



Fiddler crab spatial distributions are influenced by physiological stressors independent of sympatric interactions



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ABSTRACT

Understanding how and why organisms such as intertidal invertebrates are distributed spatially helps ecologists to determine ecosystem functioning and make predictions in the face of changing scenarios. Tropical Australian fiddler crabs (*Uca* species) are differentially distributed in mangrove habitats according to levels of canopy cover. Here we conducted experiments to test three hypotheses explaining fiddler crab distributions in a tropical mangrove. Firstly we recorded the time that it took fiddler crabs from different habitats to reorientate themselves upon being placed on their backs. Secondly we transplanted forest inhabiting *U. flammula* and clearing inhabiting *U. elegans* into enclosures set up in clearing and forest sites and measured their activities. We then excluded predators from enclosures containing *U. elegans* in the forest and monitored crab activities over 10 weeks. We found that righting-response times were longer for crabs from low compared to high intertidal zones and longer when in full sun for all crabs living in or near forests compared to those from clearings, suggesting that forest-dwelling crabs experience physiological stress in open canopy habitats. After 10 weeks, transplanted crab activities varied according to species and habitat. In the clearing, crab activities remained high with burrow-enclosure distance varying between species. Neither transplanted crab activities nor burrow-enclosure distance varied with the presence or absence of other species. Our predator exclusion experiments also found no predator effects on the activities of transplanted crabs. Our results suggest that fiddler crab spatial distributions across the mangrove ecosystem are influenced by physiological stressors independent of any sympatric interactions.

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1. Introduction

Understanding the influences affecting animal spatial distributions is an ongoing challenge for ecologists (Harrington et al., 2009; Huey, 1991). While studies demonstrate that predators may primarily affect assemblage structure (Werner and Peacor, 2003), the interactive effects of non-consumptive interactions are not well known (but see Mowles et al., 2011; Peckarsky et al., 2008). Physically stressful abiotic environments may affect the survival capacities of animals by inhibiting their ability to rapidly escape from predators or other dangers (Ruxton et al., 2004). For instance, experiments have shown heat stressed marine invertebrates to have an impaired ability to reorientate themselves when overturned (Frederich et al., 2009; Sherman, 2015; Wilson, 1989).

Intertidal invertebrates such as crabs are good models for conducting experiments aimed at determining the interactive influences of predators, competitors, and physiological stressors on animal distributions since they can be readily manipulated experimentally to compare localized spatial distributions and habitat uses between species and locations (Kristensen, 2008; Lee, 1998; Nobbs, 2003; Nobbs and Blamires, 2016). Furthermore, the nature of the interactions between different species varies across ecological contexts (Dingle, 1983; Stachowicz, 2001). For instance, the interactions between large and small or aggressive and docile crabs can vary depending on crab abundances or resource availability (Aspey, 1971; Bertness et al., 2014; Nomann and Pennings, 1998).

Organisms in intertidal ecosystems are temporally (as a consequence of the rise and ebb of tides) and spatially (along the intertidal gradient) exposed to fluctuations in temperature, salinity, water availability and other environmental factors (Helmuth, 2002; Nobbs and Blamires, 2016). Behavioral and physiological flexibility is accordingly a means by which intertidal crabs can cope with severe environmental fluctuations (López-Duarte and Tankersley, 2007; Nobbs, 2003;

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Stillman and Somero, 1996, 2000). Fiddler crabs that live at elevated intertidal locations, for instance, tolerate higher temperatures and have a greater resistance to desiccation than those that live along the more heterogeneous foreshore (Edney, 1961; Rabalais and Cameron, 1985).

Canopy cover influences temperature and water availability along the intertidal gradient (Bertness et al., 1999; Hogarth, 2015). Accordingly, if two crab species live at similar heights but one lives in a habitat with an open canopy while the other lives in a habitat with a closed canopy it is expected that they will experience significant differences in temperature and water availability. Accordingly, it might be expected that any two such species would differ in their tolerances to physiological stressors. Indeed, studies demonstrate that crabs living in closed canopy mangrove forests maintain moderate internal temperatures and experience less evaporative water losses than crabs from open clearings (Edney, 1961; Hogarth, 2015; Smith and Miller, 1973). Nevertheless, crabs in stressful environments may escape physiological stressors by behavioral means, e.g. by thermoregulating, retreating into a burrow, directed orientation or wetting their body (Davenport, 1985; Hogarth, 2015; Reid et al., 1997). Accordingly, crab spatiotemporal distributions appear to be influenced by a complex interplay between behavioral and physiological flexibility, habitat-specific adaptations to environmental stressors, and a range of dynamic sympatric interactions (Hoffmann and Hercus, 2000; Sherman, 2015). As a consequence ascertaining the influential factors on crab spatiotemporal distributions within mangrove ecosystems is problematic.

In the upper intertidal zone of the mangroves of Australia's wet-dry tropics the level of canopy cover influences the distribution of burrowing crabs (Cannicci et al., 2008; Nobbs, 2003; Nobbs and Blamires, 2015; Osborne and Smith, 1990). Here, sesarmids (Grapsidae, Sesarminae) are abundant in closed canopy forests and rarely found in sites with an open canopy, such as muddy clearings (George and Jones, 1984; Nobbs and Blamires, 2015; Osborne and Smith, 1990). Of the upper intertidal crabs, fiddler crabs (*Uca*, Ocypodidae) are most prominent. *Uca flammula* selects shaded habitats while *U. elegans* seems to prefer open clearings (George and Jones, 1984; Nobbs, 2003; Nobbs and Blamires, 2015, 2016). Another species, *U. signata*, predominantly inhabits the forest edges (Nobbs and Blamires, 2015). The foreshore contains a different suite of fiddler crabs, with *U. capricornis*, *U. dampieri*, and *U. hirsutimanus* being the predominant species (Brooksmlythe et al., 2008) in closed-canopy, open-canopy and edge habitats respectively.

By differentially distributing themselves among the different zones and habitats of the mangrove ecosystem, Australian wet-dry tropical fiddler crab species might each be expected to face a unique set of biotic and abiotic stressors. Crabs that inhabit open clearings, for instance, experience extremes in temperature and incessant drying, and may be exposed to aerial predators (Nobbs and Blamires, 2016). While crabs inhabiting the forest might be more susceptible to surface attack or subterranean predation by the larger, more aggressive sesarmids, birds or fish during high tides (Nagelkerken et al., 2008). It thus follows that predators and physical stressors may interact to influence the distributions of fiddler crabs in Australian wet-dry tropical mangroves (Kristensen et al., 2008; McGuinness, 1994; Micheli, 1993; Nobbs and Blamires, 2015). However, the relative influence of physiological stressors and competitors and predators on the differential distribution of Australian fiddler crabs remains to be experimentally explored.

Studies have shown that food availability can influence fiddler crab behavior and distribution in saltmarsh (Genoni, 1985, 1991) and tropical mangrove habitats (Bartolini et al., 2009; Penha-Lopes et al., 2009). Although controversy exists, it is likely most *Uca* species can ingest bacteria and microphytobenthos (Kristensen, 2008), the latter being more abundant in clearings than forest because light stimulates its growth (Alongi, 1994; Kon et al., 2007). Evidence suggests that, in the tropics, fiddler crabs feed on mangrove detritus in the forest but microphytobenthos in the gaps (Kon et al., 2007, 2010). Given that *Uca* are naturally abundant at low densities in both clearings and forests

in the upper intertidal zone of the mangroves of Australia's wet-dry tropics, and sediment grains found in these habitats are similarly fine-grained (Nobbs, 1999) so are able to be processed by the mouthparts of all deposit-feeding species (Robertson and Newell, 1982) irrespective of the nature of the food source, we expected food availability to not have a major impact on *Uca* distribution in these habitats.

Here we systematically conducted a series of experiments to test the following three non-mutually exclusive hypotheses as explanations for the spatial distributions of fiddler crabs in Australian wet-dry tropical mangroves: (1) the crabs differ in their capacities to cope with physiological stressors encountered in their preferred and non-preferred environments. (2) Some species of crab are more aggressive and restrict the distributions of the others. (3) Susceptibility to predation or harassment restricts certain crabs to certain areas, e.g. *U. elegans* to open habitats. To test the first hypothesis we placed six different species of fiddler crab from Darwin Harbour, each of which utilizes a habitat differing in elevation or canopy cover, on their backs in different habitats and recorded the time that it took them to reorientate themselves (Frederich et al., 2009; Wilson, 1989). To simultaneously test the first and second hypotheses we transplanted *U. flammula* and *U. elegans* into enclosures set up in the clearing or shaded forest to ascertain whether physiological stressors in non-preferred environments and/or interactions between the species resulted in one of them becoming more active over time. We tested the third hypothesis by excluding aerial, aquatic or burrowing predators from enclosures containing *U. elegans* in the forest habitat.

2. Methods

2.1. Study sites

Our sites are located in the mangrove forest at Ludmilla Creek in Darwin Harbour near Darwin, Northern Territory, Australia (12°25'S, 131°50'E) where the tides are semi-diurnal with a spring tidal range of up to 8 m. Two sites ('clearing' and 'forest') were above the high water neap level within the mid-high intertidal zone and the other site was at the north eastern foreshore of East Point Reserve within the low intertidal zone.

The two sites above high water neap were out of the visual range of pedestrian access to the Ludmilla Creek mangroves to ensure they did not suffer human disturbance. The site called 'clearing' was a muddy saltpan 23.0 m × 40.0 m and 6.68 m above sea level with a flat substratum. *Uca elegans* was the dominant species found in the centre of the clearing. *Uca signata*, and occasionally *U. flammula*, are found at the edges of the clearing. *U. flammula* and sesarmids were abundant in the adjacent *Ceriops tagal* var *australis* dominant mangrove zone (Nobbs and Blamires, 2015). The site called 'forest' was 6.36 m above sea level, close to a small tributary running off Ludmilla Creek. It had an uneven surface due to the presence of numerous sediment mounds and was faunistically dominated by *U. flammula* and sesarmids.

The foreshore of East Point Reserve was dominated by *U. capricornis* and *U. hirsutimanus* under the canopy of the *Sonneratia alba* and *Rhizophora stylosa* forest and by *U. dampieri* in the gently sloping mudflat below the tree-line.

2.2. Experiment 1—righting response times

For the first experiment individual *U. flammula* were collected from the 'forest', and *U. elegans* and *U. signata* individuals were collected from the 'clearing' sites within the mid-high intertidal zone, while individual *U. capricornis* and *U. hirsutimanus* were collected from the forest and *U. dampieri* individuals were collected from the exposed mudflat within the low intertidal zone. *Uca elegans*, *U. signata* and *U. flammula* respectively occupy increasingly more shaded, thus cooler and wetter, microhabitats in the mid-high intertidal zone of Darwin Harbour mangroves, while *U. dampieri*, *U. hirsutimanus* and *U. capricornis* respectively occupy

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