# The cost of living in mixed species populations: A fiddler crab example

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A B S T R A C T

Rising sea level is reducing the inter-tidal zone in many mangrove forests. This breaks down the normal species distribution patterns of fiddler crabs, with an increasing number of heterospecifics moving from adjacent zones into an area normally occupied by a single species. Here we examine the interspecific social and sexual interactions that have resulted. We show that male *Austruca mjoebergi* are just as likely to help their small conspecific neighbor fight off an intruder when the intruder is a conspecific or heterospecific male. It appears that keeping a known neighbor is preferable to having *any* new neighbor (even a heterospecific neighbor that would not compete for receptive females) since the costs of renegotiating territory boundaries would be the same whatever the species of the new neighbor. We also show that males court females of their own species just as vigorously as those of two heterospecific species. Courtship is costly, so the time and energy spent courting heterospecific females is wasted: a potentially high cost of living among heterospecifics.

## 1. Introduction

Climate change is already rapidly and irreversibly altering ecosystems (Hoegh-Guldberg and Bruno, 2010). Inter-tidal communities are especially vulnerable because the plants and animals that live there are adapted to a physiologically stressful environment. Marine zonation, with species restricted to very narrow bands, graphically illustrates that many individuals live within a few centimeters of their tolerance limits (Lovelock and Ellison, 2007). In this context, as sea levels comes up, mangrove communities might migrate landward up the inter-tidal gradient, with species maintaining their preferred depths, frequencies and durations of tidal inundation (Lovelock and Ellison, 2007). Unfortunately, there are now many human-induced barriers to migration: agriculture, roads, urban development and steeply sloped levees, what makes the upper inter-tidal zone one of the most vulnerable ecosystems (Gilman et al., 2008; Saintilan and Williams, 1999). In Australia, for example, four well-studied salt flats have already been reduced by rising sea level to 75%, 51%, 33% and 20% respectively of their original size (Gilman et al., 2007). Therefore, it is essential to understand the possible consequences of changes in species distribution related to rising sea level, especially those species that lives in monospecific zones and are now being forced to live in mixed-species areas.

Within mangrove ecosystems, fiddler crabs are arguably among the most ecologically important fauna, playing an essential role due to their bioturbation activities, resulting in ecosystem engineering (Cannicci et al., 2008; Citadin et al., 2016; Jones et al., 1994; Kristensen, 2008; Kristensen et al., 2012; Natálio et al., 2017; Penha-Lopes et al., 2009). Most species live in single-species populations due to specific habitat requirements (Booksmythe et al., 2011). They can be vulnerable to sea level rise, particularly those species that live in the upper inter-tidal zones. In this sense, rising sea levels and the concurrent landward migration is already eating away the mangroves and mudflats in Darwin Harbor. Over the past seven years, however, two fiddler crab species moving from adjacent zones have gradually but steadily been increasing in number within a previously monospecific population of *Austruca mjoebergi* (Backwell Personal communication). *Tubuca elegans* and, to a lesser extent *Tubuca signata*, are now commonly found within the *A. mjoebergi* population. This breakdown in the normal mosaic distribution pattern has potentially far reaching implications for the social and mating systems of these species. Species interactions, especially interference, can have profound effects on the timing and form of sexual signaling, even leading to evolutionary divergence in sexual traits (Martin et al., 1996).

From the social interactions point of view, competition for territories may be an important issue, since it is known that the most valuable resource for this group is its territory (Crane, 1975). Territory holders aggressively defend their burrow and an area in its surrounding against intruders. In addition, male *A. mjoebergi* have been shown to

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form coalitions in which neighbors help each other to defend their territories from intruders (Backwell and Jennions, 2004): a male will assist his smaller neighbor to fight of an intruder if the intruder is larger than the resident (so the resident is likely to lose the fight) and if the helper is larger than the intruder (so the helper is likely to win the fight). Coalitions are likely to be due to by-product mutualism: the helper pays to retain an established neighbor and the neighbor keeps his territory (Backwell and Jennions, 2004). Coalition formation also occurs in *T. elegans*: males helped their conspecific neighbors in 50% of the attacks; they were significantly less likely to help a heterospecific (*A. mjoebergi*) neighbor, doing so in only 15% of attacks (Booksmythe et al., 2010). As *T. elegans* and *T. signata* are being squashed together in *A. mjoebergi* areas due to rising sea level, the extent to which *A. mjoebergi* can help conspecific neighbors against heterospecific intruders might be low, what potentially has implications in habitat ownership for this species.

Species interactions can also have several important effects on mate attraction. In *A. mjoebergi*, mating occurs over a five day period every two weeks (a semi-lunar cycle). Receptive females leave their territories and wander through the population of courting males, visiting several males before selecting a mate (see Reaney and Backwell, 2007). Courting males wave their enlarged claw in a species-specific wave pattern to attract the females (Crane, 1975). Females select their mates based on numerous criteria including claw size, wave rate, the production of temporally leading waves, male size and, ultimately, burrow quality (see Reaney and Backwell, 2007; Kahn et al., 2014 and refs therein). Waving is energetically expensive (Matsumasa and Murai, 2005) and indiscriminate courtship would impose substantial costs for *A. mjoebergi* males (Booksmythe et al., 2011). Time spent courting heterospecifics would reduce a male's opportunity to attract conspecific females. Earlier work has shown that, when a conspecific or a heterospecific (*T. elegans*) female is released in the population (one at a time), nearly every male they passed waved at them (Booksmythe et al., 2011). When presented with a conspecific and heterospecific (*T. elegans*) female simultaneously, males gave significantly more waves at conspecific females (Booksmythe et al., 2011). We do not know, however, whether males adjust wave rates at conspecific or heterospecific females or take greater risks by moving further away from their burrows when courting them.

Given the background, this study aims to examine the effect of mixed-species populations on the social interactions and mating success of *A. mjoebergi*. We specifically want to understand (i) whether a male *A. mjoebergi* is as likely to assist his neighbor when it is attacked by a conspecific or a heterospecific (either *T. elegans* or *T. signata*) male; and (ii) whether a male *A. mjoebergi* alters waves rate or travel greater distances from their burrows when courting a conspecific or heterospecific (either *T. elegans* or *T. signata*) female.

## 2. Methods

The study was conducted at East Point Reserve, Darwin, Australia (12°24′31.89″S 130°49′49.12″E) from September to December 2015. Fiddler crabs (Note: *Austruca mjoebergi* was previously called *Uca mjoebergi*; *Tubuca elegans* was previously *Uca elegans; Tubuca signata* was previously *Uca signata*; see Shih et al., 2016 for details) were captured randomly in the population with the use of shovels. All individuals that were held until the use on experiments were housed individually in a cup containing 0.5 cm deep sea water in a shaded area to prevent them from overheating.

### 2.1. Cooperation

We captured males of the three species (*A. mjoebergi, T. elegans* and *T. signata*) from a distant part of the population and tethered them (a 3 cm length of cotton thread glued to their carapace and tied to a 3 cm long nail). We selected a pair of naturally occurring *A. mjoebergi* males,

where one male was considerably larger than the other, and measured the distance between their burrows. We placed a tethered male (randomizing the species of intruder between trials) 3 cm away from the smaller resident, on the opposite side of the burrow to the larger resident. The tethered male was always intermediate in size between the two resident *A. mjoebergi* males. The tethered male could approach the burrow entrance but not enter the burrow of the smaller resident. The placement of the 'intruder' on the opposite side of the burrow to the larger resident ensured that the larger *A. mjoebergi* male was not fighting the 'intruder' in order to defend his own territory (see Backwell and Jennions, 2004). We scored helping behavior when the larger resident fought (physical contact between the claws of the 'helper' and 'intruder') the tethered intruder within 5 min of all males being surface active. After each trial, we captured and measured the claw length of all three males. Each male was used in only one trial. We did not use males with regenerated claws. Males intruders sample sizes were: $N = 14$ to *A. mjoebergi*; $N = 19$ to *T. elegans*; and $N = 18$ to *T. signata*.

### 2.2. Courtship

We collected females of the three species and tethered them (a 3 cm length of cotton thread glued to their carapace and tied to a 3 cm long nail). We placed the nail 20 cm in front of an *A. mjoebergi* male burrow (this is the distance at which females make their choice: Callander et al., 2011). After the male emerged from his burrow, we counted the number of waved directed at the female and evaluate the distance the male moved towards the female while courting her within 5 min the male was surface active or until he touched the female with his legs during this time. Therefore, wave rate were evaluated by the number of waving per time of courting. We randomized the order of presentation of females between trials. After each trial, we captured and measured the male and female. Each female and male was used in only one trial. We did not use males with regenerated claws. Presented females sample sizes were: $N = 20$ to *A. mjoebergi*; $N = 10$ to *T. elegans*; and $N = 14$ to *T. signata*.

### 2.3. Data analyses

We used one way ANOVA to examine the differences between the three species in the cooperation trials (distance between male burrows; claw lengths of helper, intruder and resident males; size difference between helper and intruder and between intruder and resident males) and the courtship trials (wave rate; distance travelled towards the female; female carapace widths; male claw lengths). In addition, we used a Likelihood ratio test to determine whether there was a difference in the number of times a male helped his neighbor when the intruder was an *A. mjoebergi*, a *T. elegans* or a *T. signata* male and to evaluate if there was difference between the 3 species in the number of females were touched by males. All these variables were homoscedastic (Levene test). The analyses were performed in SPSS version 23.0 (SPSS Inc., Armonk, NY, U.S.A.). The significance level was set at $\alpha < 0.05$.

### 2.4. Ethical note

This research was approved by the Australian National University Animal Ethics Committee (permit A2015/54). We limited the handling and the amount of time each crab was used as much as possible. No crab was injured during the research, and they all continued their regular activities after release. The tethered crabs were released after the cotton thread had been cut as short as possible (such that the only thread remaining was fully glued to the carapace and would be lost at the next molt). The work was conducted under a research permit from the Darwin City Council (permit no. 2322876).