Ethology Ecology & Evolution 10: 241-251, 1998

Claw size, waving display and female choice in the European fiddler crab, *Uca tangeri*

R.F. OLIVEIRA [1] and M.R. CUSTÓDIO

Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada, Rua Jardim do Tabaco 44, 1100 Lisboa, Portugal

Received 18 September 1997, accepted 30 May 1998

Fiddler crabs present an accentuated sexual dimorphism wherein males have one of the chelipeds greatly enlarged, compared to the other chela or to the two small feeding chelipeds of females. Available observational data in the literature suggest a dual function for this trait both as an armament to fight other males and as an ornament to court females by claw waving. We experimentally tested female *Uca tangeri* for possible preferences based on the size and elevation (waving posture) of the male large cheliped and on male handedness. Dead, resin-coated males were used as test objects. Females significantly more often approached males with larger claws and males with raised claws. Male handedness had no effect on female responses. These results are consistent with a female mating preference based on claw size and position and hence with the evolution of claw size and the waving display as a result of sexual selection by female choice.

KEY WORDS: fiddler crab, female choice, sexual dimorphism, claw size, claw waving display, sexual selection.

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[1] Corresponding author (Phone: 351-1-8863184; Fax: 351-1-8860954; E-mail: ruiol@ispa.pt).

INTRODUCTION

The occurrence of exaggerated male traits, such as the hypertrophied claw in fiddler crabs, has been explained by the action of two mechanisms of sexual selection: male-male competition and female mate choice. While there is a general consensus on the role of male-male combat in producing exaggerated male traits, the mechanism through which female choice may influence the evolution of male ornaments is still a matter of debate (e.g. Fisherian models vs Handicap models, for a review see ANDERSSON 1994). Nevertheless, there has been an increasing body of evidence on the occurrence of female mate choice based on male characteristics, such as long tails in widowbirds (*Euplectes* sp.) and guppies (*Poecilia reticulata*), train size and number of ocelli in the peacock (*Pavo cristatus*), dewlap colour and display in *Anolis* lizards, sword length in swordtails (*Xiphophorus* sp.), dorsal fin length in the sailfin molly (*Poecilia sphenops*) or comb size in red jungle fowl (*Gallus gallus*), to mention only a few examples of visual signals (ANDERSSON 1994).

Fiddler crabs are an exceptional model system for studying this problem, since there is a marked sexual dimorphism in the development of one of the claws, which has an epigamic function. Males have one of their two chelipeds greatly enlarged. It has lost its function in feeding and is used both in male fighting and in a visual display (waving) consisting of a rhythmic elevation and lowering of the major chela, which attracts the females to the male's burrow during the breeding season (CRANE 1975).

Larger claws may give an advantage in male-male competition, being used both in physical fighting and in threat postures (CRANE 1967, 1975). In the species studied so far, larger males win naturally occurring fights more often, but smaller burrow-owning crabs have some competitive advantage (resident effect) (*Uca tangeri*: VON HAGEN 1962; *Uca rapax*: CRANE 1967; *Uca pugilator*: HYATT & SALMON 1978). Larger claws may also have an adaptive value in mate attraction, where an enlarged and conspicuous claw would provide an advantage in terms of detection by and/or attraction to the wandering females. *Uca rapax* exhibits size assortative mating with the larger females mating with the males which possess the larger claws (GREENSPAN 1980). This study also demonstrated a significant association between the rate of attracting females and male propodus length (GREENSPAN 1980). In *Uca pugilator* CHRISTY (1983) found that males with larger claws had a mating advantage, although larger males also constructed better burrows and female choice based on burrow quality alone was enough to account for this effect. In an independent study HYATT (1977) also found a female preference for larger males in *U. pugilator*. BACKWELL & PASSMORE (1996) showed that in *Uca annulipes* mated males are larger than the population average (carapace size), a trend that is more accentuated when claw size is compared. These authors also suggested that female mate choice in fiddler crabs is a two-stage process: first females select which males to sample based on male (claw) size, and then they decide whether or not to mate with a specific male based on burrow features. Female choice of large males (claw size) has been investigated but not found in two other fiddler crabs, *Uca vocans* (SALMON 1984) and *Uca beebei* (CHRISTY 1987).

Despite the availability of the above mentioned observational data there is a lack of experimental work on female mate choice in *Uca*. The purpose of the present study is to investigate the role of the hypertrophy of the claw in female attraction in *Uca tangeri*. For this purpose we addressed the following questions: (a) Experiment 1: do female fiddler crabs show any preference for male claw size? (b)

Experiment 2: do female fiddler crabs prefer males in a waving posture? (c) Experiment 3: do female fiddler crabs have a preference for claw handedness?

METHODS

Study area

This study was conducted at Cacela-Velha in the Ria Formosa Natural Park, Algarve, Portugal during June and July 1996. Ria Formosa consists of a coastal lagoon (approx. 55 km long with a maximum width of 7 km) separated from the ocean by a set of sand barrier islands. The inner part of the lagoon consists mainly of salt marshes and mudflats where fiddler crabs can be found.

Experimental procedures

A square test arena of 1 × 1 m was defined in the field using planks 30 cm high, so that the tested individuals were prevented from seeing beyond this area. A small pit was dug in the centre of the arena. On two opposite corners a small square area (40 × 40 cm) was defined by a line drawn in the sand. In each of these two areas a standardized burrow (opening diameter = 2.5 cm; depth 10 cm) was dug with a stick and a male dummy was placed by each burrow (see Fig. 1). The male dummies used were dead crabs which were treated with a resin coat to keep their pigments and to prevent them from deteriorating (Helfman 1983). These males were captured in the study area some days before the experiment in which they were used, and were killed by deep freezing. The large claws of the dead males were removed and

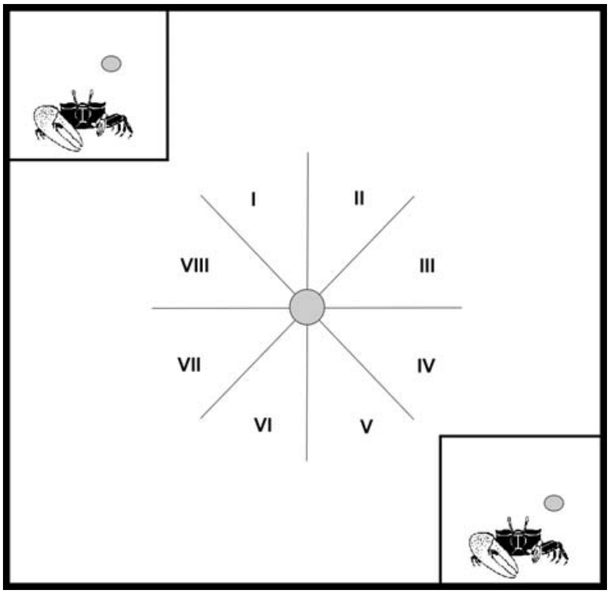


Fig. 1. — Experimental set-up (see text for details).

their inner area was cleaned of muscles. A wire was then placed so that different claws could be attached to different males.

The categories of males tested were as follows: Experiment 1: male with large claw vs male with small claw; Experiment 2: male with raised claw vs male with claw in resting position; Experiment 3: right-clawed male vs left-clawed male.

In order to control for body size influences on female choice males were matched for carapace size in all trials. Moreover, for Experiments 2 and 3 males were also matched for claw size. The claws were exchanged between the two males at every trial, so that the same number of females were presented the two possible combinations of males-claws [1-1 vs 2-2 (natural situation); 1-2 vs 2-1 (reversed claws situation)]. The morphometric measures of the males used in the experiments are shown in Table 1.

To control for physical factors (e.g. humidity, shade, temperature, etc.) males were changed between the two exhibition corners every two trials, so that each male was presented to the females the same number of times at each place.

The females were collected from the mudflats on the same low tide during which they were tested. Only receptive females, i.e. that had left their burrow and were wandering on the mudflat prior to mating, were tested. They were kept together in a large bucket between the time they where captured and the binary choice test. The size of the females varied between 13 and 30 mm carapace width, and between 16 and 29 mm carapace length. Each female was used only once.

Each trial started with the introduction of one female at the pit dug at the centre of the arena, and lasted for 20 min unless one of the following situations occurred: (a) female stayed motionless in the pit for 10 min; (b) female entered one of the male's burrows and stayed there for 10 min without leaving the burrow (in which case a choice was considered to have occurred).

On each trial the following behavioural variables were recorded: (a) direction in which the female left the central pit according to previously defined sectors of 45° centred on the pit, starting with 0° pointing in the direction of male a; these data were gathered into three categories for further analysis:

direction of male a = sectors 1 and 8,
direction of male b = sectors 4 and 5,
neutral direction = sectors 2, 3, 6 and 7;

Table 1.

Morphometirc measurements of the pairs of males used as a stimulus in the three experiments.

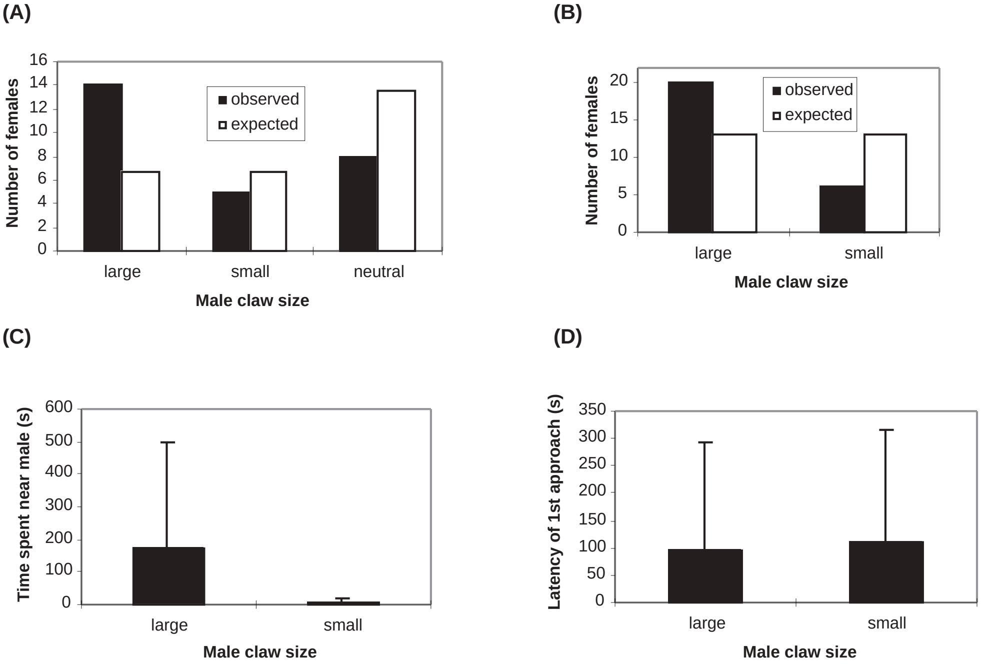
Experiment	Pair	Carapace width (mm)	Claw size (propodus length) (mm)	Claw handedness
1	1	31	28	Left
		31	61	Left
	2	30	27	Right
		30	54	Right
2	1	32	62	Right
		32	61	Right
	2	30	42	Left
		30	44	Left
3	1	31	41	Left
		30	41	Right
	2	34	60	Left
		34	61	Right
	3	32	61	Left
		32	61	Right

(b) the first male to be approached by the female (i.e. which male's corner was first entered by the female); (c) latency until first entering each male's area (corner); (d) time spent near each male, i.e. in each male's area (corner).

RESULTS

Experiment 1: Claw size

Female fiddler crabs showed strong preferences for males with larger claws. They left the central pit significantly more often in the direction of the male with the larger claw (n = 27, df = 2, $\chi^2 = 10.48$, $P < 0.01$; see Fig. 2A). Of the 27 females tested 51.8% moved in the direction of the male with the larger claw while 18.5%



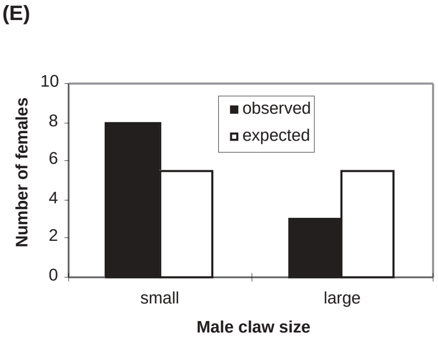


Fig. 2. — Female responses to male claw size (small vs large): (A) number of females that left the central pit in the direction of each male type, according to the previously defined sectors; (B) number of females that approached first each male type; (C) time spent (average + standard deviation) in each male's area; (D) latency (average + standard deviation) for entering the area of the first male to be approached; (E) number of females that entered and remained inside the burrow of each male type.

moved in the direction of the male with the smaller claw. The remaining 29.7% of the females walked out of the central pit in a neutral direction.

Only one of the females tested did not approach either of the stimulus males. The remaining females approached the larger clawed males first significantly more often ($n = 26$, $df = 1$, $\chi^2 = 7.54$, $P < 0.01$; see Fig. 2B), and they spent more time near the male with the large claw than near the male with the small claw (Wilcoxon matched pairs test: $n = 27$, $Z = 2.74$, $P < 0.01$; see Fig. 2C). There were no significant differences between the large and small clawed males regarding the latency of the first approach (Mann-Whitney U test: $n = 26$, $Z = 0.18$, $P > 0.10$; see Fig. 2D) and the number of females that entered each burrow ($n = 11$, $df = 1$, $\chi^2 = 2.27$, $P > 0.10$; see Fig. 2E).

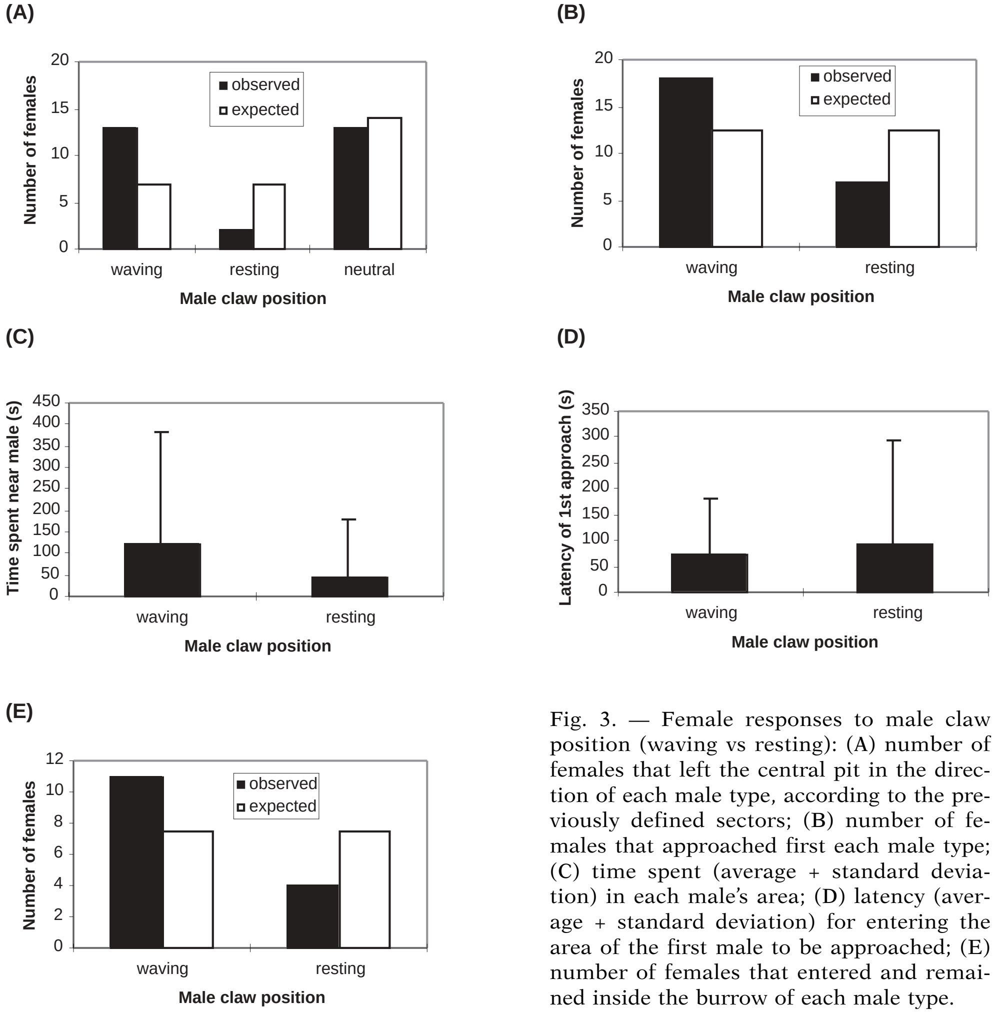


Fig. 3. — Female responses to male claw position (waving vs resting): (A) number of females that left the central pit in the direction of each male type, according to the previously defined sectors; (B) number of females that approached first each male type; (C) time spent (average + standard deviation) in each male's area; (D) latency (average + standard deviation) for entering the area of the first male to be approached; (E) number of females that entered and remained inside the burrow of each male type.

Experiment 2: Waving display posture (claw elevation)

Female fiddler crabs given a choice between a male dummy with a raised claw versus a male dummy with the claw in a resting position, showed a strong preference for males with raised claws. Of the 28 females tested 46.4% left the central pit in the direction of the male with the raised claw while only 7.2% walked in the direction of the male with the claw in resting position. The remaining 46.4% females moved out of the pit in a neutral direction (n = 28, df = 2, $\chi^2 = 8.78$, $P < 0.05$; see Fig. 3A).

Of the 28 females only 3 did not approach the stimulus males. The responsive females approached the male with the raised claw first significantly more times than the male with the resting claw (n = 25, df = 1, $\chi^2 = 4.84$, $P < 0.05$; see Fig. 3B), but they showed no significant differences in the time spent near each of the two classes of males (Wilcoxon matched pairs test: n = 28, Z = 1.03, $P > 0.10$; see Fig. 3C). They

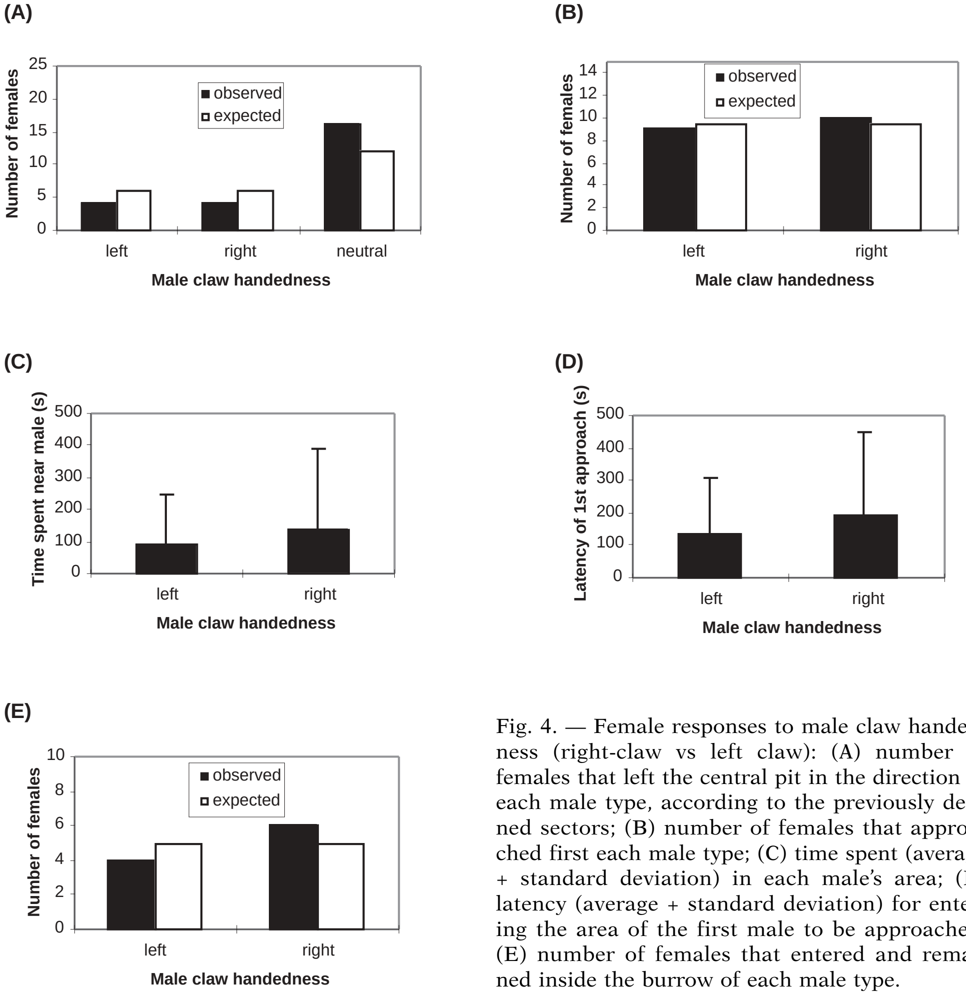


Fig. 4. — Female responses to male claw handedness (right-claw vs left claw): (A) number of females that left the central pit in the direction of each male type, according to the previously defined sectors; (B) number of females that approached first each male type; (C) time spent (average + standard deviation) in each male's area; (D) latency (average + standard deviation) for entering the area of the first male to be approached; (E) number of females that entered and remained inside the burrow of each male type.

also showed no significant differences in the latency of the first approach between the two male types (Mann-Whitney U test: n = 25, Z = 0.79, $P > 0.10$; see Fig. 3D).

Of the 25 responsive females only 15 entered and remained in a male's burrow. There was a substantial but not significant tendency for these burrow entering females to choose the burrows of the males with the raised claw (n = 15, df = 1, $\chi^2 = 3.26$, $P = 0.07$; see Fig. 3E).

Experiment 3: Claw handedness

Female fiddler crabs given a choice between a right-clawed and a left-clawed male dummy showed no preferences between the two males. Of the 24 females tested 17% left the central pit in the direction of the left-clawed male, 17% walked in the direction of the right-clawed male, and the remaining 66% moved out of the pit in a neutral direction (n = 24, df = 2, $\chi^2 = 2.66$, $P > 0.10$; see Fig. 4A). Of the 24 females tested only 5 did not approach the stimulus males. The responsive females did not show any preference in terms of the male to be first approached (n = 19, df = 1, $\chi^2 = 0.05$, $P > 0.10$; see Fig. 4B), and they spent similar amounts of time near each of the males (Wilcoxon matched pairs test: n = 24, Z = 0.59, $P > 0.10$; see Fig. 4C). Moreover, there were no significant differences in the latency of the first approach to the two male types (Mann-Whitney U test: n = 19, Z = – 0.98, $P > 0.10$; see Fig. 4D) and the number of females that entered each burrow (n = 10, df = 1, $\chi^2 = 0.4$, $P > 0.10$; see Fig. 4E).

DISCUSSION

Our data show that in binary choice tests females prefer large clawed males (Experiment 1) and males in a waving position (Experiment 2), but that they have no preferences concerning claw handedness (Experiment 3).

In Experiment 3 females moved at random away from the central pit. Although, for the females that approached one of the two stimulus males there is no detectable preference regarding male handedness, a result which is consistent with the equal proportion of right and left clawed males in this population, and the fact that these two male morphs do not show any differences that would predict a female preference (Faria 1994). In fact, in most species of fiddler crabs, males which have right and left handed major claws are present in similar proportions in the populations (except for two species of the subgenus *Thalassuca* in which males are nearly all right handed, Barnwell 1982), which suggests that the differentiation of the enlarged claw occurs randomly in respect to side (Yamaguchi 1977, Ahmed 1978).

The fact that only a small proportion of the tested females (in all three experiments) entered the burrows, and that they did not enter the burrows of the preferred males significantly more times, suggests that females detected a lack of other components of the stimulus, such as movement or other behaviour patterns. So, larger claws or raised claws are enough for attracting the females to a given male but they need further behavioural elements of the courting male to decide whether or not to enter the burrow. If one analyses the courtship sequence of this species this explanation becomes more convincing. We can broadly divide male courtship into three phases: phase 1, the male performs waving movements of low amplitude and at a low rate; phase 2, as a female approaches its burrow, the male increases both amplitude and rate of waving, with the legs becoming involved in an exaggeration of the up and down component of the movement; phase 3, when females approach the male at a distance of 10 cm the males stop waving and dash to their burrows, entering them; when males are successful, females follow the males almost immediately (VON HAGEN 1962). In our experimental situation all the dynamic components of waving were lacking, and therefore females would have to base their choices on the static components only (size and vertical position). It is reasonable that after a first stage of female choice, in which a larger claw or a raised claw would increase male detectability and/or attractiveness, females would rely on finer morphological and/or behavioural details of the male phenotype to proceed with their choice (e.g. components of the waving movement such as display rate, JENNIONS & BACKWELL 1995). This aspect was further emphasized by the fact that most females, after approaching the dummy male, remained still by it as if they were waiting for a reaction. Some females further inspected the dummy males by touching them and sometimes walking over them. This aspect of female mate choice may be overcome in the future by using miniaturized fiddler crab robots or by adopting video playback techniques (e.g. CLARK & UETZ 1992).

This study also raises an issue of interpretation that is common to almost all preferences for signals of different sizes. Females may more readily detect big signals such as larger claws. One way to test for this would be to manipulate the size of the claws while keeping the detectability the same. That is the claw size relative to body size cues would be available without giving an overall bigger target (i.e. both claws would have the same absolute size in the crab retina). We should however stress that this issue does not affect the results presented here, as it addresses the same problem at a different level of analysis — causation — while we have addressed the problem of female mate preferences at the functional level (sensu TINBERGEN 1963).

The data presented here are consistent with a female mating preference based on male claw size and elevation and hence the evolution of claw size and the waving display due to sexual selection by female choice. The evolution of male ornaments through female mate choice may be explained either by direct benefits for females or may be due to indirect genetic gains (ANDERSSON 1994). A direct benefit for females that choose larger males may result from the fact that large males may defend better breeding sites and may be more effective in reacting to crabs that open plugged burrows and disturb mating pairs than small males (CHRISTY 1983). If we feel the need to search for a genetic benefit for choosy females, then handicap models would be more supported by the available evidence (e.g. claw size and display rate are condition-dependent traits in *Uca annulipes*, JENNIONS & BACKWELL 1995).

The waving display may function as a sensory trap (CHRISTY & SALMON 1991, CHRISTY 1995) to attract the attention of wandering females. In the present study we have found a female preference for males in a waving display posture, that is with the enlarged claw vertically raised. The vertical component of the display may be exploiting the sensory mechanisms of the female receiver vision. Fiddler crabs are more sensitive to vertical than to horizontal shapes and movements (LANGDON 1971, LANGDON & HERRNKIND 1985, ZEIL at al. 1986), a preference that can be better understood if one considers that in the world of the fiddler crabs in a mudflat there are a predominance of lateral movements (e.g. wandering conspecifics, undulation of adjacent salt marsh vegetation due to the wind and even foraging seabirds). Moreover, the fiddler crab's eye has a band of greatly increased vertical resolution at the eye's equator which in living crabs images the horizon and that the crabs use the horizon in their assessment of moving objects, such as conspecifics or potential predators (LAND & LAYNE 1995, LAYNE et al. 1997). Thus, the waving display of a near fiddler male will cross the female's horizon, standing out from her view of an aggregation of conspecifics moving below her horizon line. Perhaps the function of this vertical component of the waving display is to halt or slow the female when she is walking by a male burrow.

Thus the evolution of the waving display in a mate attraction context may have been shaped by the sensory capacities of the females that show a preference for vertical shapes and movements. Mechanisms similar to this, in which males exploit a pre-existing female sensory bias, have been proposed in the literature to explain the evolution of male courtship signals, which stress the importance of the receivers sensory capabilities in shaping signal design (WEST-EBERHARD 1984, RYAN 1990, GUILFORD & DAWKINS 1991, CHRISTY 1995). That is, the way females perceive, process and react to stimuli may strongly affect the evolution of a given male courtship signal.

ACKNOWLEDGEMENTS

We thank Ria Formosa Natural Park, Portugal, for permission to work in their protected area and for logistic support. We thank Elisabet Forsgren and Vitor Almada for helpful discussions on this topic, and especially Teresa Avelar, Matthew Grober and Peter McGregor for reviewing the manuscript. We also thank John Christy and Tim Halliday for constructive comments on an early version of the manuscript.

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