

# When and Why Do Territorial Coalitions Occur? Experimental Evidence from a Fiddler Crab

Tanya Detto, Michael D. Jennions,\* and Patricia R. Y. Backwell

Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Canberra, Australian Capital Territory 0200, Australia

Submitted June 17, 2009; Accepted December 6, 2009; Electronically published March 19, 2010

**ABSTRACT:** Neighboring territory owners are often less aggressive toward each other than to strangers (“dear enemy” effect). There is, however, little evidence for territorial defense coalitions whereby a neighbor will temporarily leave his/her own territory, enter that of a neighbor, and cooperate in repelling a conspecific intruder. This is surprising, as theoreticians have long posited the existence of such coalitions and the circumstances under which they should evolve. Here we document territorial defense coalitions in the African fiddler crab *Uca annulipes*, which lives in large colonies wherein each male defends a burrow and its surrounding area against neighbors and “floaters” (burrowless males). Fights between a resident and a floater sometimes involve another male who has left his territory to fight the floater challenging his neighbor. Using simple experiments, we provide the first evidence of the rules determining when territorial coalitions form. Our results support recent models that suggest that these coalitions arise from by-product mutualism.

**Keywords:** coalitions, cooperation, dear enemy, fiddler crabs, fighting, territoriality.

## Introduction

When a male establishes a territory, he must fight with his new neighbors to demarcate the territorial boundaries. When these boundaries are established, however, neighbors are often treated less aggressively than are strangers, a phenomenon labeled the “dear enemy” effect (Fisher 1954; Jaegar 1981) that has been noted in numerous taxa (for recent references, see Booksmythe et al. 2010). It has been suggested that the dear enemy effect could extend to cases where territory owners are not simply less aggressive to neighbors but actively help them to repel intruders (Getty 1987; Mesterton-Gibbons and Sherratt 2009). Such territorial defense coalitions could arise if the immediate costs of helping a neighbor to defend his territory are smaller than the costs involved with renegotiating boundaries with a new, often stronger neighbor. In such cases,

cooperation between neighbors is a form of by-product mutualism (Mesterton-Gibbons and Dugatkin 1992; Mesterton-Gibbons and Sherratt 2009). An alternative explanation for defense coalitions is that a resident pays the current cost of helping a neighbor to retain his territory because by so doing he increases the likelihood of future help from the assisted neighbor. If this is true, territorial defense coalitions are maintained by reciprocal altruism (Trivers 1971).

Surprisingly, convincing evidence for territorial defense coalitions, wherein individuals help their neighbors to defend their territories from conspecific intruders, has been reported in only two species (with both cases involving male-male coalitions): rock pipits (*Anthus petrosus*; Elfström 1997) and the Australasian fiddler crab *Uca mjoebergi* (Backwell and Jennions 2004). In both species, territorial males enter the territory of a neighbor and help him to repel an intruder. This behavior requires that males be able to distinguish between residents and intruders. This distinction could be based on individual recognition of neighbors or on distinctive features associated with the two types of males (e.g., in fiddler crabs there is a positional cue because the resident is usually closer to his burrow entrance than is the intruder; Pratt and McLain 2006; fig. 1). In both species, it has been argued that coalitions are maintained through by-product mutualism rather than through reciprocal altruism. In *U. mjoebergi*, for example, in almost every coalition a male left his territory and helped his neighbor only when he was larger than the intruder and the intruder was larger than the neighbor. There was, therefore, a consistent size hierarchy (ally > intruder > neighbor) that makes it improbable that a small neighbor will ever reciprocate and assist a larger neighbor. Reciprocal altruism is therefore unlikely to be involved in the maintenance of coalitions.

The studies of both rock pipits and *U. mjoebergi* were solely observational and based on descriptions of natural coalition formation. Neither study quantified how often coalitions did not form under a given set of conditions (i.e., the role-based size hierarchy described for *U. mjoe-*

\* Corresponding author; e-mail: michael.jennions@anu.edu.au.



**Figure 1:** During a fight, residents can be distinguished from floaters by their proximity to the burrow entrance. Here the resident in the foreground fights off a floater while located partially in his burrow.

*bergi*). It is therefore not possible to determine whether the decision to assist a neighbor was causally related to the relative threat the intruder posed and/or the ability of the ally to repel the intruder. For example, in other fiddler crab species there is a tendency for burrowless males seeking a territory to target slightly smaller residents (Jennions and Backwell 1996) to counteract an ownership advantage (Fayed et al. 2008). If in addition, larger males are generally more aggressive and more often initiate fights, then this could explain the observed size hierarchy without requiring that helping males assess the relative size of neighbors

and intruders. Alternatively, there might be spatial and/or temporal factors that covary with the occurrence of intruders and the propensity of a male to enter his neighbor's territory.

In this study we took an experimental approach to test whether males likely use size-based rules to determine whether it will be beneficial to initiate a territorial defense coalition. We made three discoveries: First, territorial defense coalitions also occur in the African fiddler crab *Uca annulipes* (see also Milner et al. 2010). Second, the decision to help is a judicious one. Males are capable of assessing

the size of an intruder relative to both themselves and their neighbors, and size is a known predictor of fight outcome in *U. annulipes* (Jennions and Backwell 1996). Third, when a neighbor is new (so that territory boundaries are still being established), males are less likely to form a territorial defense coalition.

## Methods

### *Study Site and Species*

The study was conducted on Inhaça Island, Mozambique (26°01'51"S, 32°55'01"E), from October to November, 2008, on a large colony of *Uca annulipes* occupying an elevated sandbar surrounded by mudflats. *Uca annulipes* are typical fiddler crabs that live in dense mixed-sex colonies in which both sexes aggressively defend a burrow and the surrounding surface that makes up their territory. Burrows are vital as refuges during high tide and in which to avoid predators, and as sites for mating and incubation (Backwell and Passmore 1996). Burrowless males (hereafter, "floaters") fight residents in an attempt to acquire their burrows. As with other fiddler crab species, males appear to treat their neighbors as dear enemies, exhibiting lower levels of aggression toward their neighbors than toward floaters (Pratt and McLain 2006).

### *Natural Coalition Formation*

We scanned the mudflat looking for natural fights and noted the outcome and details of any fights involving three males. We recorded the major claw length and carapace width of all males and the distance between their burrows. In total, we collected data on 29 unique three-male fights. It is important to note that many more fights than this were observed, but it was not possible to collect data unless we observed the fight from its initiation to ensure that we could classify the floater, the resident, and the ally with certainty. We compared the outcomes of these fights with those of resident-floater fights observed at the same site over the same time period that did not involve an ally (J. Bolton, P. Backwell, and M. Jennions, personal observations).

### *Does Male Size or Interburrow Distance Predict the Likelihood of Helping?*

To experimentally test the relationship between the probability that a territorial defense coalition occurs and the relative sizes of the floater, the resident, and the potential ally, we caught a natural floater. We then located a pair of nearest neighbors of the appropriate relative sizes to evaluate the following: (1) a control based on the original

pattern (potential ally > floater > neighbor), (2) whether males still help when they are likely to successfully repel the floater but when the resident is less likely to need help (potential ally > neighbor > floater), and (3) whether males still help a weaker neighbor when they themselves are less likely to be successful in repelling the floater (floater > potential ally > neighbor). The mean difference in major claw length was  $4.6 \pm 2.4$  mm between floaters and neighbors,  $5.9 \pm 3.4$  mm between floaters and potential allies, and  $6.4 \pm 4.1$  mm between neighbors and potential allies. The floater was tethered with a 1-cm length of cotton thread that was superglued to his carapace and then tied to a nail that was inserted into the substrate. The floater was positioned 5 cm from the resident's burrow entrance (the short tether ensured that he did not enter the burrow), on the side opposite the potential ally, so that the floater did not pose a direct threat to the resident's territory. We measured the distance between the neighbor and the potential ally to determine whether it had an effect on the likelihood of helping. When we were certain that the potential ally had seen the floater and the resident interact, we observed the crabs for up to 5 min and recorded whether the potential ally fought with the tethered floater. We used different pairs of neighbors in all trials, and tethered floaters were used once per size class treatment (i.e., one to three trials, depending on whether three could be completed in a given day). Using the same tethered male across size treatments is an experimental design (randomized block) that reduces the likelihood that treatments differ due to variation among the tethered males used to elicit helping behavior. For the statistical analysis, however, we did not run a generalized linear mixed model with floater male identity as a random factor because there were too few replicates, especially given a binomial response variable, to estimate random effects. Analyses based on strict pairwise comparisons had lower sample sizes but yielded the same conclusions as those presented that treated unique neighbor-ally pairs as statistically independent.

### *Do Floaters Pose a Direct Threat to Allies?*

We tracked naturally occurring floaters to determine whether they represent a direct future threat to males that help ( $n = 20$ ). We recorded the distance traveled and the number of males the floater passed between successive fights (only those involving the floater and a resident). If they bypass several territories between successive fights, it is unlikely that a floater will go on to challenge a potential ally (i.e., the nearest neighbor) for his territory.

*Does Familiarity with Neighbors Affect the  
Decision to Help?*

To test whether neighbors that have not yet established a relationship are less likely to form a coalition, we caught the larger male of a pair of nearest neighbors. We then returned him to his burrow (control). Ten minutes after he reemerged, we tethered a floater next to the other resident (ensuring the floater was intermediate in size between the two residents) and observed whether the larger resident fought the floater. We then captured the larger male and replaced him with a male of the same size (<1-mm difference in major claw length; treatment). Again we waited 10 min for him to settle after he reemerged before tethering the same floater next to the resident and observing whether the new neighbor assisted the resident. Although this design cannot exclude an order effect, it does control for variation among pairs in how intensely the smaller resident and the floater interact. Preliminary studies suggested that this was biologically a more important source of variation in trial outcome.

*The Cost of a New Neighbor*

A posited benefit of territorial defense coalitions is based on the assumption that the potential ally will have to fight more frequently with a new (probably larger) neighbor than with an established neighbor. To test this assumption, we located and captured three similarly sized males that were not neighbors but that could be observed simultaneously. This controlled for temporal and smaller-scale spatial variation in the number of social interactions at the study site. We then returned one male to his burrow and replaced the other two males with either a smaller or a larger male, respectively (1–3-mm difference in claw length when compared with original resident), and we recorded for 30 min the number of fights they were involved in with their surrounding neighbors. We excluded males from the data set if they sealed or vacated their burrow during the trial. In each trial, we always obtained data from a control male and at least one replacement male. Pairwise analysis yielded the same conclusions as that from an ANOVA of all three male types with missing cases.

*Statistical Analysis*

Unless otherwise stated, all tests were one-tailed, with  $\alpha = 0.05$ . Predictions about directionality were based on a large-male fighting advantage (Jennions and Backwell 1996) and the effect this should have on coalition formation (see Backwell and Jennions 2004). In most cases, two-tailed tests are still significant at the  $\alpha = 0.05$  level.

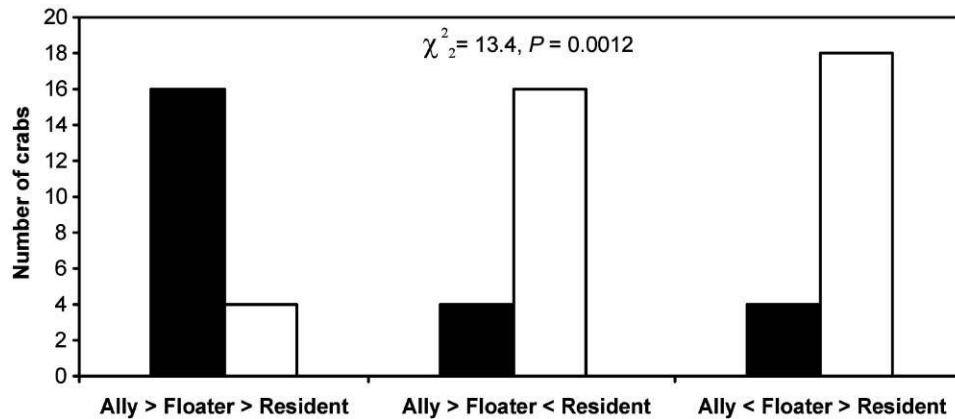
## Results and Discussion

In *Uca annulipes*, defense coalitions occurred when a fight between a resident and a floater was interrupted by the resident's immediate neighbor vacating his territory to fight the floater at the resident's burrow entrance. This intervention increased the likelihood that the resident retained his territory. The floater evicted the resident in 10% of ally-assisted fights ( $n = 3$  of 29) compared with 31% of fights when no ally intervened ( $n = 32$  of 104; Fisher's Exact test,  $P = .02$ ). Defense coalitions are therefore clearly beneficial to the receiver. In defense coalitions, the ally was much larger than both the floater ( $P < .001$ ) and the resident ( $P < .001$ ), while the floater was slightly larger than the resident ( $P = .015$ ; all Wilcoxon tests with  $n = 29$  pairs; mean  $\pm$  SD for claw size: ally,  $25.5 \pm 4.0$  mm; floater,  $21.2 \pm 1.8$  mm; resident,  $19.7 \pm 4.2$  mm). Male size predicts fight outcome, so these results suggest that allies are more likely to help when the resident is under greater threat (floater > resident) but only if the ally is likely to repel the floater (ally > floater). This pattern agrees with that for territorial coalitions in *Uca mjoebergi* (Backwell and Jennions 2004), where fight outcome also depends on male size (Fayed et al. 2008).

To test whether neighbors actually make size-based decisions, we staged fights between a resident and a tethered floater. The relative sizes of the resident, the floater, and the potential ally strongly affected the likelihood that a defense coalition formed ( $\chi^2_2 = 13.4$ ,  $df = 2$ , two-tailed  $P = .001$ ; fig. 2). When the potential ally was larger than the resident and the floater, he helped in 70% of cases (16 of 20) when the resident was smaller than the floater but in only 20% of cases (4 of 20) when the resident was larger than the floater (Fisher's Exact test,  $P < .0002$ ). When the ally was smaller than the floater, however, he helped in only 22% of cases (4 of 18) when the floater was larger than the resident (Fisher's test,  $P < .0005$ ). The decision to help therefore increased with both the likelihood that the resident would be evicted (floater > resident) and the ally's ability to win the fight (ally > floater). Our results clearly indicate that males assess the relative sizes of their neighbor, a floater, and themselves.

Helping is potentially costly, as fights can result in injury, claw loss, and death (Milner et al. 2009). Furthermore, an ally runs the risk of his burrow being usurped when he leaves his territory to assist (Hemmi and Zeil 2003). What compensatory benefits do allies gain? We considered four explanations.

First, allies pay an immediate cost by helping, but they gain later if their assistance is reciprocated (reciprocal altruism; Jaegar 1981). Given the strong trend for males to assist only smaller neighbors (26 of 29 cases; binomial test,  $P < .0001$ ), there is, however, little chance of reciprocity.



**Figure 2:** Effect of relative size on the likelihood of helping. Allies are most likely to help under very specific conditions: when the resident is most in need of help (floater > resident) and when the ally is most likely to be successful (ally > floater). Black bars represent allies that helped; white bars represent those that did not ( $n = 20, 20, 18$ ).

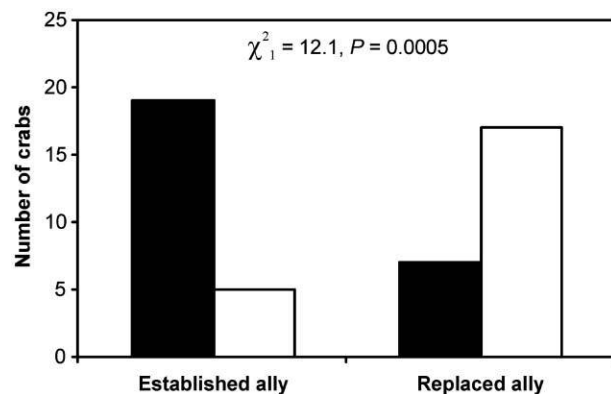
Second, early intervention reduces the likelihood that a floater who loses a fight with a neighbor will next challenge the potential ally for his burrow. However, the data do not support this explanation. (1) Allies were generally the resident's nearest neighbor (interburrow distance:  $11.3 \pm 7.6$  cm,  $n = 13$ ), but in resident-floater fights where no coalition formed, the floater moved  $62.2 \pm 41.7$  cm and bypassed  $4 \pm 2$  males ( $n = 20$ ) before next contesting a burrow. The likelihood that a floater will next challenge a neighbor who does not help is therefore very low. (2) Previous work on another population of *U. annulipes* showed that floaters tend to fight size assortatively, but with residents that are slightly smaller than themselves. Because allies are generally larger than the floaters, this is further evidence against the claim that intervention reduces the likelihood that the floater might challenge the potential ally for his burrow.

Third, allies might be more likely to help neighbors that live close to them because they are reacting to a perceived intrusion by a floater onto their own territory. Although this is a seemingly nonadaptive explanation based on a perceptual error, if the outcome of such errors is a net fitness benefit to the ally, then helping is still under selection due to its current function. The available evidence suggests, however, that interneighbor distance does not predict whether a potential ally helps (logistic regression: distance:  $\chi^2_1 = 1.399$ ,  $P = .237$ ; size class:  $\chi^2_2 = 10.95$ ,  $P = .004$ ; interaction:  $\chi^2_2 = 3.66$ ,  $P = .16$ ; helpers:  $10 \pm 3$  cm,  $n = 21$ ; nonhelpers:  $11 \pm 3$  cm,  $n = 36$ ).

Fourth, males protect established neighbors in order to maintain a dear enemy relationship and to avoid the cost of renegotiating territorial boundaries with an unfamiliar and potentially stronger individual (Getty 1987). If males

intervene in fights to reduce future territorial disputes, they should be more likely to do so when they have a history of interacting with their neighbor. In support of this prediction, 79% of males in a familiar territory came to the aid of a neighbor, while only 29% of males that had recently acquired a territory helped (Fisher's test, two-tailed  $P < .0005$ ,  $n = 24, 24$ ; fig. 3). Most males in their accustomed territories will have established relationships with their neighbors, while males in a new territory will not.

The dear enemy explanation assumes that it is costly to acquire a new neighbor. Given the large-male fighting advantage in *U. annulipes*, an evicted neighbor is usually



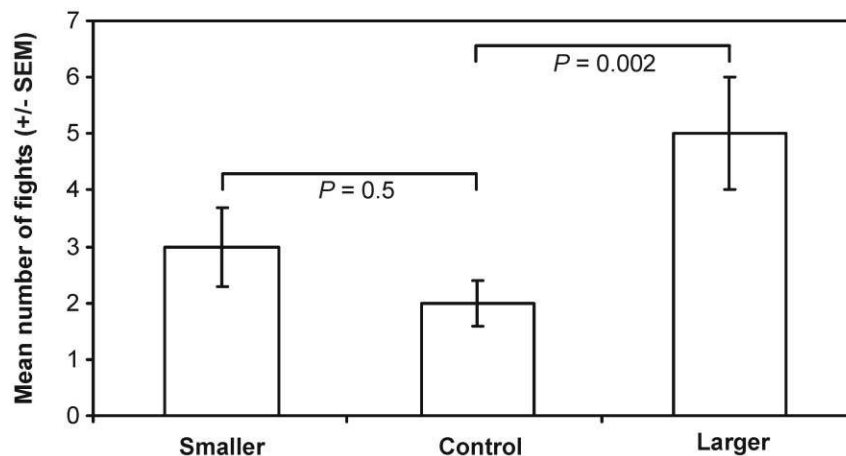
**Figure 3:** Effect of familiarity on the likelihood of helping. Potential allies are more likely to help when they have an established relationship with their neighbors. Black bars represent allies that helped; white bars represent those that did not (for scenarios from left to right,  $n = 24, 24$ ).

displaced by a larger male (Jennions and Backwell 1996). We found that replacement males who were larger than the original males were involved in significantly more fights with neighbors than were control males ( $P = .002$ ,  $n = 20$ ), but there was no difference when the replacement male was smaller than the original male ( $P = .50$ ,  $n = 20$ ; both Dunnett tests; fig. 4). This result is not due to the difference in the absolute sizes of large and small replacement males ( $F_{1,39} = 7.80$ ,  $P = .008$ ; claw size:  $21.0 \pm 4.3$  mm vs.  $24.3 \pm 3.0$  mm), because absolute male size and the number of fights were unrelated ( $r_s = -0.043$ ,  $P = .80$ ,  $n = 40$ ). Our results show that a new, larger neighbor imposes costs because of the additional time and energy spent on territorial disputes. We suspect that new neighbors who are smaller than their predecessors do not elevate costs, at least not initially (i.e., over the time interval in which we examined neighbor-neighbor interactions), because they are more likely to stay within the previous territory boundaries, while males that are larger than their predecessors more often cross these boundaries.

In summary, we have documented only the third species to exhibit male-male territorial defense coalitions. We have experimentally demonstrated that larger males help smaller neighbors to repel intermediate-sized intruders. Comparable size-dependent defense coalitions have been reported in the Australasian fiddler crab *U. mjoebergi* (Backwell and Jennions 2004), but these data were purely observational. They could therefore not confirm whether allies base their decision to help on the relative size of the fight participants or whether helping occurs more often when a male has established territorial boundaries with

his neighbors. In *U. annulipes*, however, we have shown that helping decisions depend on relative male size. In addition, as was predicted by the models of Getty (1987) and Mesterton-Gibbons and Sherratt (2009), we have shown that coalition formation is more likely when an ally has established a territorial boundary with his neighbor. We cannot be certain that an ally identifies individual neighbors (although individual recognition on the basis of carapace coloration does occur in fiddler crabs [e.g., Detto et al. 2006]). Established males might simply know the location of neighboring burrows and then assist the male whose legs are currently at the mouth of the burrow (usually the resident) as a rule of thumb (fig. 1).

The fact that decisions to help depend on the relative sizes of the three males involved, which should alter both the current cost of fighting and the likely future benefits, suggests that helping is an adaptive trait maintained by selection. Interestingly, recent work shows that males also help female neighbors repel intruders in *U. annulipes* but that these decisions are not affected by the relative size of female intruders (Milner et al. 2010). This is consistent with the potential payoffs (larger females are more fecund and males can mate with neighbors) and suggests that there is no general bias toward fighting with crabs that are of a certain size relative to that of a neighbor (see Milner et al. 2010). As with any adaptive argument to confirm that helping elevates net fitness, we must translate current fighting costs and potential gains from reduced territorial disputes into a common fitness currency. Even so, the most plausible explanation for defensive coalitions in *U. annulipes* is that they arise due to by-product mutualism if it is cheaper to help an existing neighbor than to incur



**Figure 4:** Number of territorial fights between neighboring males in relation to the size of replaced residents. Neighbors fight significantly more often when a resident is replaced by a larger male, while there is no difference in the number of fights between established residents (control) and those where a resident is replaced with a smaller male ( $n = 20, 20$ ).

the cost of renegotiating a territory boundary with a new, larger neighbor. This is likely to be the case, however, only when the ally is stronger than the intruder he must repel such that the immediate costs of fighting are low relative to the likely payoff.

### Acknowledgments

We thank the Australian Research Council for funding, L. Wickins, and everyone at Manico Camp for support.

### Literature Cited

- Backwell, P., and M. D. Jennions. 2004. Coalition among male fiddler crabs. *Nature* 430:417.
- Backwell, P., and N. I. Passmore. 1996. Time constraints and multiple choice criteria in the sampling behavior and mate choice of the fiddler crabs, *Uca annulipes*. *Behavioral Ecology and Sociobiology* 38:407–416.
- Booksmythe, I., R. N. C. Milner, M. D. Jennions, and P. R. Y. Backwell. 2010. How do weaponless male fiddler crabs avoid aggression? *Behavioral Ecology and Sociobiology* 64:485–491.
- Detto, T., P. R. Y. Backwell, J. Hemmi, and J. Zeil. 2006. Visually mediated species and neighbor recognition in fiddler crabs (*Uca mjoebergi* and *Uca capricornis*). *Proceedings of the Royal Society B: Biological Sciences* 273:1661–1666.
- Elfström, S. T. 1997. Fighting behavior and strategy of rock pipit, *Anthus petrosus*, neighbors: cooperative defense. *Animal Behavior* 54:535–542.
- Fayed, S. A., M. D. Jennions, and P. R. Y. Backwell 2008. What factors contribute to the ownership advantage? *Biology Letters* 4:143–145.
- Fisher, J. 1954. Evolution and bird sociality. Pages 71–83 in J. Huxley, A. Hardy, and E. Ford, eds. *Evolution as a process*. Allen & Unwin, London.
- Getty, T. 1987. Dear enemies and the prisoner's dilemma: why should territorial neighbors form defensive coalitions? *American Zoologist* 27:327–336.
- Hemmi, J. M., and J. Zeil. 2003. Robust judgement of inter-object distance by an arthropod. *Nature* 421:160–163.
- Jaegar, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. *American Naturalist* 117:962–974.
- Jennions, M. D., and P. R. Y. Backwell. 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biological Journal of the Linnean Society* 57:293–306.
- Mesterton-Gibbons, M., and L. A. Dugatkin. 1992. Cooperation among unrelated individuals: evolutionary factors. *Quarterly Review of Biology* 67:267–281.
- Mesterton-Gibbons, M., and T. N. Sherratt. 2009. Neighbor intervention: a game theoretical model. *Journal of Theoretical Biology* 256:263–275.
- Milner, R. N. C., T. Detto, M. D. Jennions, and P. R. Y. Backwell. 2009. Hunting and predation in a fiddler crab. *Journal of Ethology* 28:171–173.
- Milner R. N. C., M. D. Jennions, and P. R. Y. Backwell. 2010. Safe sex: male-female coalitions and pre-copulatory mate guarding in a fiddler crab. *Biology Letters*, doi: 10.1098/rsbl.2009.0767.
- Pratt, A. E., and D. K. McLain. 2006. How dear is my enemy: intruder-resident and resident-resident encounters in male sand fiddler crabs (*Uca pugilator*). *Behavior* 143:597–617.
- Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.

Natural History Editor: Craig W. Benkman



Field site: the expansive mudflat habitat of *Uca annulipes* on Inhaça Island, Mozambique. Photograph by Tanya Detto.