ORIGINAL ARTICLE

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Response of fiddler crabs (*Uca tangeri*) to video playback in the field

Abstract The fiddler crab *Uca tangeri* communicates using a visual waving display and a vibratory drumming signal, both thought to function in mate attraction. Using video playback techniques, images of an empty mudflat, a waving male, a threatening male, and a wandering female were presented to male subjects. All stimuli elicited similar levels of low-intensity waving, but significantly more high-intensity waves were elicited by the female and threatening male stimuli than the mudflat stimulus or the waving male stimulus. This concurs with other research that the waving display is used at a higher intensity to attract females. The threatening male stimulus failed to elicit the same response as an actual threatening male and we discuss the likely reasons for this. The subjects also spent a significantly greater proportion of time drumming during the male waving stimulus than during the female stimulus, suggesting that drumming functions in male-male competition as well as female attraction.

Key words Video playback · Fiddler crab · Field study

Introduction

Male fiddler crabs [genus *Uca* (Brachyura, Ocypodidae)] have a major chela, which can be as much as 30 times larger in area than the minor chela (Rosenberg 1997). This chela has a dual function, serving as a weapon in intrasexual competition and being waved to attract po-

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tential mates (Crane 1975). This conspicuous waving display is spontaneous, stereotypic, and species specific (Crane 1975; Zucker 1981).

In some species of fiddler crab the males will spontaneously perform low-intensity waves (LIW), even in the absence of females, according to the stage of the low tide and the lunar cycle. However, when a female is within visual range, a male will perform high-intensity waves (HIW) in which the body is raised and lowered and the frequency of waves is increased (Crane 1975; Layne et al. 1997). The subject of our study was the only species of fiddler crab found in Europe, *Uca tangeri*, which is considered a "broad front" on the basis of the distance between the eyestalks. Most research on the fiddler crab waving display has been conducted on broad fronts (Christy and Salmon 1991), with a consensus that the waving display plays a role in mate attraction (Christy and Schober 1994; Oliveira and Custódio 1998; Latruffe et al. 1999). *U. tangeri* only waves during the courtship and mating season, whereas threatening, fighting, and territorial behaviour continue throughout the whole active phase of the year (Wolfrath 1993), suggesting that the waving display, in *U. tangeri* at least, is for courtship purposes only.

Recent investigations into the visual system of *Uca* may have provided an insight into the waving display. *Uca* attend to an anatomical horizon (Zeil and Al-Mutairi 1996; Layne et al. 1997), so that anything larger than the crabs disrupts this horizon line (Land and Layne 1995a), allowing the distinction between predators and conspecifics (Layne et al. 1997). There is a distinct behavioural change when a male discriminates an approaching conspecific as either male or female (Land and Layne 1995a, b; Layne et al. 1997). Towards females, a male will further increase the intensity of waving, but when another male is approaching the resident will cease waving and adopt a threat posture, blocking access to the burrow (Zeil and Al-Mutairi 1996; Layne et al. 1997). Oliveira and Custódio (1998) found that female *U. tangeri* prefer males with their major chela in the raised vertical position as opposed to the lateral resting position. The vertical raising of the chela during the

waving display may be a way of exploiting the female's sensory bias for vertical movements (Christy and Salmon 1991; Oliveira and Custódio 1998).

Detailed experimental study of the function of the waving display has been limited by the lack of a suitable method for presenting visual signals. Traditional ethological methods used with visual systems, such as presenting static models or photographic slides, and manipulating the character of interest on live subjects, do not allow the waving display to be studied (Rosenthal 1999). In principle, video technology allows the production of visual stimuli that are identical in all measures but the one that you have altered. For instance, McClintock and Uetz (1996) used computer animation techniques to alter the anatomy of males performing courtship displays in two species of wolf spider (*Schizocosa* spp.). One species (*S. ocreata*) possesses bristles on their forelegs, whereas the closely related *S. rovneri* does not. Using computer animations, they were able to produce images of *S. ocreata* without the tufts and images of *S. rovneri* with the tufts of *S. ocreata*, to test female preferences.

However, as the consensus paper in this issue makes clear, video has several major limitations when used with animals with a visual system that differs from that of humans because video systems are designed for human vision [see article in this issue by Oliveira et al. (2000)]. This is particularly true of the colour balance (Fleishman et al. 1998) and the number of frames per second displayed (Clark and Uetz 1990). There are also problems related to depth perception, as most of the cues used will be absent in a video image [see article in this issue by Zeil (2000)]. The waving display of fiddler crabs avoids many of these limitations. First, all the movement is in the plane of the monitor. Second, colour arguably plays a smaller role than movement [the major chela of *U. tangeri* is white and reflects no UV (R. Oliveira, unpublished data)]. However, the use of a black-and-white monitor would have been preferable for this study (Oliveira et al. 2000).

Because of practical difficulties, video playbacks are rarely attempted in the field. Lighting conditions, intrusion of apparatus into the natural setting, weather, and performance of portable equipment are all logistical issues that make field studies problematic. However, conducting field playbacks can have advantages – the subjects are more likely to give typical responses if they are tested under natural conditions, which will aid the interpretation of results. Despite this, we are aware of only one video playback study that has been conducted in the field. Clark et al. (1997) investigated the territorial responses of male *Anolis* lizards to video images and computer animations. The lizards responded with higher-intensity threat displays to the video playbacks when tested in the field than in the laboratory, possibly because the subjects were more territorial in the field than in the laboratory (Clark et al. 1997).

This study presents the results of the first step in using video playback techniques to investigate the waving display of fiddler crabs. We describe how a population of the fiddler crab *U. tangeri* responded to video images when tested in the field.

Methods

All fieldwork was carried out during May and June 1998 in the Ria Formosa Natural Park, Algarve, Portugal. The study population inhabited the inter-tidal mudflats near Quinta do Marim.

Recording stimuli

All stimulus videos were recorded using a Sony Hi-8 Handycam video camera suspended upside down from a Benbo Trekker tripod, so that the lens axis was as close to the mudflat surface as possible. In this way we gained a "crab's-eye view" when filming. The stimuli were filmed under the shade of a parasol to reduce reflectance or glare from the carapace of the crab, and a piece of hardboard was used to create a homogenous backdrop for each. A total of 24 stimuli were recorded – 6 empty mudflats, 6 waving males, 6 threatening males, and 6 females. All crabs that were used as stimuli were measured and marked to prevent re-use. The order in which the stimuli were presented was balanced as far as possible on the six playback tapes. A Latin Square design with eight playback tapes would have been preferable, but because of temporal and logistical constraints, we were only able to make six tapes.

Empty mudflat (M)

Six different empty sections of mudflat were filmed for a total of 10 min each. This stimulus acted as a control.

Waving male (W)

All males used as stimuli were of an average or above-average size. The carapace widths of the males used as waving stimuli ranged from 2.7 cm to 3.2 cm, while the range of major chela length was 4.1 cm–5.2 cm. The video camera was 15 cm from the burrow opening of a waving male. The distance of 15 cm from the stimulus male to the video camera was used so that a life-size image would be recorded, which would subtend the same visual angle as a live crab when later viewed by the subjects at that distance. When the male surfaced and began to wave, the camera started to record. The recording was used only if the male stimulus was the only crab seen on the tape. All of the stimulus males performed both LIW and HIW, with HIW making up 22±4% (mean ± SEM, *n*=6) of waves.

Threatening male (T)

Normally, males only adopt a threat posture when another crab approaches, so we could not film a male performing the threatening display without also having a second crab in the video frame. Therefore we used males that had been captured earlier during the low tide, carapace widths ranging from 2.7 cm to 3.2 cm, and the major chela length ranging from 4.5 cm to 6.0 cm. We stimulated the males to threaten towards the camera whilst walking back and forth across the camera's field of view, at a distance of 15 cm. These clips were later edited and looped using a Sony Hi-8 VCR editing suite. This produced a 10-min sequence in which the male walked back and forth across the television monitor at irregular intervals holding his enlarged claw in the open threatening posture. The stimuli appeared on the monitor an average of 16.5±2.01 times (mean ± SEM, *n*=6) in the 10-min trial.

Wandering female (F)

These stimuli were collected in a similar fashion to the threatening male stimuli. Only large, non-ovigerous females were used, carapace widths ranging in size from 1.6 cm to 2.0 cm. Captured females were released at a distance of 15 cm from the camera so that

they would walk across the camera's field of view. Later editing created a looped 10-min sequence in which the female walked back and forth across the video monitor at irregular intervals. The female stimuli crossed the monitor on an average of 19.7±0.92 (mean ± SEM, $n=6$) occasions during the 10-min trial.
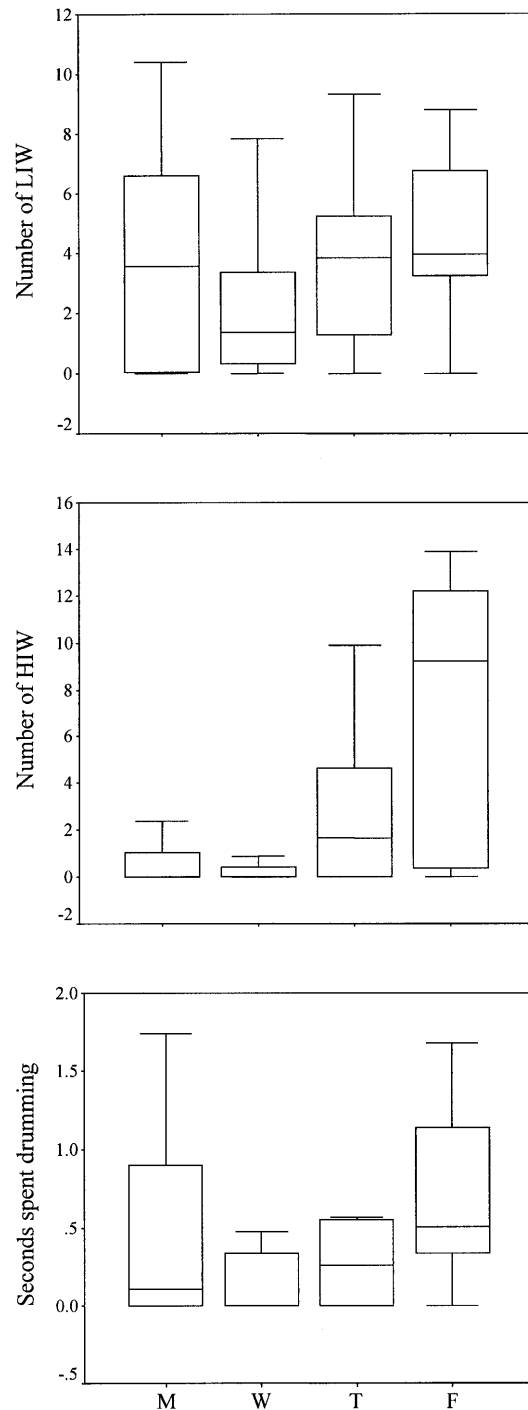
Video playbacks

Each of the six tapes was used twice, in a randomised order, giving a total of 12 playback trials. The 40-min trials (4×10-min stimuli) were carried out during the waving phase of the low tide (i.e. starting approximately 1 h after low tide, continuing for up to 2 h, Wolfrath 1993). Each trial began when the subject crab left his burrow and began to LIW. At the end of each trial the subjects were caught, measured, and marked. No crab filmed as a stimulus was used as an experimental subject. The subjects were actively displaying males of average size, both in carapace width and major chela length (the ranges being 2.8–3.2 cm and 3.4–5.2 cm, respectively). A three-sided hardboard enclosure was placed around a burrow entrance, with the video monitor (inside a protective box) making up the fourth side. The monitor used was a Sony 9" colour monitor with a horizontal resolution of over 450 TV lines, powered by a car battery. The enclosure visually isolated the subject from any source of information other than the monitor. The parasol was also used to reduce the amount of glare on the monitor. The stimulus videos were played back through a Sony Hi-8 Handycam video camera. A second Sony Hi-8 Handycam video camera was used to film each trial.

Behavioural measures were taken from the videos of the trials using the Noldus Observer v3.0 package. The crabs rarely remained on the surface for the full 10 min of each playback stimulus. We therefore looked for an effect of the time exposed to a stimulus and the level of response elicited. There was no significant correlation between the amount of exposure to the stimulus and the number of LIW or HIW produced per minute of that exposure ($r_s=-0.03$, $n=12$, $P=0.93$; $r_s=-0.20$, $n=12$, $P=0.54$, respectively). Similarly there was no significant correlation between the amount of the exposure and the length of time spent drumming per minute of that exposure ($r_s=0.11$, $n=12$, $P=0.75$).

Results

There were no significant differences in the number of LIW elicited per minute of exposure by the four stimuli (Fig. 1). However, there was a significant effect on the number of HIW elicited per minute of exposure (Friedman's $\chi^2=20.21$, $n=12$, $P<0.001$; Fig. 1). Post hoc tests showed that this effect was due to subjects producing significantly more HIW to the female stimuli than the mudflat stimuli (Wilcoxon: $z=-2.67$, $P<0.01$) and the waving male stimuli (Wilcoxon: $z=-2.67$, $P<0.01$); and more HIW to the threatening male stimuli than the mudflat stimuli (Wilcoxon: $z=-2.24$, $P<0.05$) and the waving male stimuli (Wilcoxon: $z=-2.24$, $P<0.05$). There was also a significant effect on the time spent drumming elicited by each stimulus (Friedman's $\chi^2=7.92$, $n=12$, $P<0.05$; Fig. 1). This was due to the subjects drumming for a greater proportion of the exposure to the waving male stimuli than to the female stimuli (Wilcoxon: $z=-2.12$, $P<0.05$).

The responses of the crabs may have been influenced by the order of the stimuli on the playback tape, irrespective of what the stimulus was. We looked for a difference in response to the first stimulus compared with the subsequent stimuli (without taking account of what the actual stimulus was). There was an effect of presentation order on the proportion of the exposure the subjects spent still by the burrow entrance (Friedman's $\chi^2=9.63$, $n=12$, $P<0.05$). Post hoc tests revealed that subjects spent a significantly greater proportion of their exposure to the first

Fig. 1 The effect of four video stimuli (*M* mudflat, *W* waving male, *T* threatening male, *F* female) on three measures of male behaviour [low-intensity waving (*LIW*), high-intensity waving (*HIW*), and seconds spent drumming]. All measures are expressed as per minute of exposure to video (see text). Values are medians ± quartiles, $n=12$

Table 1 Summary statistics of the amount of time spent still by the burrow opening during the first, second, and fourth stimuli. Wilcoxon post hoc tests on the presentation order of the stimuli on the playback tapes: 1 vs. 2: $z=-2.12$, $P<0.05$; 1 vs. 4: $z=-2.98$, $P<0.01$; $n=12$ for all the data. The data presented are medians $\pm$ quartiles

Stimulus placement	Time spent still
1	39.91±9.91
2	19.25±8.20
4	13.29±7.73

stimulus remaining still by the burrow entrance than during the second and fourth stimuli (Table 1).

Discussion

Under natural conditions, male *U. tangeri* wave spontaneously at a low intensity during the latter stages of the low-tide period (von Hagen 1962; Wolfrath 1993). Males wave at a higher intensity when a female is nearby, or in some cases, when a neighbouring male begins to HIW (von Hagen 1962). This pattern was also elicited by our video images in the field: the male subjects waved at low intensity during all of the stimuli, including the control (mudflat) stimulus, but produced significantly more HIW to female images. The similarity between the sort of natural stimuli eliciting waving and video stimuli eliciting waving can be interpreted as subjects responding naturally to video images.

If an animal responds to different stimuli in different ways under natural conditions, and these same differences are elicited by video stimuli, it can be said that the subjects are responding to the video playbacks in a natural way. This argument was used by Clark and Uetz (1990) to interpret the different responses of male jumping spiders (*Maevia clemens*) to televised images of prey insects, female conspecifics, and predatory heterospecifics. Furthermore, the male spiders showed no preference for either live or video prey items when presented simultaneously. Similarly, Shimizu (1998) found that male pigeons (*Columba livia*) displayed appropriately to both live female stimuli and videos of a female. In a study of wave timing in *Ilyoplax pusilla*, an ocypodid crab closely related to *Uca*, Aizawa (1998) found that males would alter the timing of their waves in similar ways to both live stimuli and to video stimuli, suggesting that the video images were recognised appropriately.

We were surprised to find that there was a significant increase in the number of HIW elicited by the threatening male stimuli, as well as the female stimuli, although there are several potential explanations. One reason for the increase in HIW could be that a male wandering back and forth across the screen was similar enough to the way that females wander to elicit a similar, but weaker response to the female stimulus. Another possible explanation stems from the finding that males threatened intruding conspecifics with a major chela smaller than their own, but switched from threatening to waving if the intruder pos-

sessed a major chela larger than that of the resident male (C. Latruffe, unpublished data). This prevents a male becoming involved in an aggressive interaction with a larger male, as the larger male would be more likely to win (Latruffe et al. 1999). A third possibility is that the movement itself was what elicited the increase in waving intensity, and the response could have been the same no matter what was shown moving across the screen. This does not seem likely though, as the waving male stimuli also moved across the screen whilst waving, either moving away from or towards their burrow entrances, and this did not result in significantly higher numbers of HIW being produced. In fact there was a non-significant tendency for the subjects to HIW more in the control stimulus than in the waving male stimulus. The lower number of HIW during the waving male stimulus than in any of the other stimuli could be due to the fact that the presence of a male waving at a lower intensity (on the video monitor) reinforced the impression of a lack of females, so the subjects did not waste energy HIW in the absence of a female. In the future, a more realistic video of a threatening male could be made using a sub-miniature camera mounted on a dummy male, so that the video images would be of a male threatening towards the camera.

Despite using looped tapes for both the threatening male and the female stimuli, which increased the repetitiveness of these stimuli, there were no signs of habituation to these stimuli. The lack of behavioural interaction with any stimulus, including video playbacks, could cause a weaker response or even habituation to the signal (Rowland et al. 1995). [However, in acoustic playbacks, there is evidence to suggest that subjects habituate more quickly to interactive playbacks than to standard playbacks; see the article in this issue by McGregor (2000).] Kodric-Brown and Nicoletto (1997) found that female guppies (*Poecilia reticulata*) responded in a similar fashion to live males and video images of males, but that the response was quantitatively smaller, possibly due to the lack of behavioural interaction. This may explain why none of the subjects in this study adopted the threatening posture to any of the threatening stimuli.

There was a significant effect of the order of stimulus presentation, with subjects remaining still by the burrow opening for a greater period of time during the first stimulus than during the second or fourth stimuli, regardless of what these stimuli actually were. This implies that the subject may have needed more time to acclimatise to the enclosure and the playback. In future it may be better to present a neutral stimulus, such as an empty mudflat, for a few minutes before beginning the trial.

An unexpected finding was the significant difference in response to the video stimuli involving the drumming signal. Fiddler crabs drum when the visual signal is ineffective, for example, during nocturnal low-tide activity or when situated in dense vegetation (von Hagen 1962; Salmon and Atsaides 1968). Von Hagen (1984) noted that in *U. tangeri*, the intervals between consecutive bouts of drumming ("drumwhirls") were the same length as the intervals between LIW, leading to the proposal that drumming acts as a direct replacement for waving when the con-

ditions are not appropriate for a visual signal. Male subjects spent a significantly greater proportion of time drumming during the waving male stimulus than the female stimulus. This may suggest that drumming is a signal used in male–male competition, or it may be that the subjects spent their time in HIW towards the female stimulus and therefore had less available time during which to drum.

This study was conducted in the field, which is unusual as far as video playbacks are concerned. There are clear advantages to conducting these experiments in the field, as can be seen in the results of Clark et al.'s (1997) study of *Anolis* lizards. In our study, the surprise finding that the amount of drumming increased significantly during the waving male stimulus may not have been seen in an artificial laboratory setting. In the study of bird song, a combination of both laboratory and field experiments has led to a broad understanding of this field. Linking laboratory studies of female choice based on song (e.g. Searcy and Marler 1981; Searcy and Brenowitz 1988) and studies in the field (e.g. Otter et al. 1998) including interactive playback (e.g. Otter et al. 1999) has given a more complete picture of the way that female birds assess and choose their mates. In the same way, combining knowledge gained from field and laboratory studies of video playbacks will increase the overall level of understanding.

This study establishes the utility of video playback techniques for studying the visual display of male fiddler crabs, at least in some contexts. These behavioural experiments have shown that fiddler crabs respond to video images. Therefore, we can conclude that it is worth continuing with video playback studies and investigating their capabilities in the future.

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