8.25 \pm 2.75 | 285.5 | 0.771 |
| Smaller replacement | 8.7 \pm 3.63 | | |
| Neighbor's size constant | 8.25 \pm 2.84 | 1179.0 | 0.747 |
| Neighbor's size changed | 8.48 \pm 3.2 | | |

SD, standard deviation. Comparisons follow the orthogonal design used to compare the likelihood of helping between treatments. We used the nonparametric Mann-Whitney test as data were not normally distributed; however, means are presented to aid comparison.

variation in carapace color markings that facilitates individual recognition in *U. capricornis*. Indirect cues (nonphenotypic, including spatial location and frequency of encounter; Sherman et al. 1997; Mateo 2004) can be sufficient to reliably discriminate between individuals under natural conditions (e.g., Chiu and Kam 2006). Strawberry poison frogs (*Oophaga pumilio*) deposit their tadpoles individually in water-filled bromeliad axils and use the deposit location to recognize their offspring for provisioning. Experimental displacement and replacement of tadpoles showed that mother frogs do not use direct phenotypic cues to recognize their offspring in a new location or to discriminate against unrelated offspring; however, as tadpoles cannot move between axils, under natural conditions location cues would reliably allow frogs to provision their own offspring (Stynoski 2009). The use of indirect cues can be susceptible to error (Tang-Martinez 2001), for example, parental identification of offspring as “young present at the nest” is exploited by cuckoos (Waldman 1988); but error rates could potentially be reduced by using more than one cue. When different cues provide information on different individual qualities, assessing multiple cues in combination can provide a recipient with more precise information than they would gain from one cue alone (e.g., in mate choice: Candolin 2003). Similarly, a cue common to members of a group can enable discrimination between individuals when used in a particular context. For example, female burying beetles (*Nicrophorus vespilloides*) use a chemical indicator of reproductive condition to discriminate between their mate and male intruders on the nest site (Müller et al. 2003). If indirect and/or contextual cues of neighbor establishment are available to fiddler crab residents, we propose that individual recognition is not necessary for judicious cooperative defense decisions. Fiddler crabs spend most of their time feeding and/or displaying on their territories, so it is relatively easy for residents to monitor neighbor continuity. Thus, residents can generally assume that a crab in a neighboring burrow is an established neighbor if they have not recently witnessed an eviction. Even if a neighbor is evicted and replaced without a resident noticing, the new neighbor’s inevitable infringement of a previously stable territorial relationship should indicate that he is an unfamiliar individual (or at least reduce the resident’s motivation to help). Our experimental design allowed visual contact between the large resident and the replacement neighbor, but trials were run before the replacement male encroached onto the larger neighbor’s territory. This “frequency of interaction” cue was therefore unavailable to residents in our study. Interestingly, however, when we compared treatments with and without a change in neighbor size, we found that the large resident was significantly less likely to help when the replacement male differed in size from the original neighbor. This suggests residents use size as a cue to recognize their neighbors and are more likely to detect a new neighbor when he differs in size from the previous neighbor. We could find few examples in the literature of size acting as a context-dependent cue to individual identity. Of course, recipients discriminate based on size when it directly corresponds to some quality of an individual, such as strength when assessing potential fight opponents or fecundity when assessing potential mates (see Andersson 1994; Bradbury and Vehrencamp 1998). However, examples of size as a cue in recognition appear to be limited to the identification of members of a particular class: client fish use size to identify cleaner wrasse (Stummer et al. 2004) and nesting yellow-browed leaf warblers use size to discriminate cuckoo eggs (Marchetti 2000). In fiddler crabs, although size does not correspond to classes of individual, it might work as a contextual cue: residents learn the size of their established neighbors and notice when a new neighbor deviates from this

template (but would not know neighbors by their size in a neutral setting). In combination, the contextual cue of neighbor size plus a simple rule based on the frequency of fights with a neighbor could provide residents with a sufficiently reliable method to determine a neighbor’s familiarity status. This would allow residents to mainly help established neighbors without the need for more sophisticated individual recognition.

In sum, our results suggest that familiarity between fiddler crab neighbors (unlike relative neighbor size) is an important factor determining when to provide help in defense. However, individual recognition of neighbors is unlikely to facilitate the decision to help, which instead depends on perceived familiarity using indirect cues.

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