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Weapons or mating signals? Claw shape and mate choice in a fiddler crab

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Abstract Males often possess traits, such as horns, claws, and tusks, which are used during male–male combat. Studies suggest that selection has fine tuned these weapons to improve their effectiveness and that the shape of these weapons provides cues for males to assess the strength of rivals. Similarly, females might also assess a male's weaponry to determine his value as a mate. The largest weapon relative to body size is the major claw of male fiddler crabs (genus: *Uca*). Males use their claws both as a weapon and as a courtship signal, waving it to attract females. We used robotic crabs in two-choice experiments to test female mating preferences based on male claw shape in *Uca mjoebergi*. First, females did not prefer conspecific claws over any of three alternatively shaped stimuli matched for color and for the rate and pattern of waving. The alternative stimuli were two different heterospecific claws and a plain rectangular shape. Second, females significantly preferred the alternative stimuli when they were presented at a faster wave rate. We conclude that claw shape in *U. mjoebergi* has not evolved under sexual selection imposed by female mating preferences and is more likely to have evolved under selection for effectiveness during male–male competition.

Keywords Female choice · Fighting · Male–male competition · Sexual selection

Introduction

There is a wide diversity of weapon-like traits among male animals. These weapon-like traits often have highly detailed features such as patterns of grooves, bumps, ridges, forks, branches, and spirals (Emlen 2008). These structures can facilitate the interlocking of male weaponry during combat (Crane 1966; Geist 1966) and are often sufficiently distinct that they are readily used for species identification (e.g., horn shape in antelope).

Sexual selection due to direct male–male competition has clearly acted on male traits to increase their efficacy as functional weapons (e.g., the closing force of claws; Lailvaux et al. 2009). There is also evidence that these traits provide cues that males can use to assess the fighting ability of potential opponents (e.g., Lappin et al. 2006). There could even have been selection for features that allow males to honestly signal their fighting ability (e.g., Arnott and Elwood 2009). This could involve either direct visual assessment of the shape of weaponry (akin to the role of status badges in rival assessment; e.g., Tibbetts and Lindsay 2008), or males possessing features that increase their ability to obtain information during physical encounters. For example, males commonly engage in fights during which they interlock weaponry. Structures that allow males to push against each other might improve the ability to assess a rival's strength (Crane 1966; Geist 1966; Barrette and Vandal 1990).

Has sexual selection due to female choice also affected the evolution of weapon-like male traits? Conspicuous armaments used during male–male competition could provide females with information used during mate choice (including for "species recognition"; Berglund et al. 1996). In many taxa, larger weapon-like male traits are favored during

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male contests as well as female mate choice (e.g., Jennions and Backwell 1996; Judge and Bonanno 2008; Milner et al. 2010). Despite this, the extent to which female choice has exerted selection on the shape, structure, and complexity of weapon-like male traits remains poorly explored (but see Rosenberg 1997, 2002; Levinton and Allen 2005; Dennenmoser and Christy 2013).

The enlarged major claw of male fiddler crabs (genus: *Uca*) is the most extreme example of an elaborate weapon-like male trait. Each fiddler crab species has a distinctively shaped claw (Crane 1975; Rosenberg 2002). The claw is used during male–male fights, but males also wave their claw to attract mate-searching females. In conjunction with claw shape, various bumps, ridges, and indentations on the claw are thought to have important functional effects (e.g., facilitating grip when males interlock their claws) during male combat (Crane 1966, 1975; Eberhard 1985). In contrast, whether female choice exerts selection on claw shape or not has yet to be determined.

Here, we tested if male claw shape affects female mate preferences in the fiddler crab *Uca mjoebergi*. In *U. mjoebergi*, the color of the claw is important for species recognition (Detto et al. 2006). Female mate choice also selects for larger claws (Reaney 2009), albeit with seasonal (Milner et al. 2010) and within breeding cycle variation in the strength of the female mating preference (Kahn et al. 2013). Females also prefer males that wave their claws at a faster rate (Reaney et al. 2008; Reaney 2009). Here, we used robotic crabs in two-choice mate choice trials to test if *U. mjoebergi* females preferentially approach conspecific versus heterospecific claws, controlling for claw coloration, wave rate, and pattern. We then tested if females actually preferred heterospecific claws when they waved at a greater rate. These experiments were also repeated with a plain rectangular object.

Methods

Study species and population

Fieldwork was conducted at East Point Reserve, Darwin, Australia (September–December 2011) during the main mating period (5–7 days centered on neap tide) of each semilunar tidal cycle. Here, *U. mjoebergi* lives in sympatry with several congeneric species, including *Uca signata* and *Uca elegans*. The three species differ in claw size, shape, color, and in courtship display movements. *U. elegans* are larger than either *U. mjoebergi* or *U. signata*, which are similar in size (largest reported carapace width: *U. mjoebergi*, 16.4 mm; *U. signata*, 18.4 mm; *U. elegans*, 26.6 mm; Crane 1975). The major claw morphology of *U. signata* differ significantly from that of *U. mjoebergi* and *U.*

elegans: it lacks prominent tubercles and have a far more pronounced pollex, angular fulcrum (dactyl pivot point), and smaller gape. The claw morphology of *U. elegans* and *U. mjoebergi* differs with respect to the thickness and shape of the tip of the dactyl and pollex fingers (Fig. 1). All three species also differ in coloration. *U. mjoebergi* have a mottled brown carapace with areas of red or yellow and a bright yellow major claw. *U. signata* have traces of blue on their carapace, a red manus, and a white major claw. In *U. elegans*, a bright blue cross is typically present on a black carapace and the major claw is a uniformly pale pink. Finally, the major claw wave pattern of these species differs dramatically. *U. mjoebergi* wave in circular lateral movements. In contrast, *U. signata* and *U. elegans* both employ vertical "up and down" wave movements. *U. elegans* exhibits a clear pause on the upward wave, a feature lacking in *U. signata* (How et al. 2009).

Female mate choice trials

We used custom-built robotic male crabs to test female mating preferences. Each robotic unit consists of a
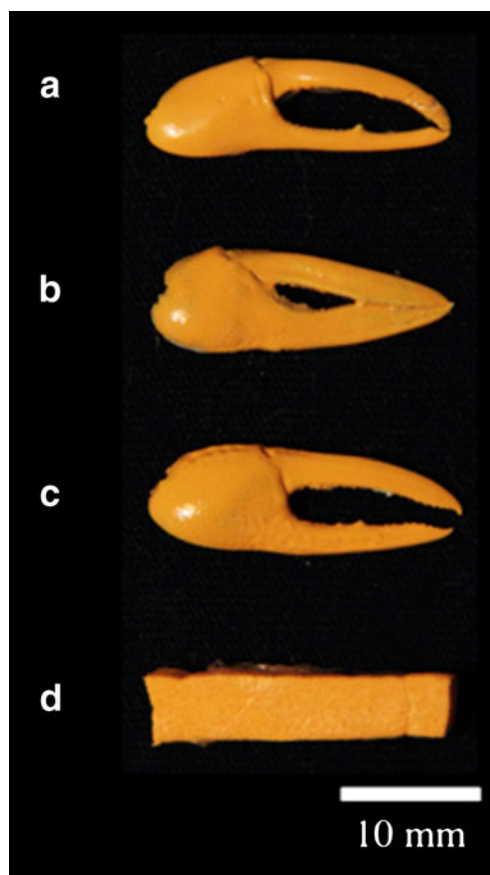
Fig. 1 The stimuli used in the female mating preference trials: (**a**) a male *U. mjoebergi* claw; (**b**) a male *U. signata* claw; (**c**) a male *U. elegans* claw, and (**d**) a rectangular shape made from a block of packing foam

motorized arm with a claw attached. The movement of the arm mimics the natural courtship waving of a male *U. mjoebergi* (for further details see Reaney 2009; Milner et al. 2010; Callander et al. 2011). Mate choice experiments were conducted in situ on a mud-covered arena (60×60 cm). The two robotic crab units were positioned so that only the metal arm (to which a claw is attached) was above the sediment and the units were 5 cm apart on an arc that was 20 cm from the female release point. We collected naturally occurring mate-searching females that had visited at least one courting male prior to capture (N=20 females/treatment). For each trial, a single female was placed in a transparent container at the release point and allowed to observe two complete waving cycles by the robots (hereafter "males"). The container was then remotely lifted and a positive mate choice scored if she directly approached a male (within 2 cm).

We conducted two sets of two-choice experiments. In all experiments, we used real claws that were autotomized by males. The size matching of the claws used within each pair was limited by the size range of the autotomized claws available on the mudflats. In each trial, the "control" stimulus was always the claw of a conspecific male *U. mjoebergi* (Fig. 1a). The three alternative stimuli were a male *U. signata* claw (Fig. 1b), a male *U. elegans* claw (Fig. 1c), and a rectangular shape made from a block of packing foam (Fig. 1d). All claws were right handed and painted to within the natural color range of a *U. mjoebergi* claw (see Detto et al. 2006).

Experiment 1: only shape differed

We presented females with a choice between two claws size matched for length that waved in synchrony at the same rate (8.4 waves/min). There were three treatments:

1. *U. mjoebergi* (22.0 mm) versus *U. signata* (21.8 mm)
2. *U. mjoebergi* (17.6 mm) versus *U. elegans* (16.9 mm)
3. *U. mjoebergi* (20.4 mm) versus rectangular shape (21.1 mm)

Experiment 2: shape and wave rate differed

We gave females the same choices as in experiment 1, except that the wave rate of the alternative stimuli male was double that of the conspecific male (16.8 waves/min). Female *U. mjoebergi* have previously been shown to have a strong preference for a faster wave rate (Reaney 2009; Callander et al. 2012). Precise doubling of the wave rate ensured that waves were still in synchrony. This prevented either male producing "leading" waves, which are preferred by females (Reaney et al. 2008).

Results

Experiment 1: only shape differed

There was no significant difference among the three treatments in the proportion of responses to the conspecific claw (log-likelihood ratio test, $G=3.66$, $df=2$, $P=0.16$). In each of the three treatments, there was no significant preference for either the conspecific or alternative stimulus (Table 1).

Experiment 2: shape and wave rate differed

There was no significant difference among the three treatments in the proportion of responses to the conspecific claw (log-likelihood ratio test, $G=3.38$, $df=2$, $P=0.18$). In each of the three treatments, there was a highly significant preference for the alternative stimulus that was presented at a faster wave rate (Table 2).

Discussion

In general, females exert a mating preference for conspecifics otherwise hybridization occurs and breeding opportunities are lost with the production of sterile or inviable offspring. This favors mate choice for traits (or combinations of traits) that are species specific. We found no evidence that, by itself, male claw shape affects female mate choice and, by extension, species recognition in *U. mjoebergi*. Females did not preferentially approach a conspecific claw over either of the heterospecific claws that were size and color matched and waved in the same pattern as a *U. mjoebergi* male. They were also equally likely to approach a rectangular shape that was matched for color, size, and wave pattern to the conspecific claw. We further found that a female preference for a faster wave rate actually resulted in females discriminating against a conspecific male waving at a slower rate.

It is not surprising that female *U. mjoebergi* did not discriminate between the relatively similarly shaped claws of sympatric heterospecific fiddler crabs. Fiddler crab eyes

Table 1 Number of females choosing the conspecific claw versus the alternative stimulus when wave rate is matched. *P* values are from exact binomial tests (two tailed)

Treatment	Number of responses		
	U. mjoebergi claw	Alternative stimuli	*P* value
U. signata claw	10	10	1.00
U. elegans claw	7	13	0.26
Rectangular shape	13	7	0.26

Table 2 Number of females choosing the conspecific claw versus the alternative stimulus when the wave rate is 8.4 waves/min for conspecific and 16.8 waves/min for the alternative stimulus. *P* values are from exact binomial tests (two tailed)

Treatment	Number of responses		
	U. mjoebergi claw	Alternative stimuli	*P* value
U. signata claw	1	19	<0.001
U. elegans claw	3	17	0.003
Rectangular shape	5	15	0.04

are located on stalks, providing 360° vision, but their resolving power is limited. They rely on color, motion detection, and a vertical zone of visual acuity (where their ommatidia are most densely congregated), to distinguish predators from conspecifics (Zeil and Hemmi 2006). It was, however, more surprising that they did not discriminate against a simple rectangular-shaped block. Therefore, our data strongly suggest that female *U. mjoebergi* do not use claw shape during mate choice. The fact that females preferentially approached the alternative stimuli when it had a higher wave rate also suggests that our results cannot readily be attributed to a generalized anti-predator response where females approach any object protruding above the mudflat (Christy et al. 2003).

How do female *U. mjoebergi* ensure that they mainly approach conspecific males? The obvious cues available to females are claw color, shape, size, and how the claw is waved. Even when males are not waving, females preferentially approach a conspecific over a heterospecific (*U. signata*) (Detto et al. 2006). This suggests that the species-specific waving display is not essential for species recognition in *U. mjoebergi*, although a higher wave rate clearly elevates a male's chances of mating (Reaney et al. 2008; Reaney 2009; Callander et al. 2012). It also remains to be determined whether females prefer conspecific wave movements after controlling for species differences in claw shape and color. This would require robotic crabs that produce different wave movements but have the same claw type. Our current study suggests, however, that claw shape itself is unimportant in mate choice. Claw size affects mate choice when females are offered a choice between conspecific claws (e.g., Reaney 2009; Milner et al. 2010; Kahn et al. 2013), but is unlikely to facilitate species recognition because of an overlap in adult size across species. This leaves claw color, which does appear to be essential for mate recognition in *U. mjoebergi* (Detto et al. 2006).

Given that we detected no effect of claw shape on female choice, why do the claws of fiddler crab species differ so markedly in shape and fine-scale details? The most plausible answer is selection driven by direct male–male competition. The claw is used extensively in male combat, during which males initially align their claws to push each other and eventually interlock their claws and grapple (Crane 1966). It seems plausible that claw shape and structure affect fight outcome. It has been argued that the teeth and indentations that line the inner surfaces of the dactyls are important contact zones to facilitate grip and leverage when males interlock their claws (Crane 1966, 1975; Eberhard 1985). The positioning of the tubercles at the contact zone near the apex of the gape may also play a role in maintaining the claw's mechanical advantage as it increases in size (Dennenmoser and Christy 2013). Fighting success is strongly selected for because fights are usually for burrows that yield direct benefits in the form of shelter, feeding territory, and mating sites (Smith and Miller 1973; Backwell and Passmore 1996; Koga et al. 2001).

One obvious question remains though: if claw shape affects fighting success, why have different species not converged on the same claw shape? This, of course, is a question that can equally well be asked of other taxa in which males show elaborate weaponry (e.g., antelope, dung beetles, ground crickets). Detailed studies of species-specific signaling and fighting behavior are required to further investigate this question (Dennenmoser and Christy 2013). For instance, even though claw shape may not have evolved under sexual selection driven by female choice for shape in *U. mjoebergi*, it may still play a role in generating claw shape variation in other species. *U. mjoebergi*, *U. signata*, and *U. elegans* all differ in their waving displays (How et al. 2009). Clear interspecific variation in wave movement pattern has long been thought to play a role in conspecific mate attraction and both morphological and muscular major claw asymmetries are correlated with wave pattern variation (Rhodes 1986; Takeda and Murai 1993). Diversity in claw shape could therefore arise due to a mechanical advantage during courtship waving displays (Rosenberg 1997). Similarly, disparate fighting tactics between species may also contribute to the diversity seen in claw morphology and sexual selection by female choice may therefore become more important in shaping diversity in claw morphology in species that employ less aggressive fighting tactics

In sum, male fiddler crabs use their claws in two very conspicuous activities: fighting and courting. Of those, however, courting does not appear to have a role in directing the evolution of claw shape in *U. mjoebergi*. Future studies should test the generality of this finding in other species. If it is widespread, this should encourage biomechanical studies investigating the effect of claw shape on fight outcome.

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