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Handedness in fiddler crab fights

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Running header: handedness in fiddler crab fights

Word count: 3479

Key words: body asymmetry; fight costs; fight outcome; handedness distribution; handedness-matching.

Asymmetric weapons are common in bilateral animals and, in some species, they can occur on either the left or the right hand side of the body (lateralisation). Fiddler crabs (*Uca* spp, Decapoda: Ocypodidae) have an enlarged claw that is used in male-male combat over territories, and in courtship displays. Males can be either right or left-handed, and most species have a 1:1 ratio. Past studies have found little effect of handedness on fighting success, fight duration or other measures of combat. Here we show that, while handedness per se. does not affect fighting, handedness-matching has a significant effect. In *Uca mjoebergi*, fights between different-handed males were more likely to escalate to grappling, suggesting that it is harder for the combatants to determine the winner. We suggest that the positioning of the claws during fighting creates distinct forces that result in different outcomes for same- versus different-handed fights. This can represent a strong selective pressure in populations with an uneven handedness distribution where handedness minority will often engage in different-handed fights. We discuss these results in light of the selective forces that may act on handedness distribution in fiddler crabs.

Morphological asymmetry in bilateral animals has independently evolved from perfect symmetry several times in evolutionary history, and is found in a variety of taxa (Palmer, 2009). Examples include eye positioning in flatfish(Schreiber, 2006), sailing forms in bluebottle jellyfish (Palmer, 2009), shell coiling direction ingastropods (Arthur, 2000), and the tusks of narwhals (Kingsley & Ramsay, 1988). Asymmetric body traits assume diverse forms and a variety of different functions, such as modified crusher and cutter claws for feeding in American lobsters (Govind, 1989), genitalia lateralization in mating strategies in insects and spiders (Huber, 2010), and specialized weapons for inter-male competition, including deer antlers (Alvarez, 1995), beetles' horns (Miller & Wheeler, 2005), and maritime earwigs' forceps (Munoz & Zink, 2012).

Behaviour lateralization (handedness) without morphological asymmetry is also common; a couple of examples are eye and foot use preferences in octopuses and parrots, respectively (Byrne et al., 2004; Magat & Brown, 2009). The effect of lateralization in combat has been studied (e.g. Elwood et al 2014) and human combat sports are well-known examples of the benefits of being left- or right-handed (Grouios et al., 2000; Pollet et al., 2013). Many crustaceans possess handedness in a morphologically asymmetrical weapon, including fiddler crabs (*Uca* spp., Decapoda: Ocypodidae). In fiddlers, males have a single enlarged claw that make up a third to a half of their body mass (Rosenberg, 2001). This claw is a weapon but is also tightly linked with courtship behaviour and is waved in a species-specific pattern to attract females for mating (How et al., 2009; Perez et al., 2012). The large claw is equally likely to be on the left or right hand side in most species (Crane, 1975) although in at least 5 of the 102 known species, the large claw is predominantly on the right (Backwell et al., 2007; Jones & George, 1982; Yamaguchi & Henmi, 2001), all in the subgenus *Thalassuca* (Rosenberg 2001)

Fiddler crab combat is generally in the context of territorial defence. The territory contains a burrow that serves as a retreat during high tide, an insulator from temperature extremes, a source of water and an incubation site for females. Not all males build their own burrows, but rather fight for and take a burrow from others. This method of gaining a burrow was successful 33.4% of the time in a study with *Uca mjoebergi* (Morrell et al., 2005). This success rate likely makes burrow taking an effective strategy to gain access to this important resource since the energy expenditure in fighting for burrows can be lower than building them (Hyatt & Salmon, 1978).

When a wandering male tries to take a resident's burrow, they often engage in combat where the two crabs align and touch claws while facing each other and pushing their claw surfaces against each other (Fig. 1a, c). The intruder generally selects an opponent that is closely-matched to his own size since he is unlikely to win against a much larger opponent, and would be unable to fit into the burrow of a much smaller opponent (Jennions & Backwell, 1996; deRivera, 2005; Bolton et al., 2013). These battles over real estate usually do not go beyond the pushing level. However, if males persist, the fight can escalate to the level of grappling, where claws interlock (Fig. 1b, d) (Backwell et al., 2007; Crane, 1975; Hyatt & Salmon, 1978; Morrell et al., 2005).

Rivals can have the same handedness, or they can have opposite handedness. Claw alignment during same- and different-handed fights differs. Figure 1 shows that, in the pushing phase of the fight, different handed opponents align their claws base-to-base and tip-to-tip (Fig 1 c); same handed opponents, however, align their claws base-to-tip (Fig 1 a). Grappling is caused by the further extension of the claws making them slide against each other from the outer surfaces reaching the point of interlock (Hyatt & Salmon, 1978). Same-handed males interlock in front of the bodies (Fig. 1 b). Different-handed males, however, need to extend their claws far away from their bodies before interlocking (Fig. 1d). The contrast between the two types of fights suggests that the source and direction of forces differ. The position of the claws relative to each other may influence the effectiveness of the pushing level in ending the fight. In fights between different-handed rivals, the claws line up tip to tip and, as observed in thousands of fights (Backwell pers. comm. and Christy pers. comm.), one male often extends his claw more than the other leading to grappling. Similarly, in same-handed fights, the claws align tip to base and the mutual force applied may push the bodies apart until the claws are extended enough that grappling is accommodated.

Several studies have examined the effect of fighting initiation and outcome and have found no difference between left- and right-handed males. In ghost crabs *Ocypode ceratophthalmus* and several species of fiddler crabs, handedness does not play a role in opponent selection (Brooke, 1981; Crane, 1975; Jennions & Backwell, 1996; Hyatt & Salmon, 1978), and handedness plays no role in winning fights in *U. pugilator* (Pratt et al, 2003). If there is any benefit in attacking heteroclawed or homoclawed opponents, it may be outweighed by the doubling in search costs involved in avoiding males of a specific handedness (J.H. Christy, personal communication).

While handedness per se. does not appear to effect the decision to fight or fight outcome, the effect of handedness-matching during combat has not been well examined. For example, same- and different-handedness may make grappling easier or harder. In turn, these factors may affect fight outcome, duration, fight level or opponents' size-matching, all potentially important aspects of fighting behaviour, energy expenditure and risk assessment. Hyatt & Salmon (1978) found that fights between same-handed opponents (in both *U. pugilator* and *U. pugnax)* more commonly escalated from pushing to grappling than different-handed opponents, but many questions remain unanswered.

Here we investigate effects of handedness-matching in fight dynamics in *U. mjoebergi*, a fiddler crab species with a left- to right-handedness ratio that is very close to 1:1

(Backwell, unpublished data). This species is in the subgenus *Celuca* and is distantly related to the predominantly right-handed *Thalassuca* (Rosenberg 2001). We address the following questions: Do same- and different-handed fights differ in their fight level, duration, the size-matching between rivals and whether the intruder or resident wins?

METHODS

We studied a population of *U. mjoebergi* at East Point Reserve, Darwin, Northern Territory, Australia, from October-December 2003 and September-December 2013. Data were collected during the low tide period (up to 6 h a day) during both neap and spring tides. We examined fights between intruders and burrow-owning resident males. There are two possible methods to examine fights. First, with no interference by observing natural intruder males engaging in fights with residents. Second, creating intruders by capturing a resident, releasing in a different area and waiting until he fought with a resident. We employed the second method since it eliminated several potentially important problems: (i) it prevented winner–loser effects since both males were burrow-owners and must therefore have won their last fights (see Hsu & Wolf, 1999); (ii) it overcame the possibility that wandering males are a class of weaker individuals that are unable to hold territories successfully (Bradbury & Vehrencamp, 1998; Olsson & Shine, 2000); and (iii) it avoided the possibility of size-assortative fighting if individuals are distributed in a size-assorted patches within the population (Christy, 1980).

We captured a burrow-owning male, measured his carapace width and major claw length, noted whether he was left- or right-handed and then released him at least 2 m away from his territory. We did not document any behaviour that we considered to be a scare response after we released the male. Instead, we waited for the released male to approach and instigate a fight with a resident. A fight was defined as any interaction in which the males touched claws. We recorded the level of fights as either pushing or grappling. Fights start with males aligning their large claws and pushing each other; if this does not end the encounter, they escalate to grappling where they interlock claws and twist (Crane, 1975). After the fight, we recorded fight outcome, captured and measured the resident's carapace and claw, and noted his handedness.

We only included fights between males with original claws since regenerated claws are known to be inferior weapons (Backwell et al., 2000). We also only included fights in which both males remained on the surface: we excluded those where one male fought from within the burrow shaft or where one male attempted to dig the opponent out of the burrow, as these situations did not represent equivalent fighting conditions for both opponents. We avoided re-recording the same males by using distinct parts of the population on successive days. The population is large (tens of thousands of animals) so we are unlikely to have re-used the same males in different trials.

The data collected in 2003 were part of a larger study (Morrell et al., 2005) but were not analysed in terms of male handedness. This made it ideal data for minimising observer bias since the observer was unaware of the question being addressed. Additional data were added in 2013 to boost the sample size. In total, we collected data from 156 fights where 81 were same-handed and 75 were different-handed.

Data analysis:

We used Fisher's exact test to determine whether same- and different-handed fights differed in fight level. We further evaluated the effects of size-matching and fight type (same- or different-handed fights) on fight level by running a binary logistic regression with fight level as the dependent variable, size difference between rivals as continuous covariate, fight type as categorical covariate. To test for differences between fight type and duration, we ran a General Linear Model with duration $\log_{10}$ transformed as the dependent variable and push/grapple and same/different-handedness as fixed factors, hence controlling for fight level when examining the durations of same- and different-handed fights. We also checked if grappling fights were longer than pushing fights by running a Mann Whitney U test and if same-handed fights are longer than different-handed fights by running a Student's t-test equal variances not assumed. To determine whether same- and different-handed fights differ in their level of size-matching, we ran correlations between the claw lengths of the opponents for each fight type and compared the correlations (computing the value of Z). Carapace width and claw length are highly correlated in this species (Morrell et al., 2005; Reaney & Backwell, 2007), therefore we opted for using claw length. Finally, we performed a Fisher's exact test to investigate if fight type influenced whether the intruder or resident wins. All analyses were carried out in SPSS ver. 22.0 (SPSS Inc, Armonk, NY, U.S.A.).

Ethical Note:

All procedures performed in studies were in accordance with the ethical standards of the Australian National University. Relocating residents causes minimum disturbance since males often loose their burrows in fights or abandon them after mating with a female (Backwell per observation). Handling the animals during measurements was minimal to avoid any effects on animal behaviour during data collection and guarantee animal welfare.

RESULTS

Do same- and different-handed fights differ in their fight level?

Of the 81 fights between same-handed males, 51 (63%) ended at the pushing level and 30 (37%) escalated to grappling. Of the 75 fights between different-handed males, 32 (43%) ended at the push phase and 43 escalated to grapple (57%). Fights between different-handed males were more likely to escalate to grappling (Fisher's exact test: $P = 0.02$).

If fights between more closely sized-matched rivals are more likely to escalate than fights between disparate sized rivals this could affect the above result. We separated these effects through a binary logistic regression that showed that size differences between rivals partially explained the escalation from push to grapple (closely size-matched opponents were more likely to escalate; Wald test: $Wald_1 = 4.91$, $P = 0.027$). Fight type (same- or different-handed) was, however, a stronger predictor of fight level (different-handed opponents were more likely to escalate; Wald test: $Wald_1 = 7.59$, $P = 0.006$).

Do same- and different-handed fights differ in their duration?

Grapple fights (12.35s) are longer than push fights (3.16s) (Mann Whitney U test: $U = 495.5$, $P < 0.001$) and different-handed fights (9.15s) are longer than same-handed-fights (5.91s) (t-test: $t_{93} = 2.09$, P two-tailed: 0.039). Given that we found different-handed fights were more likely to escalate to grappling, we controlled the effects of the fight level to enable analysis of the relationship between fight type and duration. Same- and different-handed fights did not differ in duration when controlled for fight level (General Linear Model: $F_1 = 0.104$, $P = 0.75$).

Do same- and different-handed fights differ in the size-matching between rivals?

To determine whether same- and different-handed fights differ in their level of size-matching, we ran correlations (separately for same-handed and different-handed fights) between the claw lengths of the opponents (Pearson correlation same handed: $r = 0.32$, $n = 81$; different-handed: $r = 0.57$, $n = 75$) and compared the correlations ($Z = 1.39$, P two-tailed $= 0.17$; Zar, 1984). There was no difference in the size-matching between same- and different-handed fights.

Do same- and different-handed fights differ in whether the intruder or resident wins?

Of the 81 same-handed fights, 57 residents won and 24 intruders won (70.4% against 29.6%). Of the 75 different-handed fights, 54 residents won and 21 intruders won (72%

against 28%). Intruders were just as likely to win when they fought same-handed or different-handed opponents (Fisher's exact test: $P = 0.80$).

DISCUSSION

Our results suggest that there is difference in fight efficiency when claws are lined up in the same or the opposite direction. We found that fights were more easily resolved when the males were same-handed, since these fights were less likely to escalate from a simple push to a grapple. In same-handed fights, the positioning of the claws may result in a more efficient transfer of force, and pushing may therefore be sufficient to determine a winner. In contrast, for different-handed fights, a push was not sufficient and these fights were more likely to escalate to grappling.

Hyatt and Salmon (1978) explored a range of variables correlated with fight outcome, including the opponents' handedness, in *U. pugilator* and *U. pugnax*. They describe the fight in detail and found that same-handed fights were more likely to escalate, the opposite of our results. Fiddler crab species commonly show quantitative and qualitative differences in fighting behaviour and different claw morphology (grooves and tubercles) may play an important role in gripping ability, fight structure, and outcome (Crane, 1975; Dennenmoser & Christy, 2013). The diversity of weapons in animals (size, shapes, ridges, grooves, forks) is likely to be the result of different fighting tactics (Emlen, 2008). In dung beetles, for instance, the horn morphology is related to the strategy of fighting in confined spaces (Emlen & Philips, 2006). To elucidate the differences in the results found in the present study and the study by Hyatt and Salmon (1978), future work on aggressive behaviour in other species of fiddler crabs should routinely document male handedness.

We propose that the positioning of claws during fighting (Fig. 1) creates distinct forces that result in different outcomes for same- versus different-handed fights. A push might have a higher propensity to escalate to grapple when rivals are different-handed because of the direction of force that is being employed and how it propagates to the opponent. The study of the interaction of physical forces in animal contests is essential to unveil weapon efficiency (e.g. beetles mandibles, bovid horns, Goyens et al., 2014; Kitchener, 1988). Fight biomechanics in crabs is well explored with special focus on muscle force and fight outcome where winners possessed greater claw height and length (Sneddon et al., 2000), or when there is a trade-off between closing speed and force relative to claw size (Levinton & Allen, 2005). Furthermore, Dennenmoser & Christy (2013) suggested that different-handed fights had differential use of tubercles on the claws. Future studies testing or modelling the physics of fight scenarios in fiddler crabs are still needed in order to understand handedness influence in fight outcomes.

Size-matching of opponents did not differ between same- or different-handed fights when fight level was controlled. Intriguingly, fight duration also did not differ between same- and different-handed fights when fight level was controlled. If the position of the claws influenced the higher tendency of different-handed fights to escalate to grappling, then one would expect to see differences in the duration of the pushing or grappling level between same- and different-handed fights (i.e. if there is a higher tendency to move directly to grappling in different-handed opponents, same-handed opponents would have shorter grappling duration).

The increased likelihood of escalation in different-handed fights suggests that the pushing level for this fight type is not as decisive in ending the fight as it is in same-handed fights. The costs of engaging in a different-handed fight are probably higher than for a same-handed fight. This is because the duration of escalated fights is longer (Morrell et al., 2005). Since different-handed fights are more likely to escalate to grappling they are also longer overall and thus likely to be more costly. In addition, grappling is more likely to end in injury or claw loss (Hardy & Briffa, 2013). Moreover, we found that residents have the same likelihood of winning regardless of the handedness of the fight (see also Hyatt & Salmon, 1978; Morrell et al., 2005; Pratt et al., 2003). This evidence would suggest that fighting same-handed opponents is advantageous. So why do males still fight different-handed opponents?

Previous fiddler crab studies have shown that males do not fight opponents with specific handedness (Jennions and Backwell, 1996; Pratt et al., 2003) and that same- and different-handed fights are equally likely (Hyatt & Salmon, 1978). Male fiddler crabs fight opponents of a similar size so they have a reasonable chance of winning, and so that the burrow being fought for will have an appropriate size (Bolton et al., 2013; deRivera, 2005). Avoiding an opponent with a different handedness would likely increase search effort, energetic costs, risks of predation and overheating (J.H. Christy, personal communication).

Most fiddler crab species have a 1:1 ratio of left and right-handed males, although the exact proportions would vary over space and time (Jones & George, 1982; Rosenberg, 2001). If there is an advantage to fighting same-handed males, any drift away from exactly 1:1 would be magnified and the handedness that occurs in the lower proportion would be under higher selective pressure and possibly slowly be eliminated from the population. So why do they retain their 1:1 handedness? In fiddler crabs, handedness is thought to be developmentally plastic and not heritable (Palmer, 2004). Handedness is determined early in the growth period, when very young male crabs still have symmetric claws (Ahmed, 1978). When the young male loses one claw, the remaining claw develops into the enlarged claw (Ahmed, 1978; Morgan, 1923; Yamaguchi, 1977; Yamaguchi & Henmi, 2001). The selection maintaining the 1:1 ratio of left and right-handed can only act early in the growth period and is still unclear. Possible explanations can lie in environmental effects acting on physiological paths (Yamaguchi, 1977) such as the differential use of claws, as in lobsters (Govind, 1992). However, fight would unlikely be the reason for the maintenance of the 1:1 ratio according to our previous explanation of searching efforts outweighing fight costs. In a study with *U. lactea,* Yamaguchi (1977) argues that in early growth period there are rare agonistic encounters since they feed in a small radius from the burrow and hardly leave the area.

However, there are at least five (out of 102) fiddler species that are predominantly (>95%) right-handed (Backwell et al., 2007; Jaroensutasinee & Jaroensutasinee, 2004; Jones & George, 1982; Rosenberg, 2001; Takeda & Murai, 1993). The fact that they are all right-handed (no convincing evidence of a predominantly left-handed species exists, but see Gibbs 1974) and that they all belong to the subgenus *Thalassuca* (Rosenberg, 2001) suggests that this trait originated only once (Jones & George, 1982). The predominance of a single handedness could have become fixed by genetic assimilation when the ancestor had a previous developmental plasticity (Palmer, 1996; Palmer, 2004; Palmer, 2012; Pigliucci *et al*., 2006). As suggested by Palmer (2004), if a fiddler crab population has an uneven handedness distribution, even if by chance, and there is a disadvantage of being the less abundant handedness in fights, the selective pressure of fight mechanics would then act and favor the predominant handedness. The costs of maintaining developmental plasticity increase favoring a heritable variation, a phenomenon known as genes-as-followers or genetic assimilation (Palmer 2012; Pigliucci *et al*., 2006).

ACKNOWLEDGEMENTS

The study was funded by an ARC Discovery Grant to P.R.Y.B.. We thank the North Australian Research Unit for facilities and Michael Jennions for assistance.

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FIGURE CAPTION

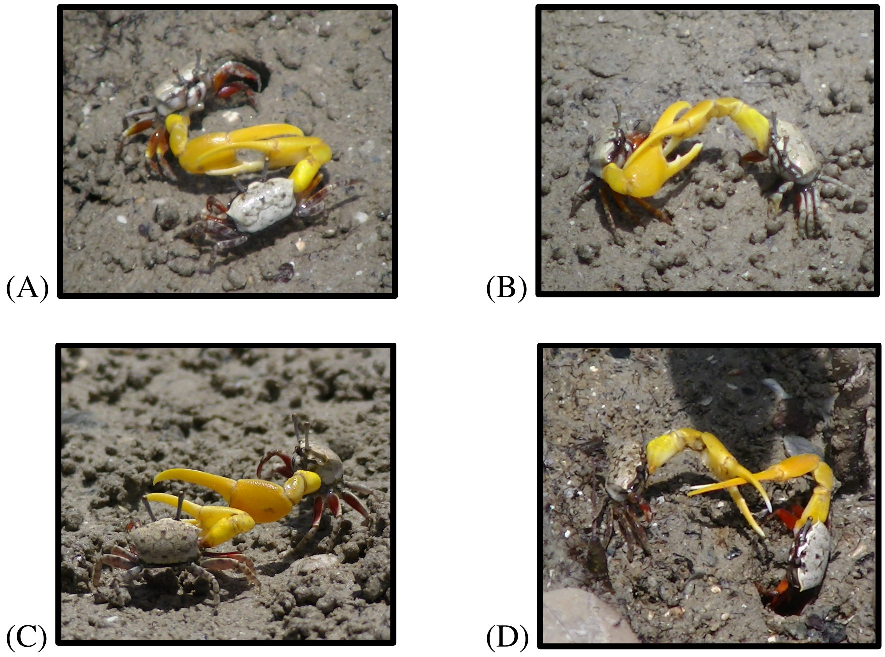

Figure 1. Fiddler crab fights. Fight of same-handed males of *U. mjoebergi* starts with a push (a) and escalates to grappling level (b). Same for fight of different-handed males in pushing level (c) and grappling level (d).