



# 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 (Brooksmaythe 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

increasingly shaded microhabitats in the low intertidal zone (Brooksmythe et al., 2008; Hagen and Jones, 1989; Nobbs and Blamires, 2015).

We used 28 adults ( $N = 14$  males and 14 females) of each of the six fiddler crab species that were collected. Prior to testing, crabs were assigned to one of the following three treatments: (i) 'Restrained in sun' crabs were restrained in the sun for 2.5 h without access to water prior to testing. (ii) 'Restrained in shade' crabs were restrained in the shade for 2.5 h without access to water prior to testing. (iii) 'Control' crabs were tested immediately after capture. Upon receiving the above treatments the crabs were then placed dorsal side upward within a large bucket containing 5 cm of substratum collected from the clearing at Ludmilla Creek. The time it took for the crabs to reorientate themselves to their normal posture was measured using a stopwatch. The time recorded was the righting response time (RRT: Burger et al., 1991; Wilson, 1989). To avoid excessive handling prior to experimentation, the carapace width (CW) of all crabs was measured after RRT had been measured.

We used RRT as it is the most useful repeatable measure of physiological duress in crabs in the field since it is: (1) nonlethal (Frederich et al., 2009; Lutterschmidt and Hutchison, 1997), (2) fast and cheap, i.e. it requires no machinery, just a stopwatch and can be done anywhere by one person, and (3) strongly correlates with metabolic and thermal stress in crabs (Frederich et al., 2009; Wilson, 1989). Moreover, since crabs can become overturned, especially during male combat (Crane, 1975; Mokheles et al., 2011) it represents a realistic physiological challenge that crabs face in their natural environment.

### 2.3. Experiment 2—visual counts of resident crabs

This experiment was conducted to monitor and compare the activities of naturally occurring resident fiddler crabs in the 'clearing' and 'forest' sites within the mid-high intertidal zone for comparisons with transplanted crabs (see Experiment 3) and to ascertain the influence that the presence of the Perspex enclosure and consequent substratum disturbance had on fiddler crab activities.

During March and April 1998 three replicates of the following treatments were set up at each of the 'clearing' and 'forest' sites (Fig. 1): (i) Enclosure with disturbance—an enclosure was constructed out of a strip of  $2.4 \times 0.5$  m clear Perspex bent into a circle and secured using metal screws. A shovel was used to break up the substratum so that the enclosure could be hammered to a depth of  $\sim 15$  cm into the substratum in the clearing, or down to the level of the root mat (5–15 cm into the substratum) in the forest thus enclosing a  $0.47 \text{ m}^2$  area of substratum surface. A series of randomly spaced holes (5 mm diameter) were drilled into the Perspex above the substratum to allow water to escape during low tide. It was unfortunately not possible to construct an 'enclosure and no disturbance' treatment. (ii) No enclosure and no disturbance—the circumference of a circular-shaped plot that enclosed a  $0.47 \text{ m}^2$  area of substratum surface was marked out with vinyl flagging tape lying on the substratum surface secured with thin wires pushed into the substratum. Disturbance was minimal as no further alteration was made to the plot. (iii) No enclosure with disturbance—the substratum was disturbed using a shovel in such a way so as to mimic the kind of disturbance caused when implanting the Perspex enclosure. Then, the circumference of a circular-shaped plot was marked with flagging tape as previously described.

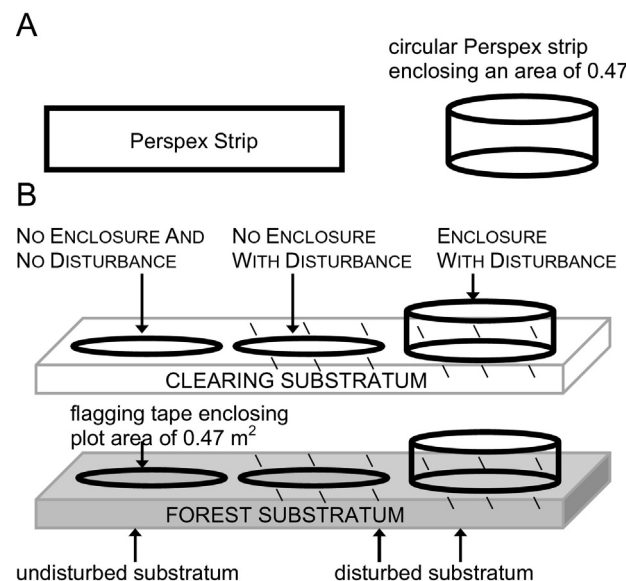
Resident crabs naturally found within treatments at each site were not moved. Visual counts were done on the resident crabs of each species that were seen within treatments over a 10 minute observation period during the spring low tide at the commencement of the experiment and after four, six and ten weeks. After ten weeks the distance between each occupied burrow and the edge of the enclosure (burrow-enclosure distance, BED) was measured within the enclosures at both sites.

### 2.4. Experiment 3—visual counts of transplanted crabs

During March and April 1998 a further nine Perspex enclosures were set up at each of the 'clearing' and 'forest' sites. All of the crabs found residing within these enclosures were removed and the enclosures were monitored over the following 48 h to be certain that all crabs present in the enclosures had been removed before five adult (three males and two females) *U. flammula* collected from the 'forest' and/or five adult *U. elegans* collected from the 'clearing' were transplanted into the empty enclosures. We used 5 crabs per  $0.47 \text{ m}^2$  as this represented the approximate density of these crabs within Darwin Harbour (Nobbs and McGuinness, 1999). The CW of all transplanted *U. flammula* and *U. elegans* were recorded before transplantation to ensure that approximately similar-sized individuals (CW for both species combined: mean  $\pm$  SE =  $18.71 \text{ mm} \pm 0.19$ ,  $N = 120$ ) were used [two factor (site, species) analysis of variance (ANOVA):  $F(1, 116) = 3.50$ ,  $P > 0.05$ ].

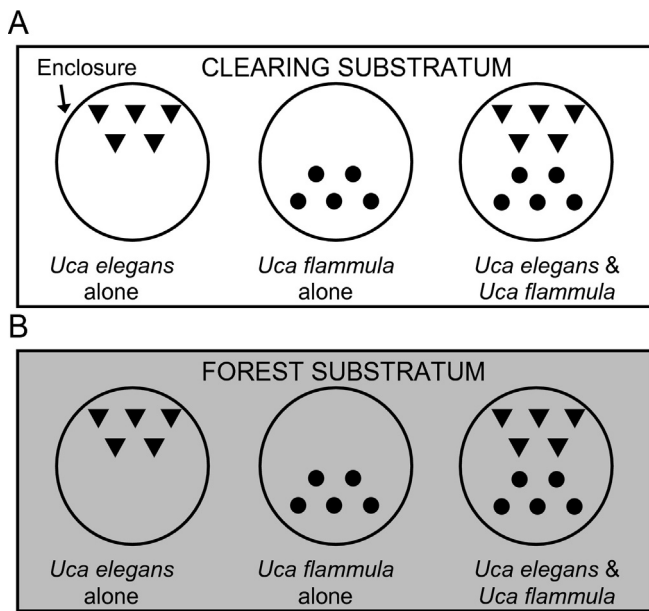
Upon transplantation of crabs, three replicates of the following enclosures were set up at each of the 'clearing' and 'forest' sites (Fig. 2): (i) *Uca elegans* alone—five individuals of *U. elegans* from the 'clearing' were transplanted into an empty enclosure. (ii) *Uca flammula* alone—five individuals of *U. flammula* from the 'forest' were transplanted into an empty enclosure. (iii) *Uca elegans* and *Uca flammula*—five individuals of *U. elegans* from the 'clearing' and five individuals of *U. flammula* from the 'forest' were transplanted into an empty enclosure.

Visual counts were done on the crabs of each species that were seen within the enclosures over a 10 minute observation period during the spring low tide after four, six and ten weeks post transplantation. After ten weeks the species of occupant and the BED of each burrow within the clearing enclosures were measured. BEDs were not measured in forest enclosures because some enclosures contained no *U. elegans* after ten weeks.



**Fig. 1.** Diagrammatic representation of the construction and installation of treatments set up for experiment 2. (A) Construction of enclosure. A strip of  $2.4 \times 0.5$  m clear Perspex was bent into a circle and secured with metal screws to enclose an area of  $0.47 \text{ m}^2$ . (B) Installation of treatments. The types of treatments installed in the 'clearing' (top panel) and 'forest' (bottom panel) sites were—No enclosure and no disturbance, No enclosure with disturbance, Enclosure with disturbance. The  $0.47 \text{ m}^2$  circular plots used for treatments with no enclosures were marked with flagging tape secured to the substratum with thin wire. Resident crabs naturally found within all treatments at each site were not moved.



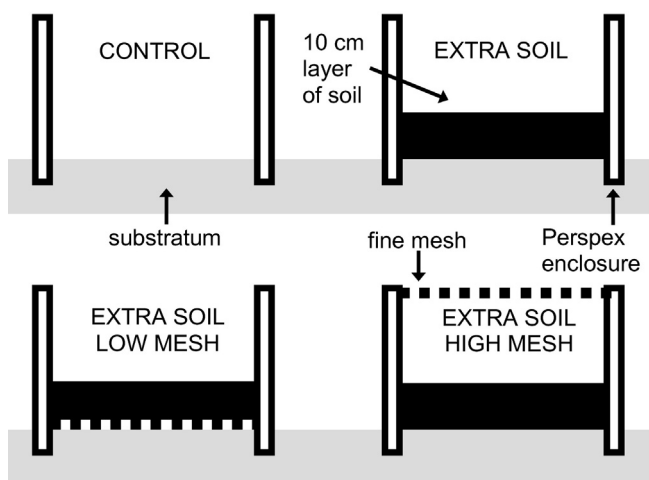


**Fig. 2.** Diagrammatic representation of the enclosures set up for experiment 3. Five adult *U. elegans* (black triangles) and five adult *U. flammula* (black circles) were transplanted into empty enclosures in the (A) 'clearing' and (B) 'forest' sites as follows—*Uca elegans* alone, *Uca flammula* alone and *Uca elegans* and *Uca flammula* together. Resident crabs were removed prior to transplantation.

#### 2.5. Experiment 4—crab predation in forest enclosures

We conducted a further experiment to examine whether predators entering forest enclosures might influence the activities of fiddler crabs within enclosures, and whether predators might influence the distribution of the crabs in the mangrove ecosystem. We specifically tested here whether different types of predators accessed the enclosure via one of two methods: (1) aerial or aquatic predators, such as fish and birds, entering the enclosure from above, or (2) burrowing predators, such as sesarmids, entering from underneath.

We thus placed five *U. elegans* from the 'clearing' into each of twelve empty Perspex enclosures (set up as outlined above) within the 'forest'. Three replicates of the following treatments were set up (Fig. 3): (i) Control—no soil or mesh was added to the enclosure. (ii) Extra



**Fig. 3.** Diagrammatic representation of forest enclosures set up for experiment 4. Five adult *U. elegans* were transplanted into each of the following empty enclosures set up in the 'forest'—Control, Extra soil, Extra soil low mesh, and Extra soil high mesh.

soil—a ~ 10 cm layer of soil was added to the base of the enclosure. (iii) Extra soil low mesh—a fine (~1 cm spacing) fiberglass mesh was added to the base of the enclosure and covered with a ~ 10 cm layer of soil. This treatment excluded predators from entering the enclosures from underneath. (iv) Extra soil high mesh—a ~ 10 cm layer of soil was added to the base of the enclosure and the top of the enclosure was sealed with fiberglass mesh. This treatment excluded aerial and aquatic predators.

We subsequently recorded the number of transplanted *U. elegans* active within each enclosure over a 10 minute observation period during the spring low tide at two and six weeks after commencement of the experiment. The number of sesarmids within enclosures was also counted after six weeks.

#### 2.6. Statistical analyses

##### 2.6.1. Experiment 1—righting response times

Data on RRT were analysed by 4 factor ANCOVA with CW as the covariate and the factors Zone (mid-high, low), Species nested in Zone (*U. flammula*, *U. signata*, *U. elegans* in mid-high zone; *U. capricornis*, *U. dampieri*, *U. hirstimanus* in low zone), Treatment (control, restrained in sun, restrained in shade) and Sex. All data were log transformed prior to analysis for normalization. Cochran's test was significant ( $0.01 < P < 0.05$ ) for log transformed data so the significance level for the ANCOVA was adjusted to  $P = 0.01$ . A Bryant-Paulson generalisation of Tukey's HSD *post-hoc* test ( $\alpha = 0.05$ ) was used to identify the significantly differing means across treatments (Huitema, 1980).

##### 2.6.2. Experiment 2—visual counts of resident crabs

Data on visual counts of resident crabs per treatment ( $N = 3$ ) were compared across treatments by a three-factor repeated measures analysis of variance (rmANOVA) with the factors Species (*U. elegans*, *U. flammula*), Treatment (no enclosure and no disturbance, no enclosure with disturbance, enclosure with disturbance) and Time (repeated measures at 0, 4, 6, 10 weeks). Cochran's test was not significant upon square-root transformation of the data ( $P > 0.05$ ). Tukey's honest significant difference (HSD) tests ( $\alpha = 0.05$ ) were used to compare means where the rmANOVA indicated there were significant differences across treatments. Data on BED was averaged for each enclosure, and a *t*-test was done to compare mean BEDs at the two sites.

##### 2.6.3. Experiment 3—visual counts of transplanted crabs

Data on visual counts of transplanted crabs per enclosure ( $N = 3$ ) after 4, 6 and 10 weeks were analysed by three factor ANOVA with the factors Site (forest, clearing), Sympatry (presence or absence of another species) and Species (*U. elegans*, *U. flammula*). A Cochran's test of the raw data was not significant ( $P > 0.05$ ) so no transformations were made. Data on BED was averaged for each species per clearing enclosure, and analysed by a two factor ANOVA with the factors Sympatry and Species.

##### 2.6.4. Experiment 4—crab predation in forest enclosures

Data on visual counts of transplanted *U. elegans* and resident sesarmids per forest enclosure ( $N = 3$ ) after 2 and 6 weeks were analysed by one factor ANOVA with the factor Treatment (control, extra soil, extra soil low mesh, extra soil high mesh). A Cochran's test of the raw data was not significant ( $P > 0.05$ ) so no transformations were made.

### 3. Results

#### 3.1. Experiment 1—righting response times

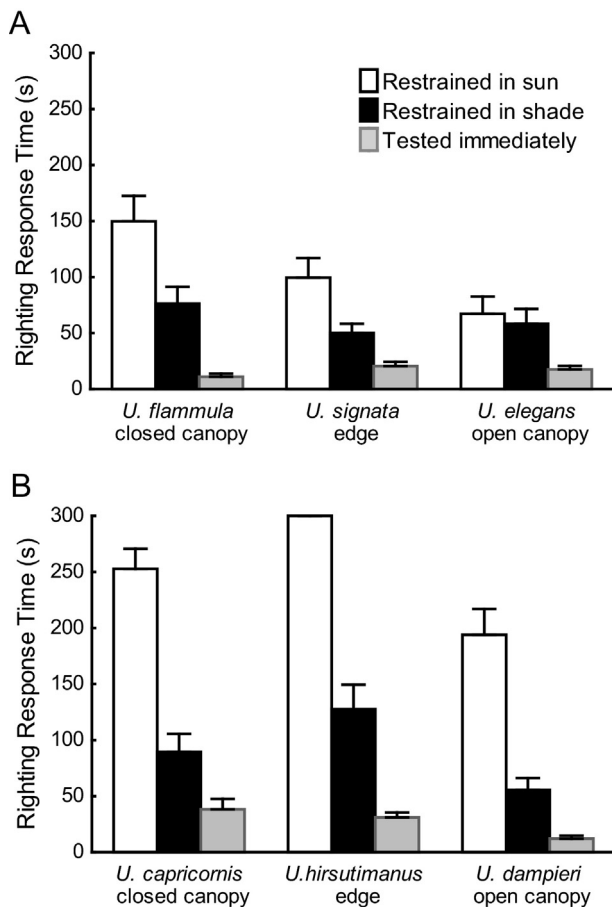
Carapace width-corrected RRT did not vary significantly with sex of the crabs (Table 1). The RRT of control crabs did not vary significantly between zones or between species in the mid-high intertidal zone

**Table 1**

Results of experiment 1: ANCOVA on righting response times and carapace widths. Cochran's test was significant ( $P > 0.05$ ) for log transformed data, therefore the significance level for ANCOVA was increased to  $P \leq 0.01$ . Significance is indicated as: \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; and \*\*\* =  $P < 0.001$ .

Factor	df	MS	F
Species	4	6.21	6.58***
Zone	1	32.29	34.21***
Sex	1	2.03	2.15
Treatment (Tt)	2	194.24	205.78***
Species $\times$ sex	4	0.47	0.50
Zone $\times$ sex	1	0.35	0.37
Species $\times$ Tt	8	2.77	2.94**
Zone $\times$ Tt	2	10.58	11.20***
Sex $\times$ Tt	2	0.18	0.19
Species $\times$ sex $\times$ Tt	8	1.15	1.22
Zone $\times$ sex $\times$ Tt	2	0.91	0.97
Error	467	0.94	

(Fig. 4). Our experiment for all control crabs from the low intertidal zone showed the RRT of *U. dampieri* was shorter than either of the other species. Restrained crabs from the low intertidal zone took longer to right themselves than those from the mid-high intertidal zone. Our experiment for all restrained crabs from the low intertidal zone showed



**Fig. 4.** Carapace width-corrected righting response times of different *Uca* species in (A) the Mid-high zone and (B) the Low zone. Within each zone the different species occupy habitats that experience different levels of canopy cover: *U. elegans* and *U. dampieri* live in open habitats, *U. signata* and *U. hirsutimanus* live in edge habitats, while *U. flammula* and *U. capricornis* live in closed habitats. Each bar represents the mean righting response time (in seconds) of 28 adult crabs (N = 14 males and 14 female crabs). White bars = crabs were restrained in the sun for 2.5 h prior to testing; black bars = crabs were restrained in the shade for 2.5 h prior to testing; and grey bars = crabs were tested immediately after capture. Error bars show means  $\pm$  SE.

the RRT of *U. dampieri* found in open habitats was shorter than either of the other two species that live in or near habitats with closed canopy. The RRT of high intertidal crabs restrained in the shade did not vary significantly between species, but for those restrained in the sun the RRT were, in order, *U. elegans* (open canopy) < *U. signata* (edges of canopy gap) < *U. flammula* (closed canopy). We accordingly concluded that crabs that live in the low intertidal zone or close to habitats with a closed canopy take longer to right themselves and are therefore more vulnerable to stressors in open habitats than are those crabs that live in the high intertidal zone and/or in open habitats. These results thus confirmed hypothesis (1), i.e. that the capacity for different crabs to cope with stress across different environments is associated with the habitat they are found within.

### 3.2. Experiment 2—visual counts of resident crabs

For our experiment testing the influence of the enclosure and substratum disturbance on activities of resident fiddler crabs we found a mean ( $\pm$  SE) of  $5.28 \pm 0.40$  (N = 36) *U. elegans* within the clearing and  $2.56 \pm 0.17$  (N = 36) *U. flammula* within the forest. Significantly fewer *U. flammula* than *U. elegans* were active and crab counts did not vary significantly with treatment i.e. enclosure with disturbance, no enclosure with disturbance, no enclosure and no disturbance (Table 2). Our Tukey's (HSD) tests showed that crab counts differed across time periods in the following order: 4 weeks < 10 weeks < 6 weeks = 0 weeks. After 10 weeks, mean ( $\pm$  SE) BED was  $16.83 \pm 2.04$  cm (N = 18), which did not vary significantly between sites ( $t(16) = 0.07$ ,  $P > 0.05$ ). Combined, these findings suggest that neither natural variations in crab abundances nor disturbances associated with setting up the experiments could influence the results of our transplantation experiment (i.e. Experiment 3).

### 3.3. Experiment 3—visual counts of transplanted crabs

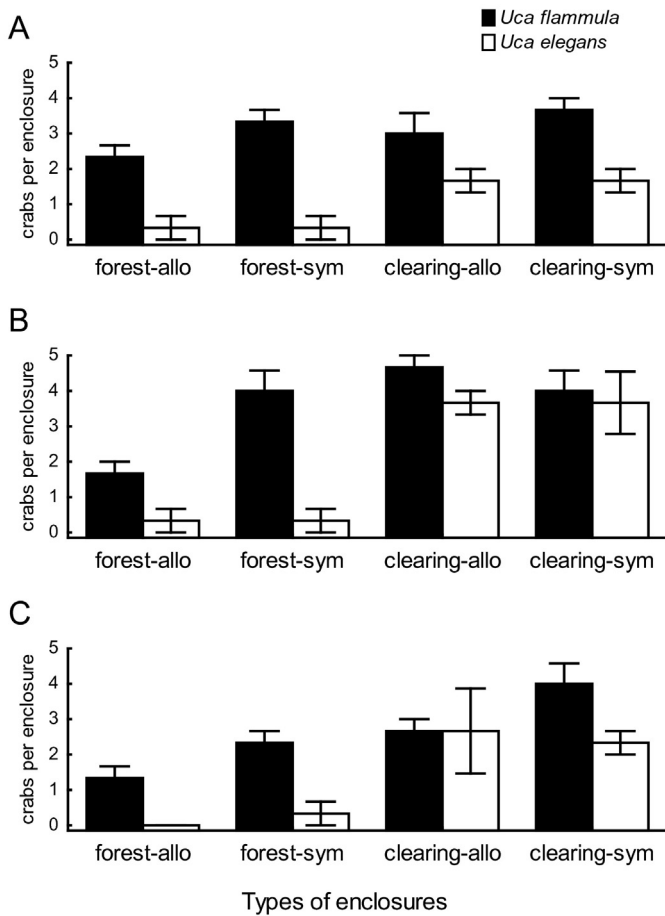
Enclosures, into which we had transplanted crabs, contained significantly fewer *U. elegans* than *U. flammula* and we found significantly fewer transplanted crabs of either species within the forest compared to the clearing (Fig. 5; Table 3). These results were unexpected given *U. elegans* occupies the clearings, whereas *U. flammula* occupies the forest. After 6 weeks, but at no other time, the interaction of all three factors had a weakly significant effect on crab counts within enclosures. Interaction between the two sympatric fiddler crab species cannot, on its own, explain their temporal distributions, particularly in light of the finding that counts of *U. flammula* were higher when transplanted into the clearing than when transplanted into the forest.

At the 'clearing' site *U. flammula* burrows were closer to the edge of the enclosures than were *U. elegans* burrows (mean BED  $\pm$  SE: *U. flammula* =  $8.2 \pm 2.9$  cm and *U. elegans* =  $18.2 \pm 2.9$ ; F (1, 10) = 5.98,  $P < 0.05$ ). Nevertheless, BED did not vary significantly with the presence of the other species or with the interaction of these factors. These results imply that the burrow locations of both species were

**Table 2**

Results of experiment 2: rmANOVA on visual counts of resident crabs per treatment to determine the effect of the enclosure and associated substratum disturbance on crab activity over time. Cochran's test was not significant upon square-root transformation of the data ( $P > 0.05$ ).

Factor	df	MS
Species	1	20.61***
Treatment (Tt)	2	0.00
Time	3	4.34*
Species $\times$ Tt	2	0.37
Species $\times$ time	3	2.71
Tt $\times$ time	6	2.16
Species $\times$ Tt $\times$ time	6	0.91
Error	12, 36	0.30, 0.11



**Fig. 5.** Visual counts of crabs transplanted to enclosures in the clearing and forest in the presence and absence of another species. The figure shows mean ( $\pm$ SE) crab counts per enclosure ( $N = 3$ ) after (A) four weeks, (B) six weeks and (C) ten weeks. Enclosures in the forest and clearing had their original crabs removed and replaced with individuals of *U. flammula* or *U. elegans* alone i.e. allopatric (forest-allo or clearing-allo) or both species together, i.e. sympatric (forest-sym or clearing-sym). Five individuals (3 males and 2 females) per species were added to the appropriate enclosure. Black bars = counts of *U. flammula* and white bars = counts of *U. elegans*.

affected by habitat and were independent of the presence of other crabs. Accordingly, we expect sympatric interactions to not influence the distribution of fiddler crabs across mangrove habitats in Darwin Harbour.

#### 3.4. Experiment 4—crab predation in forest enclosures

We found no significant differences in the number of fiddler crabs between the (1) control, (2) extra soil, (3) extra soil low mesh, and (4) extra soil high mesh treatments (Table 4). As expected, sesarmid

**Table 3**

Results of experiment 3: ANOVA on visual counts of transplanted crabs to determine the effect of site, sympatry and species on crab activity. A Cochran's test of the raw data was not significant ( $P > 0.05$ ) so no transformations were made.

Factor	df	4 weeks		6 weeks F		10 weeks F	
		MS	F	MS	F	MS	F
Site	1	5.04	12.10**	35.04	46.72***	22.04	25.19***
Sympatry	1	1.04	2.50	1.04	1.39	2.04	2.33
Species	1	26.04	62.50***	15.04	20.06***	9.38	10.71**
Site $\times$ sympatry	1	0.04	0.10	3.38	4.50*	0.04	0.05
Site $\times$ species	1	1.04	2.50	5.04	6.72*	1.04	1.19
Sympatry $\times$ species	1	1.04	2.50	1.04	1.39	2.04	2.33
1 $\times$ 2 $\times$ 3	1	0.04	0.10	3.38	4.50*	0.38	0.43
Error	16	0.04		0.75		0.88	

**Table 4**

Results of experiment 4: mean counts ( $\pm$ SE) of *U. elegans* and sesarmids per enclosure ( $N = 3$ ) after 2 and 6 weeks. F values are for one factor ANOVA comparing the means.

Treatment	Mean crabs per enclosure		
	<i>U. elegans</i> 2 weeks	<i>U. elegans</i> 6 weeks	Sesarmids 6 weeks
Control (no mesh)	0.3 $\pm$ 0.3	0	2.3 $\pm$ 0.3
Soil (no mesh)	0.7 $\pm$ 0.3	0	2.7 $\pm$ 0.5
Soil and low mesh	1.0 $\pm$ 1.0	0.3 $\pm$ 0.3	0.7 $\pm$ 0.3
Soil and high mesh	2.7 $\pm$ 0.3	1.0 $\pm$ 0.6	3.0 $\pm$ 0.5
F values (df = 3, 8)	3.2	2.0	4.3*

counts were significantly lower in the enclosures with low mesh compared to the other three treatments. The results of this experiment suggested that predation did not affect the abundances of fiddler crabs across our treatments and insinuated that predators are unlikely to affect the distributions of fiddler crabs across habitats within the Darwin Harbour mangroves.

#### 4. Discussion

Here we performed field experiments to test three explanations for the differential spatial distributions of fiddler crab species across habitats in Darwin Harbour (Nobbs, 2003; Nobbs and Blamires, 2015, 2016) and found that the crabs differed in their capacities to cope with stressors when in different habitats, and that each species is adapted to their preferred habitat independent of interactions with sympatric species. We concede that it is unlikely that interspecific competition or aerial, aquatic, or burrowing predators have no influence on the spatial distributions of fiddler crabs in the Darwin Harbour mangroves (Kristensen et al., 2008). Rather our results suggest that the influences that habitat-specific competitors and predators exert on any one species of fiddler crab are no different from the influences they exert on any other species and are not as important as physiological stressors or other influences.

Since our enclosures were embedded into the substratum, *Uca* burrows usually consist of a single vertical shaft (Kristensen, 2008), no crabs were seen attempting to climb up or dig underneath the sides of the enclosures, and escaped crabs were never found during subsequent field trips the following year, we were confident that no fiddler crabs escaped from the enclosures. Furthermore, our exclusion of predators would have also prevented *Uca* from escaping, but our results showed no effect of predator exclusion on *Uca* counts. The presence of the enclosures and soil disturbance did not affect any resident crab activities within the enclosures across habitats. Despite taking such protracted measures to control all lethal effects, we were unable to ascertain the survivorship rates of any of the transplanted fiddler crabs as the density of the root mat prevented us from excavating the crabs to determine how many resided within burrows. Nevertheless, we thoroughly measured the activities of crabs at the surface during spring low tides, i.e. when they are known to be most active (Nobbs and Blamires, 2016), so our measurements provided reliable information about the suitability of the forest and clearing habitats for sustaining the activities of crabs. Accordingly, it seems that both the clearing and forest habitats are suitable for resident fiddler crab activities, implying that the different habitats are selectively utilized by the different fiddler crab species.

Many studies suggest that abiotic interactions are equally or more important than biotic interactions in driving the spatial distribution and abundance of crabs in mangrove ecosystems (Nagelkerken et al., 2008; Ribeiro et al., 2005), with factors such as vegetation structure, organic matter, water content, salinity and temperature of critical importance in affecting fiddler crab spatial distributions (César et al., 2005; Ewa-Oboho, 1993; Thurman, 1984; Mouton and Felder, 1996; Reinsel and Rittschof, 1995; Ribeiro et al., 2010). We showed previously that abiotic factors, such as canopy cover, temperature and water availability have significant impacts on fiddler crab distribution and abundance in

the mangroves of Darwin Harbour (Nobbs, 2003; Nobbs and Blamires, 2015, 2016). The RRT of fiddler crabs confirmed that crabs from different habitats have different capacities to cope with abiotic stressors, while biotic interactions (namely interspecific competition and predation) have little or no influence on the activities of fiddler crabs in Darwin Harbour regardless of their habitat preferences. It would be presumptive, however, to suggest that abiotic interactions appear to be more important than biotic interactions in driving the spatial distribution and abundance of crabs in Darwin Harbour, given that the role of food as a limiting resource and driver of distribution has not been elucidated.

We observed that *U. flammula* remained active within enclosures in the clearing after 10 weeks of experimentation. Subsequently, we observed *U. flammula* feeding within clearing enclosures one year after the experiment had ceased. These results seem inexplicable, as this species is naturally found within the forest habitat (Nobbs, 2003; Nobbs and Blamires, 2015). According to our results *U. flammula* seems to be physiologically and behaviorally adept at living within either habitat. Nevertheless, our first experiment showed *U. flammula* experiences greater physiological stress when restrained in the sun compared to either *U. signata* or *U. elegans*, both of which live in clearings. We reconcile these apparent disparities in our results by predicting that the different species of fiddler crab are capable of living in any habitat but cope differently with extreme physiological stressors across habitats. We thus expect that the differential ability among species to with cope with stressors primarily drives the spatial distributions of fiddler crabs in Darwin Harbour. We consider it reasonable to hypothesize that other factors within habitats, such as food availability and those associated with courtship behavior, reproduction or burrowing, might interact with predation, competition and abiotic factors to render certain habitats more or less stressful to certain crab species (Allen and Lovinto, 2014; Cannicci et al., 2008; Koga et al., 2000; Thurman, 1984). We recommend that more experiments be done to assess the reproductive and burrowing requirements of different fiddler crabs across different environments (sensu Allen and Lovinto, 2014) to test such hypotheses.

We expected predators such as sesarmids to influence the spatial distributions of fiddler crabs in the Darwin Harbour mangroves to some extent (see Nobbs, 2003; Nobbs and Blamires, 2015), nevertheless we could not ascribe any influence of sesarmids or other predators on crab activities based on our fourth experiment. These results surprised us because within unprotected forest enclosures that contained transplanted crabs we had observed sesarmids attacking *U. elegans* and observed dead and mutilated *U. flammula*. Furthermore, other studies suggest that forest inhabiting fiddler crabs are susceptible to surface and subterranean predation such as large, aggressive sesarmids, birds, and fish across the circatidal cycle (Nagelkerken et al., 2008). As sesarmids were still present, albeit in low numbers, in the enclosures designed to exclude them we considered it a possibility that sesarmids could be responsible for the loss of some transplanted *Uca* in the forest enclosures. However, numbers of resident *U. flammula* (i.e. crabs naturally present within the forest enclosures) were not affected by the enclosures nor, presumably, by the many sesarmids that were present. Transplanted crabs have to build themselves a new burrow thereby putting themselves at an increased risk of predation or harassment by sesarmids in a way that resident crabs that can retreat to safety do not. If this were the case, this would represent an experimental artefact that would need to be addressed in any future studies.

Throughout Experiments 2, 3 and 4 more crabs were seen active within enclosures in the clearings than within enclosures in the forest, thus suggesting that the forest was a more stressful environment for all of the transplanted fiddler crabs. Nevertheless, Experiment 4 showed predation not to be a delimiting factor on fiddler crab activities within the forest. Of the abiotic factors, we expected the higher temperatures in the clearings to induce thermal and dehydrative stress in transplanted fiddler crabs. We, nevertheless, found that throughout Experiments 2 and 3 *U. elegans* and *U. flammula* remained active within

enclosures placed in the clearing. Thus, it seems perplexing as to why *U. flammula* prefers to occupy the forest habitat, especially considering predatory stress is higher in this habitat (Hogarth, 2015). We were also unable to deduce what factors drove the activities of both *U. flammula* and *U. elegans* within the forest enclosures to be lower than those within the clearing enclosures. Perhaps the high root mat density of the soil in the forest prevented burrowing activities (Marinelli and Waldbusser, 2005; Micheli et al., 1991; Nomann and Pennings, 1998), which may affect the willingness of the crabs to forage or engage in social activities. On the other hand the complexity of the forest habitat might have reduced the visual capacities of the crabs, thus limiting their foraging and communicative activities (Zeil and Hemmi, 2006).

An intriguing further possibility is that food is a limiting resource for mangrove-dwelling *Uca* species and, as such, may act as a driver of distribution. We transplanted 5 crabs per species into each test-enclosure. Which is, as Experiment 2 showed, similar to the density of resident crabs naturally found in the clearing enclosures (*U. elegans*), but approximately double the density of resident crabs naturally found in the forest enclosures (*U. flammula*). It is surprising that our results did not find the occurrence of other species to have a significant effect on crab activity given that crab density was increased to 10 crabs in sympatric enclosures, which we assume would increase the risk of inter- and intraspecific encounters and exhaust the food supply quicker compared to allopatric enclosures. In a Thai intertidal mangrove forest microphytobenthos, a highly nutritious food source that is abundant in canopy gaps, is responsible for increases in invertebrate biomass in canopy gaps compared to the shaded areas (Kon et al., 2007). The food availability within our enclosures may sufficiently support ten crabs in the clearing, yet insufficiently support five crabs in the forest. It is thus recommended that further study be done to determine if fiddler crab distribution is food-limited in some tropical mangrove habitats as shown to be the case in a saltmarsh environment (Genoni, 1985).

In summary, we conducted a series of experiments to assess the influences of various factors on fiddler crab activities to make predictions about the factors influencing their spatial distributions in an Australian tropical mangrove ecosystem. We found support for the hypotheses that crabs differ in their capacities to cope with stressors among environments and that each species is adapted to their preferred habitat independent of the influence of any sympatric interactions. Our subsequent experiments could not find any evidence that interactions with other crabs or differential susceptibility to predation affects fiddler crab spatial distributions. Our study provides significant insights into the influences affecting the spatial distributions of intertidal animals, but some of our results were contrary to what we had expected. Such information might be imperative for making predictions about the rates of spatial expansion or contraction of intertidal animal distributions under climate change scenarios (Helmuth, 2009; Sanford and Kelly, 2011; Somero, 2010) or the consequences of introduced invasive predators on native fauna (Jensen et al., 2002; Lohrer et al., 2000).

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