



## Both size and gender of mud crabs influence the outcomes of interference interactions

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### ABSTRACT

Many crab fisheries target large males, which can cause their densities to differ greatly in areas where they are fished and areas where they are protected, such as inside marine reserves. The size and gender of crabs potentially affect their ability to compete for resources, with competition likely to favour larger male crabs, raising the potential for cascading effects on females or smaller crabs in reserves. The role of size and gender in structuring the outcomes of competitive interference interactions between mud crabs (*Scylla serrata* Forskal) was tested by placing crabs in tanks with a competitor of smaller, equal or greater size, and of the same or differing gender. The behaviour of crabs was recorded for 15 min, and the times spent feeding, attacking, threatening and avoiding were compared among the different size and gender combinations. Male and female crabs spent less time feeding and more time avoiding in the presence of larger male than larger female crabs. Female crabs spent more time avoiding male crabs of equal size than female crabs of equal size. Male crabs of equal size spent the most time attacking. The size and gender-dependent responses of mud crabs to competition may lead to quite unexpected effects inside marine reserves.

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### 1. Introduction

Intraspecific competition often plays a major role in determining the dynamics and distribution of populations (Begon et al., 2006). Competition can occur indirectly, where competitors limit resources, or individuals can come into direct contact with each other near a resource and engage in interference competition (Birch, 1957; Miller, 1967). Due to differences in competitive ability among individuals within a population, interference is often asymmetric (Maynard Smith and Parker, 1976). Asymmetries in competitive ability can result from differences in size, age, gender, condition or experience. In either case, the outcome of competition for the inferior competitor is usually detrimental, e.g., reduced feeding rate, loss of energy, injury or death (Briffa and Sneddon, 2007). Reduction in the density of particular individuals, i.e., through size and/or gender-selective fishing (Fenberg and Roy, 2008; Zhou et al., 2010), or the reverse, i.e., through the implementation of a marine reserve (e.g. Cox and Hunt, 2005; Edgar and Barrett, 1999; Kleczkowski et al., 2008), may therefore have cascading effects on individuals that compete in a population (Lizaso et al., 2002). Determining the characteristics of animals that influence the outcomes of interference interactions is therefore important for predicting which animals will potentially be affected by changes in density and structure of populations.

The behaviour of animals during interference interactions has often been explained by Game Theory (Maynard Smith and Price,

1973). Game Theory aims to predict the behaviour of individuals during a contest based on the benefits and costs to Darwinian fitness. During a contest, individuals are thought to assess each other's competitive abilities, or resource-holding potentials (RHPs) (Enquist and Leimar, 1983; Parker, 1974). The perceived differences in RHPs then determine the behaviours that result. Behaviour that maximises fitness, in a particular situation, is expected to become an evolutionary stable strategy (ESS) within a population. For example, when there are large differences in RHPs between individuals, Game Theory models predict that the individual with the lower RHP will likely disengage early or avoid a fight, because fighting would likely have greater costs and, thus, is unlikely to have become an evolutionary stable strategy (ESS). When differences in RHPs cannot be easily established, fights may be longer and more intense because both individuals have a similar chance of winning. Fighting is therefore more likely to have a greater benefit than avoiding in these situations (Enquist and Leimar, 1983; Parker, 1974).

Crabs often interact aggressively, with the outcomes usually consistent with the predictions of Game Theory. For example, in aquarium-based experiments on interference competition between two male shore crabs (*Carcinus maenas*) over mussels, crabs with the larger claws mostly dominated interactions and fed on more mussels than their opponent (Smallegange and Van Der Meer, 2007). In addition, crabs that were similar in size tended to have longer or more intense fights and fed less than crabs that differed in size (Smallegange and Van Der Meer, 2007). Similar behaviour was observed during agonistic interactions between two male crabs of similar and differing carapace widths that were placed in aquariums (Glass and Huntingford, 1988; Smith et al., 1994). Crabs with larger carapace widths were also dominant

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during agonistic interactions between two female crabs in aquariums (Thorpe et al., 1994).

Male and female crabs are likely to come into contact with each other near shared resources and, thus, engage in interference competition. However, there is a lack of studies that examine interference competition between male and female crabs. Agonistic interactions between male and female stone crabs (*Menippe mercenaria*) have, however, been examined in an aquarium-based experiment (Sinclair, 1977). Larger *M. mercenaria* were usually dominant and male crabs were usually dominant over female crabs during fights. Fights were also more frequent between crabs of similar size or the same gender than crabs of different size or gender (Sinclair, 1977). Morphological and physiological differences between male and female crabs will likely influence the outcome of interference interactions between them. For example, male crabs often have larger chelae than females of equivalent body size (Schenk and Wainwright, 2001). As chelae size and strength can strongly determine the outcome of agonistic interactions (e.g. Smallegange and Van Der Meer, 2007; Sneddon et al., 1997, 2000), males are generally expected to dominate females.

Mud crabs (*Scylla serrata*) are large aggressive predators and scavengers, found in mangrove-lined estuaries and coasts throughout the Indo-West Pacific region (Fratini et al., 2009; Hill, 1976). They are heavily fished throughout most of their range (Fratini et al., 2009). Major fisheries for mud crabs exist along the coast of Queensland (QLD). Commercial fishers are responsible for most of the catches (estimated 1192 tonnes in 2010), but recreational and indigenous fishers catch some crabs (QLD Dept of Emp., Econ Dev., and Innovation, 2011). Male crabs less than 150 mm carapace width (CW) and all females are protected from harvesting in QLD. Moreton Bay Marine Park (MBMP) in southeast QLD is comprised of multiple zones, several of which are no-take marine reserves. Surveys using baited crab pots found that catch rates of legal size male mud crabs were about twice as high in some of the marine reserves than in adjacent unprotected areas in MBMP (Haywood et al., 2009; Pillans et al., 2005). The surveys suggest that higher densities of large male crabs occur in areas where they are protected from fishing than where they are fished. The frequency of interference interactions is therefore expected to be greater in the marine reserves than in the unprotected areas.

To understand the potential consequences of differing densities of large male mud crabs, it is necessary to determine the influence of size and gender on the behaviour of mud crabs during interference interactions. This study, therefore, tests the hypothesis that the combination of gender and relative size of a crab and its competitor determines its behaviour during interference interactions. Specifically, it was expected that female crabs would spend more time avoiding and less time feeding with a male than a female crab of equal and larger body size (carapace width) and crabs with equal body size and gender will spend the most time attacking.

## 2. Methods

### 2.1. Mud crab collection and storage

Mud crabs were collected using pots, baited with pieces of fish (*Mugil cephalus*), that were soaked for 18–24 h overnight in estuaries in southern Morton Bay, QLD, between February and May 2011. A total of 192 crabs were collected, comprising 60 small male (mean CW = 116.5 mm, SD = 16.2), 60 large male (mean CW = 155.5 mm, SD = 11.6), 36 small female (mean CW = 120 mm, SD = 15.6) and 36 large female (mean CW = 159.4 mm, SD = 9.3). Crabs were kept separately in individual 50 l containers filled with seawater (salinities of 32–34 ppt) that were constantly aerated in a constant temperature room (23.5 °C) on a 12 h light/dark cycle. Crabs were fed pilchard and mullet *ad libitum* for 4 days and then starved for 4 days to standardise hunger prior to trials. This starvation time was chosen as it was intermediate between previous competition and feeding experiments

conducted using *S. serrata* (7 days; Webley, 2008) and those using *C. maenas* (2 days; Smallegange and Van Der Meer, 2007). Seawater and any remaining food were removed and the holding containers refilled with new seawater after each day of feeding. Crabs were kept for another 7 days after the trials to ensure they were not in proecdysis (none were).

Collection and experimentation were carried out in four stages between February and May 2011, as storage space was limited to 50 crabs. Treatments were randomly interspersed over the experimental period to eliminate potential temporal confounding. Each crab was used only once in the experiments (192 total crabs used). Mud crabs are mostly nocturnal and tend to forage more at night (Hill, 1976). All experiments were, therefore, conducted between 7:00 pm and 4:00 am in darkness.

### 2.2. Food source

Small crabs are a common prey item of mud crabs (Hill, 1976). However, mud crabs are also scavengers of carrion and are likely to consume dead shore crabs in the wild. Male and female mud crabs (90–170 mm) readily consumed dead shore crabs (*Australoplax tridentata*) (8–15 mm CW) in preliminary trials. These crabs were therefore used as the food source during all trials. Shore crabs were collected by hand from the banks of estuaries in southern Moreton Bay during low tide. Shore crabs were frozen and then thawed before they were used in trials.

### 2.3. Preliminary study: Size of experimental tank

The behaviour of crabs may be influenced by the size of experimental tanks. For example, crabs are more likely to come into contact with each other in smaller tanks and, therefore, may spend more time attacking or avoiding contact. A preliminary study was conducted to determine if crabs behaved differently in two different sized circular tanks (1 m and 1.8 m diameter). Two combinations of crabs were used in trials, small versus large male crabs and two large size-matched male crabs. Each treatment was replicated 6 times and a total of 24 trials were conducted.

Tanks were filled with a layer of washed live sand (2 cm) and seawater (13 cm depth, 23–25 °C, 33–34‰). In each trial, two crabs, a focal crab and competitor crab, were placed under buckets at opposite sides of the tanks and allowed to become accustomed for 10 minutes (e.g. Smallegange and Van Der Meer, 2007; Thorpe et al., 1994). Twenty shore crabs were placed on the surface of the sediment in the centre of the tanks. Buckets were then removed and the activities of the crabs were recorded immediately for 30 min. Experiments were filmed using an infrared CCTV camera (Defender Security, model LICG40SHQ 540TVL, with built in infrared LEDs), which was suspended above the tanks and recorded videos to a computer using a 4 Channel USB Adapter. To avoid disturbance to crabs during a trial, all persons vacated the room immediately after buckets were removed and did not enter until the trial was finished. Although sensitivity of *S. serrata* to infrared light is not known, observations of *S. serrata* in laboratory tanks found that they were much more active under infrared than visible light (Hill, 1976). Before being reused in subsequent trials, tanks were emptied, rinsed twice with freshwater and once with seawater, to remove any residual organic material or odours, and then refilled with new seawater.

The times spent by the crabs carrying out four types of behaviour (Table 1) were obtained from the videos. No overt behaviour was observed upon release of the buckets and therefore behaviours were scored immediately. Behaviour of only the focal crabs was analysed to maintain independent observations. The duration of each of the behaviours was analysed separately using two-way ANOVAs, with tank size (2 levels: small, large) and relative size of competitor (2 levels: equal, larger) as the two fixed factors. Cochran's C test revealed heterogeneity of variances for time spent feeding and attacking, which were consequently  $\ln(x + 1)$  transformed to homogenise variances. All

**Table 1**  
Behaviours of mud crabs recorded from videos.

Type of behaviour	Description
Feeding/ foraging	Scooping food into mouth with chelipeds or walking legs or probing with chelipeds or walking legs
Threatening	Raising of one or both chelipeds with chelae open and holding them at about 180 degrees to the body
Avoiding/ retreating	Focal crab moves away from the competitor when approached or after contact occurs
Attacking	Focal crab pushes the competitor using its chelipeds or grasps using its chelae

analyses were conducted using the programme “GMAV 5” for Windows (Underwood and Chapman, 1998) and all results were compared to an alpha level of 0.05.

## 2.4. Size and gender

### 2.4.1. Experimental design and procedure

To determine the influence of relative size and gender on behaviour during interference competition, gender of focal crabs and gender and relative size (smaller, equal and larger CW) of competitor crabs were varied in an orthogonal design, resulting in 12 different treatments. Each treatment was replicated 6 times and a total of 72 trials were conducted. Relative size was based on carapace width and not the size of chelae because the females collected had smaller chelae than all large males and most small males.

Preliminary trials did not show differences in the mean duration of each of the behaviours of crabs in large and small tanks when with a competitor of equal or larger size and, therefore, subsequent trials were conducted in small tanks. The experimental procedure, including equipment used, laboratory conditions, acclimation of crabs and washing of tanks, was the same as that described for the preliminary study. However, trials were recorded for only 15 minutes, as it was observed in the preliminary study that most feeding and interference behaviour occurred within this period.

### 2.4.2. Statistical analyses

The durations of each of the four behaviours were analysed separately using 3-way ANOVAs, with size of competitor (3 levels: smaller, equal, larger), gender of focal crab (2 levels: female, male) and gender of competitor (2 levels: female, male) as the 3 fixed factors. Cochran's *C* test revealed heterogeneity of variances for all variables and variances could not be stabilised by transformation. However, the tests were conducted using  $\ln(x + 1)$  transformed data and the results were interpreted cautiously. Where significant effects were found SNK post hoc tests were conducted to determine which means differed. Because behaviours were not independent (i.e. multiple types of behaviour were recorded on the same individual within a single trial), correlations between the durations of each type of behaviour were investigated using Spearman's rank correlation tests. Correlations were conducted using the  $\ln(x + 1)$  transformed data for each behaviour, across all trials. In addition, Spearman's rank correlation tests between Julian day of the trials and the transformed times of each behaviour were conducted to determine whether any cumulative effects (e.g. due to residual odours remaining in tanks or sand) occurred over the experimental period. All tests for correlations were conducted using the R Package V2.15.1 (R. Core Team, 2012).

## 3. Results

There were significant three-way interactions among the crab's gender, the competitors' gender and the competitors' relative size for the durations of attacking, avoiding and feeding (Table 2). Pair-wise (SNK) comparisons of the durations of these behaviours of crabs with female

and male competitors within each size combination were considered to be the most informative and are, thus, explained below. However, results of all other pair-wise comparisons are presented in the supplementary material. Female crabs spent similar amounts of time attacking smaller female and male crabs, but spent two to three times longer attacking equal size female than equal sized male crabs and larger female than larger male crabs (Fig. 1). Male crabs spent similar amounts of time attacking smaller and larger female and male crabs, but when paired with crabs of equal size, spent approximately five times longer attacking male than female crabs (Fig. 1). Female crabs spent more time avoiding males than females when paired with crabs of greater or equal size, but, despite there being a trend for females to spend more time avoiding males than females that were smaller than them, the trend was not statistically significant (Table 2; Fig. 2). Male crabs did not avoid smaller female or male crabs, but spent more time avoiding equal size male than equal size female crabs and larger male than larger female crabs (Fig. 2). Female crabs spent twice as long feeding when paired with smaller female than smaller male crabs, similar amounts of time feeding with equal size female and male crabs, and almost no time feeding when paired with larger crabs, regardless of their gender (Fig. 3). Male crabs spent similar amounts of time feeding with smaller female and male crabs, but more time feeding with equal size females than equal size male crabs and larger female than larger male crabs (Fig. 3). All crabs, regardless of their gender and the gender and size of their competitors, spent similar amounts of time threatening (average 57 s, S.E. = 5.8; Table 2). Crabs spent the remaining time (average 64%, S.E. = 1.6%) inactive on top of the sand or slowly moved about the tank.

A significant negative correlation existed between the times spent feeding and avoiding ( $r = 0.69$ ,  $p < 0.001$ ). However, there were no significant correlations between other behaviours (Table 3). In addition, there were no significant correlations between the Julian day of the trial and the duration of the four behaviours, verifying the independence of trials.

## 4. Discussion

The hypothesis that the interaction between the gender of crabs and the gender and relative size of their competitors determines their behaviour during interference interactions was supported for the behaviours of attacking, avoiding and feeding. Both female and male crabs spent more time avoiding larger males than larger females and equal size males than equal size females. The dominance of males over females was also reflected in the times spent feeding, i.e. males spent more time feeding with females than males that were equal and larger. Although food was not used in experiments involving male and female *M. mercenaria*, male crabs were usually dominant over female crabs during fights (Sinclair, 1977). Size dimorphism is not present in *M. mercenaria* (Sinclair, 1977); however, large asymmetry in size and strength of chelae occurs between male and female mud crabs, which would have likely played an important role in determining the outcomes of interactions. Size and strength of chelae was found to be a more reliable predictor of the outcome of pair-wise fights than body size (CW) for male *C. maenas* (Sneddon et al., 1997; Sneddon et al., 2000). During interference interactions between two male *C. maenas*, crabs with larger chelae often displaced their opponents, and crabs with chelae of equal size fought for the longest and fed for the least (Smallegange and Van Der Meer, 2007). Matching male and female mud crabs based on size of chelae may lead to different results than those found here. For example, females may spend less time avoiding and more time attacking males with chelae of similar size. However, such a design was not possible because of the rarity of females with chelae large enough to match or exceed those of males.

The behaviours of mud crabs matched with an opponent of the same gender but differing relative sizes were generally similar to those observed in other species of crabs. Both male and female mud crabs dominated smaller crabs of the same gender, causing them to

**Table 2**  
Results of 3-way ANOVAs for the effects of focal crab's gender (F), competitor crab's gender (C) and relative size (S) on times spent attacking, feeding, avoiding and threatening. The denominator of the *F*-ratio was the residual mean square for all tests.

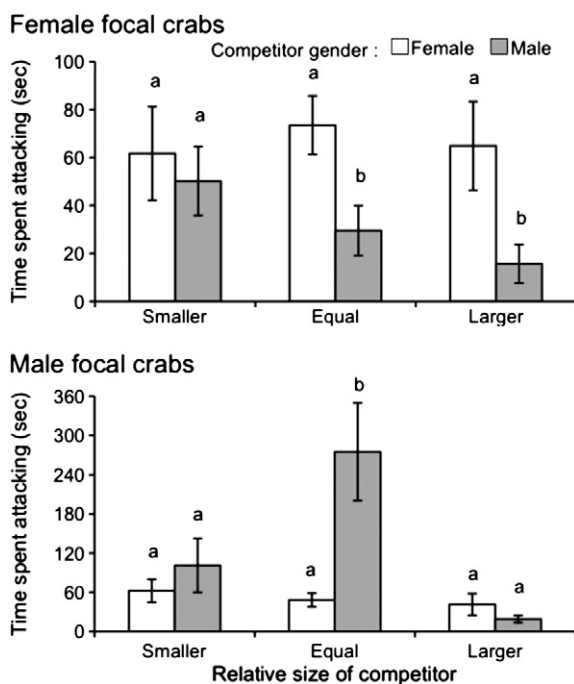
Source	df	Attacking		Avoiding		Feeding		Threatening	
		SS	P	SS	P	SS	P	SS	P
S	2	61,055	0.003	42,880	<0.001	152,415	<0.001	5759	0.351
F	1	31,752	0.011	1840	0.087	40,233	0.001	253	0.761
C	1	9660.5	0.154	57,460	<0.001	69,688	<0.001	82	0.862
S×F	2	45,588	0.011	3009	0.093	14,033	0.143	3294	0.548
S×C	2	49,248	0.008	13,340	<0.001	16,113	0.108	3581	0.52
F×C	1	60,668	0.001	329	0.465	14,450	0.046	415	0.697
S×F×C	2	54,276	0.005	6218	0.009	35,777	0.009	1172	0.806
Residual	60	277,787		36,561		209,855		162,454	

spend more time avoiding, and crabs that were similar in size and gender spent the most amount of time attacking. During agonistic interactions between 2 male *Liocarcinus depurator*, the larger crab was generally dominant and size-matched crabs fought for the longest durations (Glass and Huntingford, 1988). Similarly, male and female *Necora puber* tended to dominate fights with smaller opponents of the same gender (Smith et al., 1994; Thorpe et al., 1994). Male *N. puber* that were similar in size also fought for longer durations than those that differed in size (Smith et al., 1994). However, female *N. puber* that were more similar in size fought for shorter durations than those that differed in size (Thorpe et al., 1994). Attacks by female mud crabs against another female of equal size were generally less intense (e.g. they mainly involved pushing) and occurred for less time than attacks by male mud crabs against another male of equal size. A possible explanation for these differences is that male mud crabs are inherently more aggressive and are better adapted morphologically and physiologically for intense and prolonged fighting. For example, male decapod crustaceans usually have greater amounts of serotonin and androgenic hormones, which are associated with aggressive behaviour or willingness to fight (e.g. Barki et al., 2003; Huber and Delago, 1998). These traits along with enlarged claws would presumably benefit mud crabs

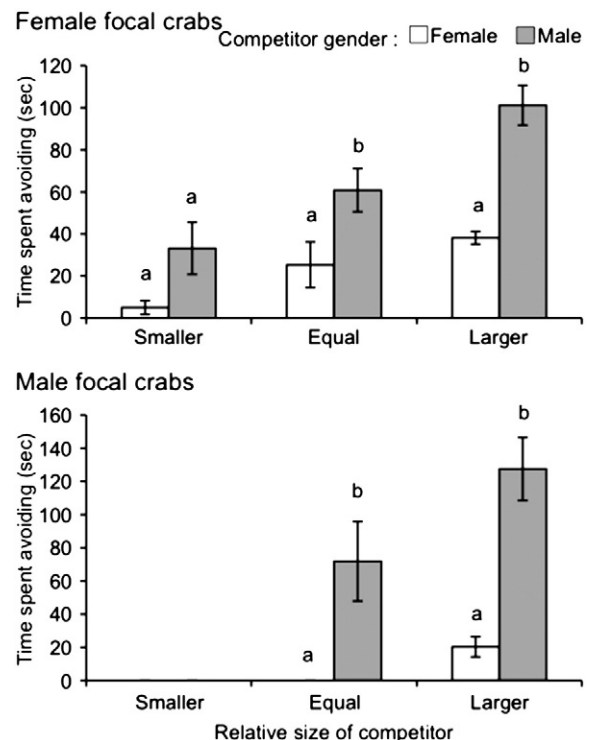
competing for mating opportunities, which may involve the defence of females or breeding sites (Christy, 1987; Knuckey, 1996).

Several aspects of the observed behaviour of mud crabs during the trials were consistent with the predictions of Game Theory (Enquist and Leimar, 1983; Maynard Smith and Price, 1973; Parker, 1974). The use of threat displays by animals to symbolise RHP is an important strategy to avoid potentially costly fights (Caryl, 1979; Parker, 1974). Mud crabs seemed to commonly adopt this strategy, as the use of threat displayed by both males and females was frequent and independent of the gender or relative size of the competitor. Differences in RHPs seemed to be determined rapidly when crabs were matched with larger or male (if female) competitors, as they either avoided contact or retreated immediately after contact was made. When differences in RHP were more difficult to determine, i.e. when crabs were with a competitor of equal size and gender, they attacked for longer periods of time (Fig. 1).

The times spent by crabs displaying a type of interference behaviour would not have been limited by the times spent displaying other types of behaviour, as crabs spent a considerable proportion of the time stationary or moving slowly around the tank during trials (average 64%, S.E. = 1.6%). However, relationships between the durations of some behaviours were expected. A strong negative correlation was only found between feeding and avoiding (Table 3). Crabs that avoided for longer



**Fig. 1.** Time spent attacking (mean, S.E.) by female and male mud crabs with smaller, equal and larger female and male competitors. Different letters indicate differences between times spent attacking with female and male competitors within a relative size category (SNK,  $p < 0.05$ ).



**Fig. 2.** Time spent avoiding (mean, S.E.) by female and male mud crabs with smaller, equal and larger male and female competitors.

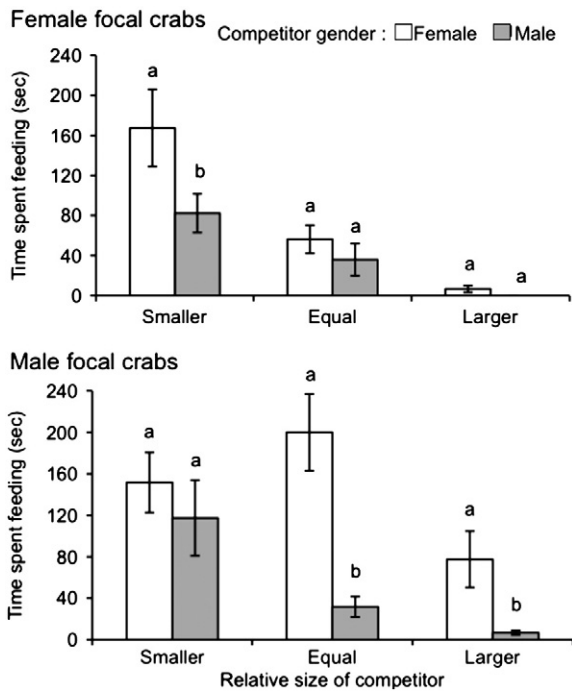


Fig. 3. Time spent feeding (mean, S.E.) by female and male mud crabs with smaller, equal and larger male and female competitors.

tended to feed for less, probably because these crabs were also avoiding the higher risks of confrontation near the food. Crabs that attacked for longer durations were also expected to avoid for less and vice versa. However, no significant relationship was found between these variables, probably because a crab placed with a similar competitor may have attacked for long durations but then spent time avoiding the competitor once it was found to be superior.

The response of crabs to competitors of varying size and gender within the enclosures may differ to that in the field. The preliminary study attempted to determine whether available space affected the behaviour of crabs and did not find differences in their behaviour in large (1.8 m diameter) and small (1 m diameter) tanks. However, the greater space available in their natural habitats may enable crabs to avoid an interaction more easily and, thus, behave differently. Observing interference behaviour of mud crabs in situ is largely constrained by the low transparency of estuarine waters and the infrequency of interactions. For example, baited remote underwater videos were deployed in estuarine areas throughout Moreton Bay Marine Park, QLD, on five occasions over a period of 4 years, resulting in over 500 hours of video recordings. The videos recorded mud crabs scavenging on dead fish but no interactions between crabs were observed (Webley, 2008; Beattie et al., 2009). Catch rates of mud crabs in baited pots could, however, provide some information on interference behaviour occurring in situ. Analyses of catch rates often reveal that the presence of a mud crab in a pot reduces the probability of further captures, which is likely due to agonistic behaviour between crabs (Robertson, 1989; Williams and

Hill, 1982). In addition, catch rates are often skewed towards large male crabs (Robertson, 1989; Williams and Hill, 1982), suggesting that large females or smaller crabs are often prevented from entering or remaining in a pot by the presence of a large male crab.

Despite potential differences in the behaviour of crabs in the laboratory and in more “natural” conditions, it is possible to make some broader inferences from the findings of this study. More frequent contact by smaller crabs and large female crabs with large male mud crabs may occur in marine reserves, where densities are greater than in fished areas (Haywood et al., 2009; Pillans et al., 2005). Small crabs and large female crabs may, consequently, spend more time avoiding or retreating and have less access to food. These individuals may then be forced to alter their foraging behaviour or move to areas where there is less chance of encountering large male crabs, such as outside the boundaries of small marine reserves. For example, higher densities of subadult Dungeness crabs (*Cancer magister*) experienced more frequent physical interactions, forcing smaller crabs to emigrate from intertidal shell habitat into suboptimal habitats (Iribarne et al., 1994). More intense density-dependent competition between fish was observed in a marine reserve in the Philippines (Abesamis and Russ, 2005). Larger fish usually chased smaller fish away from food, suggesting that smaller individuals were more likely to be forced out of the reserve (Abesamis and Russ, 2005). This hypothesis was further supported by the gradient of decreasing mean size of fish found at greater distances from the marine reserve (Abesamis and Russ, 2005).

In addition to mud crabs, many species of crabs are subjected to size and gender selective fisheries, including *Callinectes sapidus* (Abbe, 2002), *C. magister* (Taggart et al., 2004), *Paralithodes camtschaticus* (Kruse et al., 2000) and *Paralithodes brevipes* (Sato et al., 2007). Studies assessing abundance, size, and gender ratios of most of these species in protected areas are lacking. However, abundances of large male Dungeness crabs dramatically increased following exclusion of commercial fishing in Glacier Bay, Alaska (Taggart et al., 2004). Aggressive interactions over food (Barber and Stanley Cobb, 2009) and space (Iribarne et al., 1994) among size classes of Dungeness crabs have been observed. Size dimorphism also occurs between male and female Dungeness crabs (Smith and Jamieson, 1991), suggesting that interactions between them could have similar outcomes to those observed in this study. Females and small male Dungeness crabs may therefore also be affected by more intense competition with large male crabs within protected areas.

Instances of cannibalism or aggression-associated mortality of mud crabs did not occur during the experiments. However, they are common among size classes of crabs and are likely to be strongly density-dependent. For example, higher rates of cannibalism or aggression-associated mortality of mud crabs occurs at higher stocking densities within aquaculture holding tanks (Mann and Paterson, 2003; Qunitio et al., 2001; Triño et al., 1999). Higher rates of cannibalism among Dungeness crabs at higher densities were also observed in experimental studies (Fernandez, 1999) and density-dependent cannibalism may be an important mechanism of regulating their populations in the wild (Fernandez, 1999; Higgins et al., 1997). Cannibalism may also occur more frequently where densities of large male crabs are higher in the wild, such as in marine reserves.

This study has shown that the size and gender of mud crabs have important consequences for how they respond to competitors in the presence of food. As larger male crabs tend to dominate interactions, there is potential for individuals to experience negative effects from more intense interference competition with large male crabs in marine reserves. Given that most assessments of interference behaviour in crabs have focused on a single gender, studies of competition between male and female crabs, such as this study, can improve our understanding of potential drivers of the dynamics and distribution of crab populations. Finally, these findings prompt further research into the potential indirect effects of manipulating the structure of populations through size and gender selective fisheries and the establishment of marine reserves.

Table 3

Spearman's correlation coefficients ( $r$ ) between the durations of the four behaviours.

	Fighting	Avoiding	Feeding	Threatening
Fighting	1	-0.187	0.145	0.009
Avoiding		1	-0.690 <sup>a</sup>	0.036
Feeding			1	0.013
Threatening				1

<sup>a</sup> Significant,  $p < 0.01$ .

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2012.07.025>.

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