



Major claws make male fiddler crabs more conspicuous to visual predators: a test using human observers

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Abstract

One of the possible costs of the male fiddler crabs enlarged claw can be conspicuousness to predators. This hypothesis was tested using human observers as a model of visual predators. In the European fiddler crab, *Uca tangeri* Eydoux, the males' major claw is white contrasting with the orange-brownish colour of the carapace and of the feeding claw, and the mudflat background. The following morphotypes were created from close-up photographs taken in nature using an image processing software: male, male without claw, female, female with enlarged claw, male with enlarged claw of the same colour of the feeding claw, male with 75% sized claw, male with 50% sized claw. These morphotypes were then presented in a randomised order to students, using a psychology test software, which allows the measurement of response time in msec. The subjects were allowed to look at the images for an unlimited amount of time, until they detected the individual or until they decided to pass on to another image. Backgrounds (i.e. mudflat picture) without individuals were also presented as a control. Male crabs were detected significantly sooner than females. When we compared males with the claw removed with females with an enlarged claw added, the pattern is reversed and the latter are detected significantly faster. Thus, the enlarged claw seems to be the key feature that makes the individuals more conspicuous. Size and colour seem to be the main aspects of the claw's conspicuousness. The data of these experiments support the initial prediction of males being more conspicuous than females because of their enlarged claw. The possible costs and benefits of this trait, related to predation, are discussed.

Introduction

Advertising traits are assumed to be costly to produce or maintain in order to be considered 'honest' signals. Hypothesised costs include the energetic demands of trait development, maintenance and production (e.g. Vehrencamp et al., 1989), attraction of parasites (e.g. Cade, 1975), higher risk of mortality due to violent fights (Clinton & Le Boeuf, 1993), among others. By far, the most frequently demonstrated cost related to traits that enhance male's attractiveness to females is conspicuousness to predators. In the guppy (*Poecilia reticulata*), for example, more colourful males are preferred by females (Houde, 1997) but are also more susceptible to predators (Endler, 1987). Populations where predator density is high are composed of much duller males than populations where predation risk is

low (Endler, *op. cit.*). Similar situations are reported for other species (for a review see Andersson, 1994).

Fiddler crabs are well known for their high degree of sexual dimorphism (Crane, 1975). Females have two isomorphic feeding claws, whereas males possess one feeding claw and one highly enlarged claw reaching up to 40% of the individual's total body weight (Rosenberg, 1997). In the European fiddler crab *U. tangeri*, the major claw of the males is used both in fighting and threatening displays (intra-sexual selection) and in a waving display that attracts females to the male's burrow for mating (inter-sexual selection). Thus, in this species, the major claw plays a dual role of an armament and an ornament.

Larger claws are, generally, preferred by females. Experimental data by Oliveira & Custódio (1998) shows that female *U. tangeri* spend more time near

models of males with larger claws in binary choice tests. This female preference is confirmed by field observational data which shows that females visit males with larger claws more often (Latruffe et al., 1999). There is also observational evidence of this fact for other species. Backwell & Passmore (1996) showed that females of the species *Uca annulipes* mate with males with claw size larger than the population average. Greenspan (1980) demonstrated a significant association between the rate of attracting females and male major claw length for *Uca rapax*. In *Uca pugilator*, Christy (1983) observed that males with larger claws had a mating advantage that, however, could be on the account of the fact that larger males built better burrows, and Hyatt (1977) also found a female preference for larger males. On the other hand, no preference for males with larger claws was found in *Uca vocans vocans* (Salmon, 1984) and *Uca beebei* (Christy, 1987). Males with larger claws also have an advantage in male-male competition (Crane, 1967, 1975).

Apart from the benefits of mate attraction and male-male competition, larger claws also involve a cost for the male. The male's enlarged claw is not used in feeding and thus, feeding in males is restricted to one minor claw. Although, different species have different mechanisms to cope with this disadvantage. *Uca panacea* (Caravello & Cameron, 1987) and *U. vocans vocans* (Murai et al., 1983) males spend the same amount of time as females in feeding activities but the rate of the feeding claw's movement is significantly higher. In both *Uca pugnax* (Valiela et al., 1974) and *U. tangeri* (Faria, 1994), males spend more time feeding than females.

Another potential cost of the male fiddler crab's enlarged claw is its apparent conspicuousness due to its size and colour, contrasting with the rest of their orange-brownish coloured body and the mudflat background, suggesting that males may be more easily detected by predators than females.

In the present study, we intend to (a) test the hypothesis, using humans as a model of visual predators, that the enlarged claws of male fiddler crabs makes them more conspicuous to visual predators and, if so, (b) whether its effect depends on size or colour of the enlarged claw, and then, (c) discuss the costs and possible benefits of this trait in relation to predation.

Methods

Several morphotypes, all of the same size, of the fiddler crab *U. tangeri* were created from close-up photographs taken in nature (Parque Natural da Ria Formosa, Algarve, Portugal) using the image-processing software Adobe Photoshop 4.0: a right-handed male (M) with the major claw in the resting (horizontal) position and an identical male with no major claw (MNC); a female (F) with two feeding claws and an identical female with an enlarged claw (identical to M's) added (FWC); a male identical to M with the major claw of the same colour (orange-brownish) of the feeding claw (MOC); and two males, identical to M, but with smaller claws (M75–75% sized claw, and M50–50% sized claw).

Using the software SuperLab 1.04, these morphotypes were pasted in a random position on a background picture of their natural habitat (i.e. mudflat) and were presented in a randomised order to students, who were asked to detect them. The average age of the students was 24 years old; 18 males and 71 females, a sex-bias that reflects the student's population registered in that year at the Instituto Superior de Psicologia Aplicada (Lisbon): 82% females and 18% males. We looked for possible differences in detection abilities between female and male students, which could bias our results, using a two-way ANOVA, but we found none ($F_{1,6}=2.07$; $P=0.163$). The subjects were allowed to look at the images for an unlimited amount of time, until they detected the individual or until they decided to pass on to another image (non-detection). Backgrounds without individuals were also presented as a control. Response time was registered in msec by the psychology test software SuperLab 1.04.

The following *a priori* planned comparisons were made: (a) to test for the importance of possessing a claw, we compared M with F and FWC with MNC; (b) to test for claw colour, we compared M with MOC; (c) to test for claw size, we compared M with M75 and M50, and M75 with M50; (d) to test for the importance of claw colour versus claw size, we compared MOC with M75 and M50. To avoid the assumptions of parametric statistics we used the non-parametric Wilcoxon matched pairs test. Since there is a different number of non-detections for each morphotype, the N value of the matched pairs differs for each comparison.

To keep the joint level of significance at the desired value (0.05), the level of significance of each individual test was reduced using the Dunn–Bonferroni procedure. Individual levels of significance for each

Table 1. Differences between percentages of non-detections for all morphotypes

Comparison	Percentage of non-detections		<i>p</i>
M vs. F	M=2.25	F=17.05	< 0.001 *
FWC vs. MNC	FWC=2.25	MNC=39.33	< 0.001 *
M vs. MOC	M=2.25	MOC=28.09	< 0.001 *
M vs. M75	M=2.25	M75=3.41	0.322
M vs. M50	M=2.25	M50=6.74	0.075
M75 vs. M50	M75=3.41	M50=6.74	0.157
MOC vs. M75	MOC=28.09	M75=3.41	< 0.001 *
MOC vs. M50	MOC=28.09	M50=6.74	< 0.001 *

* Indicates significant differences.

comparison are as follows: M vs. F, $p=0.010$; FWC vs. MNC, $p=0.025$; M vs. MOC, $p=0.007$; M vs. M75, $p=0.007$; M vs. M50, $p=0.007$; M75 vs. M50, $p=0.008$; MOC vs. M75, $p=0.008$; MOC vs. M50, $p=0.008$.

The occurrence of order effects was controlled *a posteriori* by testing the order of the presented stimuli (Wilcoxon matched pairs test). No significant differences were found.

Comparisons of the percentage of non-detections of each morphotype were also used to assess the claw's conspicuousness using a significance test for differences between two percentages (Statistica for Windows 5.0).

Results

Presence of major claw

Male fiddler crabs of *U. tangeri* (M) were detected significantly sooner than females (F), (Wilcoxon matched pairs test; $N=71$, $Z=3.770$, $P<0.001$). When we compared males with the claw removed (MNC) with females with an enlarged claw added (FWC), the pattern was reversed and the latter were detected significantly sooner (Wilcoxon matched pairs test; $N=53$, $Z=5.838$, $P<0.001$), (see Fig. 1).

Colour

The subjects took significantly more time to detect males with the enlarged claw artificially coloured with the same colour as the feeding claw (MOC) when compared to males with claw of its natural colour (M), (Wilcoxon matched pairs test; $N=62$, $Z=5.809$, $P<0.001$), (see Fig. 2).

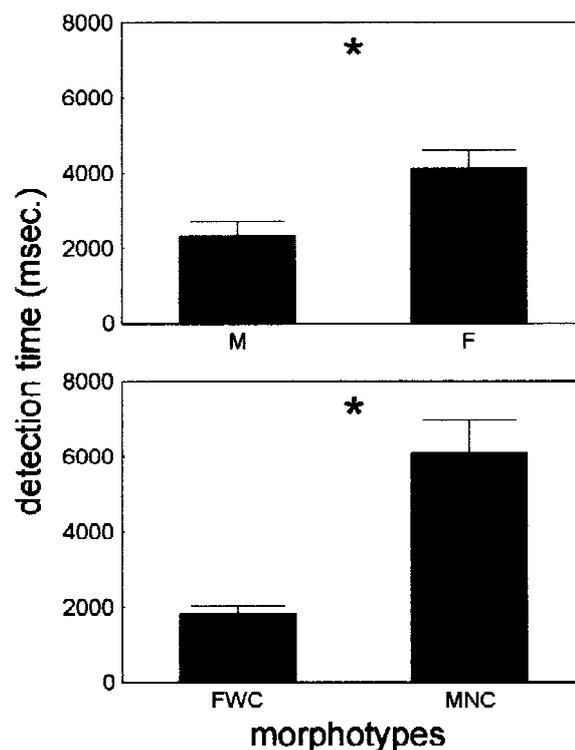


Figure 1. Detection time of morphotypes with major claw (M and FWC) and without major claw (F and MNC). Values are means \pm se (msec). * indicates significant differences.

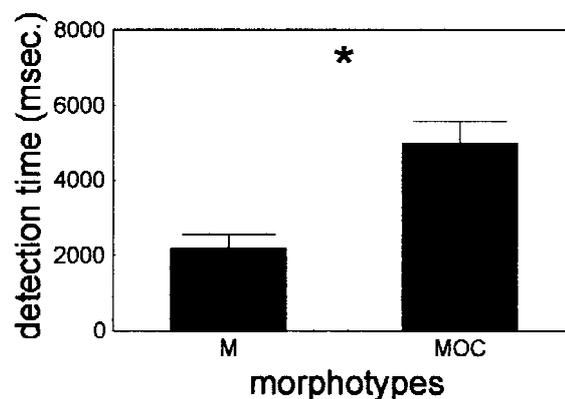


Figure 2. Detection time of morphotypes with chela of the same colour as feeding claw (MOC) and with natural coloured chela (M). Values are means \pm se (msec). * indicates significant differences.

Size

Crabs with smaller claws took longer to be detected but there were only significant differences when the relative size difference is of 50% (M vs. M50), (Wilcoxon matched pairs test; $N=83$, $Z=1.689$,

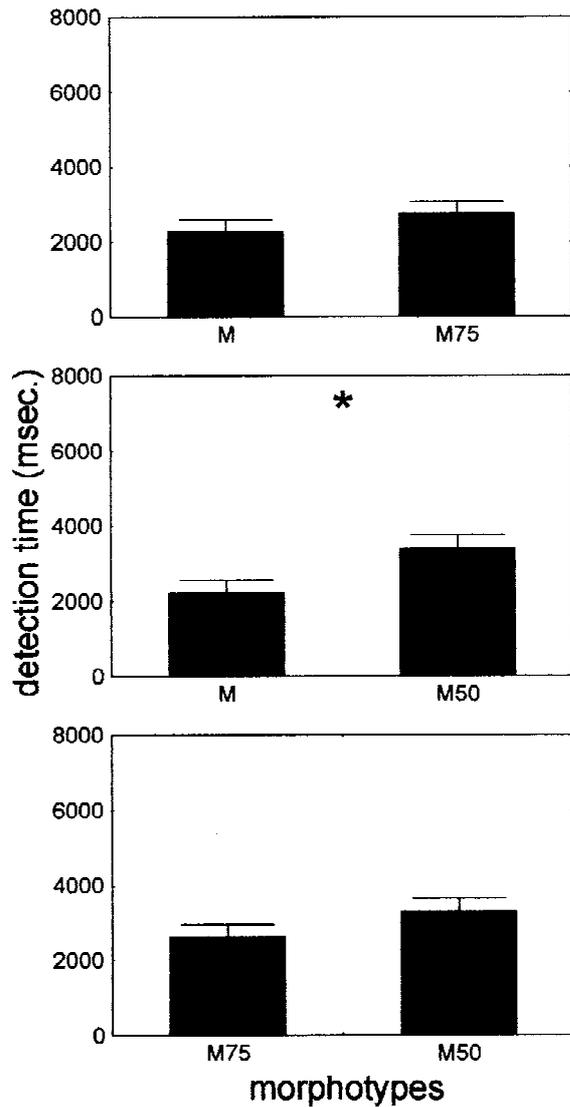


Figure 3. Detection time of morphotypes with different sized claws. Values are means \pm se (msec). * indicates significant differences.

$P=0.091$; M vs. M50: $N=82$, $Z=4.052$, $P<0.001$; M75 vs. M50: $N=79$, $Z=2.353$, $PN=0.019$) (see Fig. 3).

Colour vs. size

To assess the relative importance of claw colour and size for its conspicuousness, we compared the male with the coloured claw (MOC) with males with smaller claws of their natural colour (M75 and M50). Males with natural coloured claw were still detected significantly sooner than males with a claw of the same colour of the feeding claw, even when it is 50% smaller (Wilcoxon matched pairs test; MOC

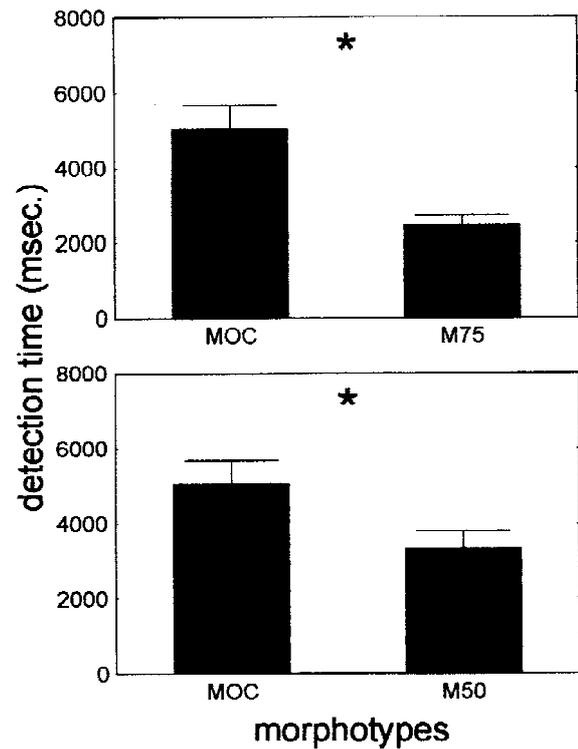


Figure 4. Detection time of morphotypes with chela of the same colour as feeding claw (MOC) and natural coloured claws of smaller sizes (M75 and M50). Values are means \pm se (msec). * indicates significant differences.

vs. M75: $N=61$, $Z=4.593$, $P<0.00$). As relative claw size increases, differences continue to be significant (Wilcoxon matched pairs test; MOC vs. M50: $N=60$, $Z=3.147$, $P=0.002$), (see Fig. 4).

Non-detections

Percentages of non-detections (as shown in Table 1) are consistent with the previous results. Individuals with no major claw (F and MNC) had a significantly higher percentage of non-detections than crabs with major claw (M and FWC, respectively), and crabs with the major claw of the same colour as the feeding claw were significantly less detected compared to crabs with major claw of its natural colour, independently of its size. However, there were no significant differences in the percentage of non-detected crabs with different claw size, even when the relative size difference was of 50%.

Discussion

Our data suggests that, as hypothesised, the enlarged claw of male fiddler crabs is a very conspicuous trait. Males with larger claws had a non-significant tendency to be detected sooner when relative claw size difference was of 25% and there was a significant difference when the claw was 50% larger. However, claw colour seems to be the main aspect that makes males easier to detect. Males with an orange-brownish coloured claw were detected significantly slower compared to males possessing a white major claw, even when it was 50% smaller.

An evolution towards cryptic coloration in fiddler crabs is suggested by the fact that chromatophores of five species of the genus *Uca* (*U. subcylindrica*, *U. panacea*, *U. spinicarpa*, *U. longisignalis* and *U. rapax*) exhibit dispersion patterns indicating statistically significant background adaptation (Thurman, 1990). Although, despite the fact that many species of fiddler crabs are cryptically coloured when the animals are feeding or constructing burrows, when social activities become more frequent the large claw, and sometimes even the carapace and other appendages, become brighter in some species (Weygoldt, 1977). This is not an intriguing fact, given the social signalling function of the major claw.

From an evolutionary perspective, a signal is constrained by the properties of the sensory system of the receivers (Endler, 1992). Thus, the bright colour of the male's major claw should be the result of a selection pressure imposed both by conspecifics and predators. Waving the major claw is the main mechanism of visual communication among fiddler crabs and a conspicuous claw could make it more effective.

However, from a conspecific point of view, the background for a waving claw is the sky, not the mudflat (like we used in this experiment), unless the male is displaying in an area with a steep slope (e.g. creek) or against salt marsh vegetation background. So our results may not apply for a flat environment, and the claw-background contrast is yet to be evaluated in those circumstances. Also, the eyes of fiddler crabs appear to be especially well designed to resolve objects in the vertical plane. Zeil et al. (1986) have shown that two species of *Uca* have narrow vertical corneal pseudopupils on each eye equator, yielding an acute zone of high vertical resolving power. They also use their visual horizon to distinguish between predators and conspecifics. If an object's image does not extend above the horizon, it is smaller than the receiver

which perceives it as a conspecific. If an object image extends above the horizon it is perceived as a predator (Zeil et al., 1986; Land & Layne, 1995; Layne et al., 1997). When a male waves its claw it does intrude into the space above the horizon, but not very high. This may capture the attention of another fiddler crab but not evoke a full escape response (Layne et al., 1997). Thus, size more than colour, seems to be main feature involved in signalling to conspecifics. Nevertheless, colour discrimination has been described for two species of fiddler crabs (Hyatt, 1975), but only one pigment has been found in the rhabdoms using microspectrophotometry (Scott & Mote, 1974). This apparent contradiction can be solved by the finding that in another brachyuran crab, *Scylla serrata*, colour discrimination occurs with a single visual pigment due to the existence of different colour filters in different photoreceptors (Leggett, 1979). In *Uca*, photoreceptors screening pigments have also been described (Cronin & Forward, 1988) which may account for the behavioural evidence for colour discrimination. An alternative causal explanation for colour discrimination in *Uca* would be the existence of a violet/UV receptor in the smaller 8th reticular cell, like the one described for crayfish and other brachyuran crabs (Cummins & Goldsmith, 1981; Martin & Mote, 1982). Despite which is the causal mechanism underlying colour discrimination in fiddler crabs, colour could amplify the effect of size on conspecific detection of the male enlarged claw.

From the predators point of view, our results suggest that colour would be the key feature that makes the claw conspicuous. But we should be conservative when applying our results to natural predators of fiddler crabs since colour is not property of an object, but the result of the nervous system that perceives it (Bennett et al., 1994), and human vision is different from other organism's. The main natural predators of *U. tangeri* African populations are sea birds (Ens et al., 1993). The only described predator in Ria Formosa was the ashly curlew *Numenius arquata* (Von Hagen, 1962) but indirect evidence of predation by seagulls (*Larus* spp.), whimbrels (*Numenius phaeopus*), turnstone (*Arenaria interpres*) and rats also exists (Von Hagen, *op. cit.*; Faria, 1994; pers. obs.).

To what extent the results present here are relevant for the natural predators is a major issue.

Humans have three colour channels associated with different receptors that absorb maximal light at different wave lengths. This way, accordingly to which receptor is being stimulated, there are three primary

colour sensations: blue, green and red. If all cones are stimulated at the same time, the sensation of white is produced (Bennett et al., 1994; Finger & Burkhardt, 1994). Most birds, except maybe some nocturnal species (Bennett & Cuthill, 1994), possess another cone which absorbs UV light, thus producing another primary colour, and a system of oil droplets that filter the light entering individual cones (Bennett et al., 1994; Finger & Burkhardt, 1994). Thus, most probably, fiddler crab colours would look different to humans and to sea birds. However, the efficiency of a visual signal depends critically on the difference in radiance between the object and the background in a range of wavelengths (Dusenbery, 1992). Thus, contrast more than colour is the more relevant feature for increasing detectability. The fact that neither the white colour present in the claw nor the mudflat reflect UV (M.C. Cummings & R. F. Oliveira, unpublished data) suggests that at least brightness contrast (for the measurement of brightness contrast see Bradbury & Vehrencamp, 1998) between the white claw and the mudflat background could be equally perceived both by humans and by birds, and thus the present result could be extrapolated, with caution, to natural predators. Nevertheless, further experimental studies with conditioned birds in captivity are being planned to test the present hypothesis with a closer model to the natural predators.

Although, using humans as models for visual predators was not inappropriate since the main fiddler crab predators in the Algarve population are fishermen that remove the male's major claw, used in local gastronomy. The males are then released again in the mudflat to regenerate their claws (see Oliveira et al., 2000). In this particular population there is a sex-biased 'predation' and the conspicuousness of the claw is, indeed, a cost for male *U. tangeri*.

In spite of the possible disadvantage of making males easier to detect by visual predators, it must be taken into account that the enlarged claw is also a powerful weapon used in defence and might function as a deterrent for predators. Formanowicz & Brodie (1988) reported that only males adopt a threatening behaviour in the presence of a potential predator. This advantage may compensate for the conspicuousness cost imposed by the claw. In fact, Bildstein et al. (1989) demonstrated that when given a choice between intact males and females or between intact males and males with the major claw removed to a natural predator, white ibis (*Eudocimus albus*), they chose the individuals without the major claw. When

they chose the male with the major claw, on many occasions, the crab grasped the ibis bill. Situations like this result on a much longer handling time for the predator, risk of injury and risk of loosing its prey in case the crab autotomizes its claw.

If the major claw makes males such unprofitable prey, then it would be expected that they would be less exposed to predation pressure in the field than females, and be passed over by predators. Despite that, Backwell et al. (1998) did not find a selective predation pressure in either sex for *U. stenodactylus* and *U. princeps*. We suggest that the benefit of easy detection of male fiddler crabs in the mudflat may compensate for the costs involved in handling the prey. This way, the conspicuousness of the claw may not increase the risk of predation of males compared to females, but it may be sufficient to overweight the benefit of its anti-predator function.

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