Body Size, Burrow Ownership and Handedness Affecting Fighting Success of the Fiddler Crab, *Uca annulipes* (H. Milne Edwards, 1837)

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ABSTRACT

In this study, the effects of body size, burrow ownership and handedness on fighting success of male fiddler crab, *Uca annulipes* (H. Milne Edwards, 1837) were investigated. Forty-six pairs of naturally engaged combats between residents and intruders were observed, and their fighting durations were recorded. After finishing each combat, the character of the winner (larger/smaller, resident/intruder) was identified, and afterwards the crabs were caught to identify their handedness (right/left claw), and to measure their carapace widths and major claw lengths. In addition, 40 non-fighting male crabs were caught randomly from the population, their handedness identified, and carapace widths and major claw lengths measured. Results showed that only larger males in the population were involved in combats. Residents, as well as, larger males won higher numbers of combats. Heteroclawed (opposite handed) combats were more common than homoclawed (same handed). Fighting duration was negatively correlated with body and claw size asymmetries of fighting pairs. This study clearly indicates that large resident males tend to win fights in a shorter time.

Keywords: Fighting duration, Fighting success, Handedness, Burrow ownership, *Uca annulipes*

INTRODUCTION

In animals, engaging in combats concurs high energetic costs, risk of injury and predation (Huntingford and Turner, 1987; Jacobsson *et al*., 1995; Copeland *et al*., 2011). If individuals can accurately assess the fighting ability of opponents prior to fighting that should be a selective advantage (Maynard Smith and Parker, 1976). In a typical combat between two males of the same species, the winner gains mates, dominance rights, desirable territory and other advantages (Maynard Smith & Prince, 1973) which are beneficial for them. Combats between *Uca* fiddler crab males are very common throughout the year (Hyatt and Salmon, 1978; Christy and Salmon, 1984; Rosenberg and Enquist, 1991). Males compete vigorously to acquire new burrows (Mautz *et al*., 2011)

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because gravid females select males based on the burrow features, and remain in the chosen males' burrows while their eggs develop (Backwell and Passmore, 1996). Wandering males fight with resident males in order to acquire new burrows, and residents defend their burrows from intruders (Milner *et al*., 2010).

During combats between residents and intruders, residents tend to win the fights and hold territory, because stronger individuals tend to own valuable resources (Maynard Smith and Parker, 1976; Leimar and Enquist, 1984). On the other hand, fighters with larger body sizes than their opponents are physically stronger, and thus may cause more damage upon their opponents (Maynard Smith, 1982; Riechert, 1998). One male may be more likely to win because of its greater size (Le Boeuf, 1974; Jaroensutasinee and Tantichodok, 2003) or resident ownership advantage (Parker, 1974, Tina *et al*., 2015), but it is difficult to understand which factor has effect on fighting success (Hammerstein and Parker, 1982; Leimar and Enquist, 1984; Waage, 1988). The fighters can determine fighting duration and intensity based on body size asymmetry (Hammerstein and Parker, 1982; Neat *et al*., 1998), and fighting duration is negatively correlated with body size asymmetry of fighters (Leimar and Enquist, 1984; Jaroensutasinee and Tantichoodok, 2003; Tina *et al*., 2015).

Handedness also may have an effect on fighting behaviour of fiddler crabs. Jennions and Backwell (1996) suggested that heteroclawed (opposite-handed) combats should be more common in a population than homoclawed (same-handed) combats, because heteroclawed males might be able to assess each other's claw and body size more easily and with great accuracy, as their claws act as mirror images.

The objective of this study was to test the effects of body size, resident status, and handedness on the fighting success of fiddler crabs, *Uca annulipes* (H. Milne Edwards, 1837). Four hypotheses were tested: (1) residents, as well as, larger males should win more combats, (2) heteroclawed combats should be more common than homoclawed combats, (3) only larger males in the population should get engaged in combats, and (4) fighting duration should be negatively correlated with body and claw size asymmetries of fighting pairs.

MATERIALS AND METHODS

Study site and observation of fighting behaviours

We observed fighting behaviours of 46 pairs of *U. annulipes* inside mangrove vegetation in Pakmeng Sea Beach, Sikao District, Trang province (7° 30' 25.3859" N and 99° 18' 40.2540" E), in November 2015. Combats between residents and intruders were observed. Whenever two males started fighting, their fighting behaviour was observed, and fighting duration (second) was recorded. After finishing each combat, the character of the winner (i.e. resident/intruder;larger/smaller) was recorded. Afterwards, we caught both crabs to identify their handedness (right or left hand), and to measure their body size (carapace width) and claw size (major claw length) using digital Vernier callipers. In addition, we collected 40 non-fighting

crabs randomly, identified their handedness, and measured their carapace width and major claw length. After measuring, each crab was released back to the natural habitat immediately with a minimal handling time on each crab.

Statistical analysis

Before analysing data, normality was assessed. Parametric statistics were used when normality or other assumptions of parametric tests were met. Fighting duration (second) was log transformed to achieve normality of data. The differences in carapace width, and major claw length were calculated as larger males minus smaller males of the combat pairs. In this study, we used major claw length instead of carapace size to test whether body size affects fighting outcomes, as major claw size is a more important indicator of fighting ability than carapace size (Jennions and Backwell, 1996). One-way ANOVA tests were used to test the differences in body size (carapace width), as well as in claw size (major claw length) among residents, intruders, and non-fighting crabs. The relationships between carapace width and major claw length of non-fighting males, residents, and intruders were identified using simple linear regressions. We used analysis of covariance (ANCOVA) to test whether relationships between carapace width and major claw length differed for non-fighting males, residents, and intruders. We used chi-square tests to see the differences in the numbers of (1) combats won by larger and smaller males, as well as by residents and intruders, (2) homoclawed and heteroclawed combats, and (3) right and left handed males in the population. Spearman's correlation was used to analyse the relationships between body/claw size of intruders and residents, as well as between body/claw size differences and log fighting duration. All tests were two-tailed with a significant level of $P < 0.05$.

RESULTS

Crab body and claw size of non-fighting crabs, residents and intruders

Body and claw sizes of non-fighting crabs, residents and intruders differed significantly (carapace width: $F = 4.98$, d.f. = 2, 129, $P = 0.008$, major claw length: $F = 6.49$, d.f. = 2, 129, $P = 0.002$, Fig. 1a, b). Post-hoc Tukey showed that non-fighting crabs were smaller than residents (carapace width: $P = 0.015$, major claw length: $P = 0.008$) and intruders (carapace width: $P = 0.022$, major claw length: $P = 0.004$), but these measures did not differ between residents and intruders (carapace width: $P = 0.990$, major claw length: $P = 0.981$).

The positive linear relationships between carapace widths (CW) and major claw lengths (MCL) of non-fighting males (NF), residents (R), and intruders (I) were: $MCl_{NF} = 1.69CW_{NF} - 0.978$ ($F = 61.49$, d.f. = 1, 38, $r^2 = 0.618$, $P = 0.000$, Fig. 2), $MCL_R = 2.068CW_R - 5.219$ ($F = 153.57$, d.f. = 1, 44, $r^2 = 0.777$, $P = 0.000$, Fig. 2), and $MCL_I = 1.603CW_I + 1.162$ ($F = 300.41$, d.f. = 1, 44, $r^2 = 0.872$, $P = 0.000$, Fig. 2). Non-fighting males, residents, and intruders had different relationships between their carapace widths and major claw lengths (ANCOVA interaction: $F = 3.295$, d.f. = 2, 126, $P = 0.04$). Non-fighting males had smaller major claw lengths than residents at CW >11.2 mm, and intruders at any carapace

width (Fig. 2). Intruders had larger major claw lengths than residents at CW <13.75 mm, but residents had larger major claw lengths than intruders at CW >13.75 mm (Fig. 2).

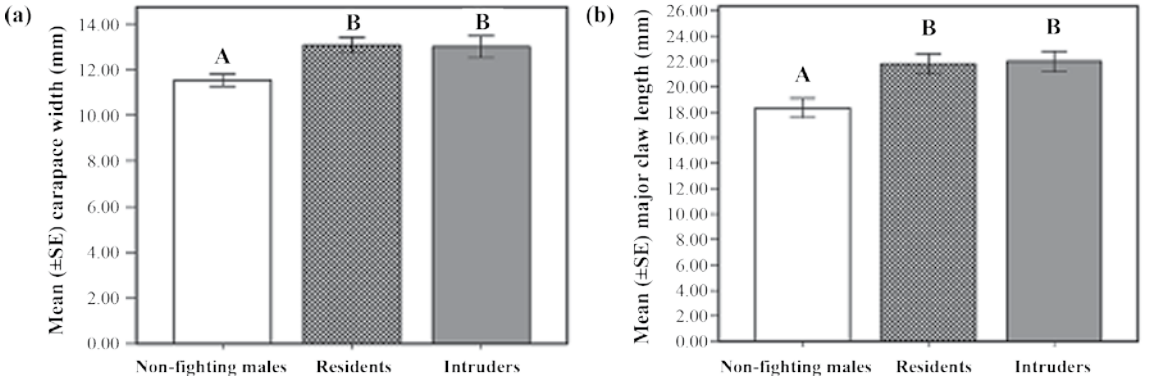

Figure 1. Carapace width (a) and major claw length (b) of non-fighting males, residents and intruders. A and B indicate significant differences among non-fighting males, residents and intruders ($P < 0.05$).

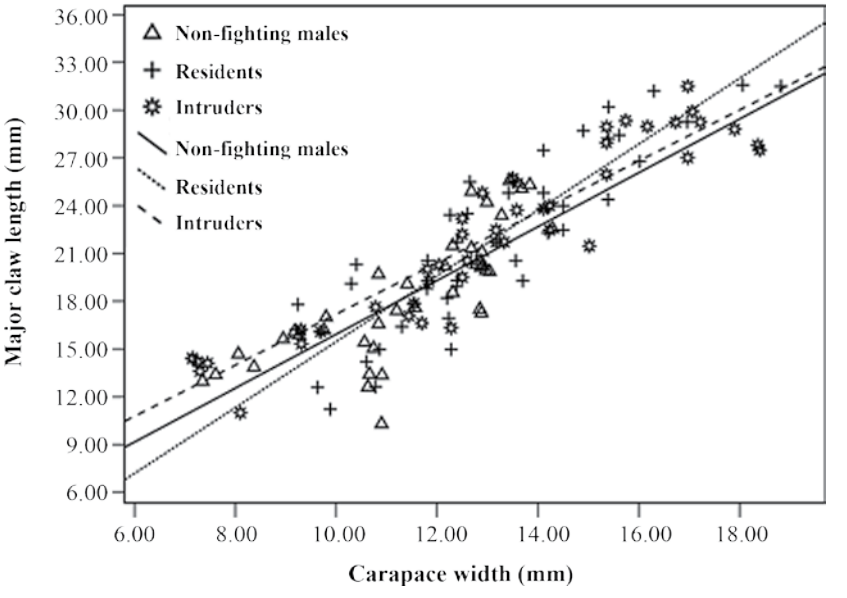

Figure 2. Carapace width and major claw length of non-fighting males, residents and intruders of *Uca annulipes*

Crab fighting, body size, burrow ownership and handedness

Higher numbers of combats were won by larger, as well as resident, males (Table 1). The intruders that won combats had larger major claws in 75% of combats (larger won- 12, smaller won- 4, $\chi^2 = 4.00$, d.f. = 1, $P = 0.046$). However, when the residents won, the number of winners with the larger major claws were not significantly different than the number of winners with the smaller major claws (larger won- 20, smaller won- 10, $\chi^2 = 3.33$, d.f. = 1, $P = 0.068$). Heteroclawed combats were more common than homoclawed combats (Table 1). Sampled males from the population had equal handedness (right major claw- 22, left major claw- 18, $\chi^2 = 0.4$, d.f. = 1, $P = 0.527$).

Table 1. Fighting status, body size, burrow ownership and handedness in *Uca annulipes* males

Parameters	Fighting status		Statistical tests
Body size	Larger won 32	Smaller won 14	$\chi^2 = 7.04$, d.f. = 1, $P = 0.008$
Burrow ownership	Residents won 30	Intruders won 16	$\chi^2 = 4.26$, d.f. = 1, $P = 0.039$
Handedness	Heteroclawed 34	Homoclawed 12	$\chi^2 = 10.52$, d.f. = 1, $P = 0.001$

Body and claw size of intruders and residents

Carapace width, as well as major claw length of intruders were positively correlated with carapace width and major claw length of residents (Fig. 3a, b). Intruders did not initiate fights randomly but they selected same sized residents to engage in fighting (i. e. carapace width and major claw length).

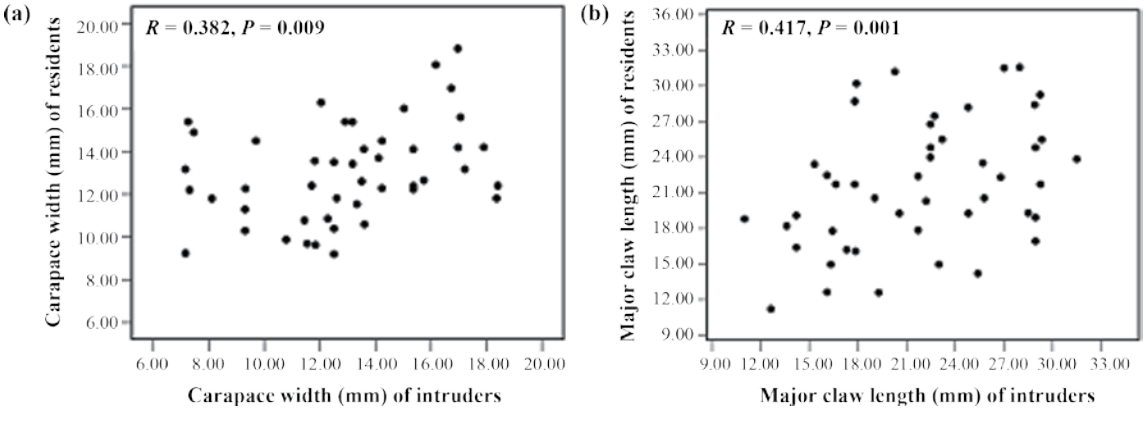

Figure 3. Carapace width (a) and major claw length (b) of intruders and residents

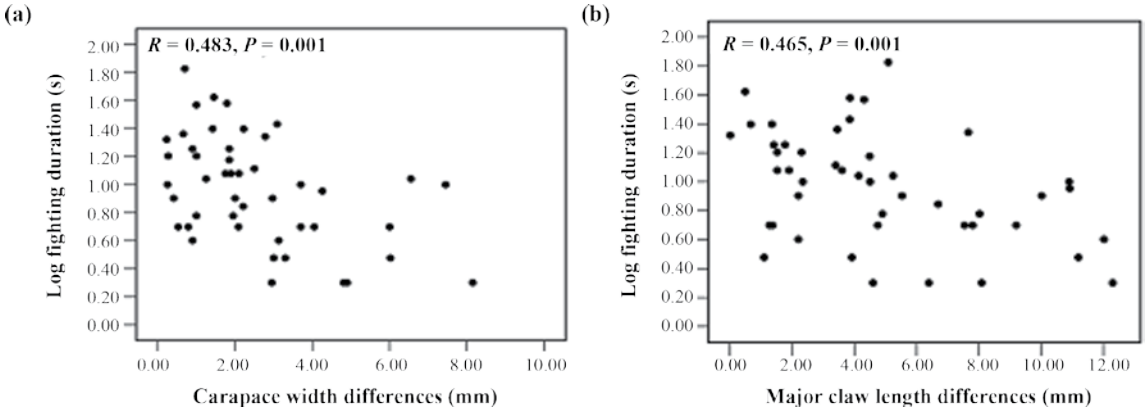

Figure 4. Log fighting duration, and carapace width differences (a), and major claw length differences (b)

Body and claw size asymmetries, and log fighting duration

Body and claw size asymmetries were negatively correlated with log fighting duration (Fig. 4a, b). As body and claw size of residents were similar in size with intruders, they spent longer time engaged in fighting.

DISCUSSION

We observed that non-fighting males were smaller in size than fighter males. This finding is very common in *U. vocans* hesperiae, and *U. bengali* (Jaroensutasinee and Tantichodok, 2003; Tina *et al*., 2015). So, in a fiddler crab population, only larger males get engaged in combats, because the chances for larger males to win a combat are higher than smaller males (Tina *et al*., 2015).

In the case of *U. annulipes*, body size, burrow ownership and handedness all played major roles in fighting success. The effects of these three factors are different in different fiddler crab species. Such as in *U. pugilator*, *U. pugnax*, and *U. bengali*, both body size and burrow ownership showed effects on fighting success (Hyatt and Salmon, 1978; Tina *et al*., 2015), but in *U. vocans hesperiae*, males only assessed body size asymmetry to settle combats, not the burrow ownership (Jaroensutasinee and Tandichodok, 2003). During combats, the chances are higher for the larger males to win more combats, as fighters with larger bodies are usually physically stronger than their opponents (Maynard Smith, 1982; Riechert, 1998). On the other hand, burrow owners have a positional advantage; they can anchor onto the entrance of their burrows (Christy, 1982; Adams and Caldwell, 1990). During fighting, when a resident crab retreats into its burrow during fighting and does not show its behaviour, the intruder needs to down-push until the resident reappears at the surface; otherwise, the intruder moves away. This down-pushing behaviour may make the fighting cost greater for intruders than residents, and reduces the chance of winning for intruders (Hyatt and Salmon, 1978; Hammerstein and Parker, 1982).

In this study, we proved our hypothesis that heteroclawed combats were more common than homoclawed combats, but previous studies could not prove this hypothesis (Jennions and Backwell, 1996; Tina *et al*., 2015). Another study observed that in *U. vocans hesperiae*, homoclawed combats were more common than heteroclawed combats, although 96% males of the population were right handed (Jaroensutasinee and Tantichodok, 2003). Therefore, there was a high possibility of observing significantly more homoclawed combats than heteroclawed combats. In the case of our study, we found that *U. annulipes* population had equal numbers of right and left handed males. So, handedness influenced fighting initiations, and most of the cases, crabs started combats when they were opposite handed.

The body and claw size of intruders were positively correlated with body and claw size of residents. Intruder males tend to initiate combats with similar body and claw sized resident males, as intruders need to acquire burrows compatible with their body sizes, into which they can enter easily (Jennions and Backwell, 1996; Jaroensutasinee and Tantichodok, 2003; Tina *et al*., 2015).

Negative correlations were observed between body/claw size asymmetries of *U. annulipes* and fighting duration. Previous studies showed similar results in the case of *U. vocans hesperiae*, *U. mjoebergi*, and *U. bengali* males (Jaroensutasinee and Tantichodok, 2003; Morrell *et al*, 2005; Tina *et al*., 2015). According to Rosenberg and Enquist (1991), negative correlation between body size asymmetry and fighting duration indicates that combats between two males involve a cost that is greater for the smaller individual than larger one, and for this reason fighting duration is shorter when body asymmetry is higher.

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