

## Research Papers

# Chorusing by male European fiddler crabs, *Uca tangeri*: a study of visual communication networks.

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Chorusing behaviour, in which males aggregate and advertise to attract females, has been extensively studied in acoustically signalling orthopterans and anurans. Species which aggregate and signal visually have comparable behaviour but chorusing aspects have been studied infrequently. Male fiddler crabs (genus *Uca*) signal by waving an enlarged claw and form signalling aggregations, therefore, they have the potential to form a visual chorus. This study investigated the chorusing behaviour of male European fiddler crabs, *Uca tangeri*. The timing of waving by groups of three males (trios) was studied when each male was alone and when all three males were present. When waving in a trio, the male with the largest claw significantly increased the length of its interwave interval and some such males tended to wave soon after the other males. This pattern of waving may enhance the effectiveness of the large-clawed male's signal by avoiding visual object grouping and by allowing females to assess relative claw size more readily.

Key words: Waving, signalling, sexual selection/signal.

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## Introduction

A chorus is a group of conspecific males signalling simultaneously to attract females (Ryan et al., 1981; Minckley et al., 1995). Choruses are very clear examples of communication networks, that is, groups of individuals within signalling and receiving range of each other rather than simple signaller-receiver dyads (McGregor & Dabelsteen, 1996). In communication networks a variety of signaller and receiver behaviours can occur, for example, females can assess several signalling males simultaneously and males can adopt strategies to maximise the effectiveness of their individual signals depending on the signalling behaviour of the other males (McGregor, 1993; McGregor & Dabelsteen, 1996).

Most research on choruses has been conducted on acoustic systems (e.g. anurans: Grafe, 1996; Rose & Brenowitz, 1997; insects: Otte, 1974; Greenfield, 1994; Greenfield et al., 1997). Yet communication networks will exist in all sensory modalities where signals can propagate long distances relative to the average spacing between individuals and will, therefore, be received by many individuals (McGregor & Dabelsteen, 1996). However, well-studied examples of aggregations of males signalling visually (e.g. male ruff *Philomachus pugnax*, van Rhijn, 1973) are rarely considered from a signalling perspective. Even those species where visual signalling is considered, for example, the strikingly synchronous flashing of *Pteroptyx* tropical fireflies (Buck & Buck, 1978) are rarely considered from a chorus perspective (Carlson & Copeland, 1985). Signals of different modalities have different properties (e.g. persistence and directionality) yet may have been subject to similar selection pressures in a chorus context. Therefore a consideration of visual choruses may illustrate signalling strategies that are common to all communication networks as well as identifying strategies specific to the features of the visual modality.

Some of the basic ways in which signal timing can be affected by others in the communication network have been described in studies of call timing in anuran choruses (e.g. Ryan et al., 1981). These are overall strategies in which all signallers in the chorus either synchronise or alternate. Synchronous signalling is developed to an extreme degree in some cicada (Cicadidae) choruses (Alexander, 1975) and occurs in anurans to a lesser extent (Lörcher, 1969; Wells, 1977). Alternating signals with close neighbours prevents signal overlap (Brush & Narins, 1989) and this form of antiphonal chorusing has been described in male painted reed frogs, *Hyperolius marmoratus broadleyi* (Grafe, 1996). However, individuals in the same chorus can vary in the strategy adopted; in the green tree frog, *Hyla cinerea*, some individuals signal at random with respect to others, while some lead other callers and some follow, furthermore individuals can change signalling strategies over relatively short time periods (Klump & Gerhardt, 1992).

Fiddler crabs (genus *Uca* [Brachyura, Ocypodidae]) are an ideal group for studying visual chorusing because males signal visually by waving in aggregations (acoustic/vibrational signals have also been noted in *Uca*, Burkenroad, 1947; von Hagen, 1962). Males are characterised by their major chela (Christy, 1988), a greatly enlarged claw which can constitute up to 40% of male body weight and be up to 30 times larger than the other chela (Crane, 1975; Hyatt & Salmon, 1978; Greenspan, 1980; Rosenberg, 1997). This enlarged claw can no longer be used for feeding (Valiela et al., 1974; Carvello & Cameron, 1987), rather it functions mainly in visual signalling (it is waved to attract females) and in male-male fights over breeding burrows. An early

observation of fiddler crabs noted a degree of waving synchrony between males in small groups and drew the somewhat surprising conclusion that synchronous waving in male *U. annulipes* was "probably best described as a physical expression of abundant energy in a sun-loving genus" (Gordon, 1958). Therefore one aim of our study of *Uca tangeri* was to discover whether the timing of waving in male fiddler crabs could be best described as synchronous. A second aim was to study the timing of waving in trios of males in close proximity as a tractable first stage in describing whether individuals in a communication network adopted different visual signalling strategies and if so, why.

## Methods

The study species was *Uca tangeri* which is the only species of fiddler crab to occur in Europe (Crane, 1975; Wolfrath, 1992). Fieldwork was conducted between June 20 and June 25, 1996 at the Ria Formosa Natural Park, located on the Algarve coast of Portugal (near Faro). The Ria Formosa is approximately 55 km long with a maximum width of 7 km and consists of a system of mudflats and salt marshes, sheltered from the Atlantic Ocean by a series of sand barrier islands (Wolfrath, 1992). Large populations of *U. tangeri* are found on most of the mudflats at Ria Formosa. Two sites at opposite ends of the Park were used: Quinta do Marim and Cacela-Velha. The average male density at Quinta do Marim was 2.1 m<sup>-2</sup> and at Cacela-Velha was 5.5 m<sup>-2</sup>.

Video recordings of interactions between neighbouring males were made during the 1.5 hours when the most waving occurred, i.e. during the last 2 hours of the low tide. A Sony 8mm camcorder was mounted on a tripod at a height of 1.5 m, pointing downwards at an angle of 30°, which gave a field of view measuring about 4.7 m<sup>2</sup>. A ruler was included in the field of view to aid assessments of relative chela size and separation distances. Three males within close proximity were monitored from each video recording. The males were referred to by the relative length of the major chela because a large-clawed male (L), a medium-clawed male (M) and a small-clawed male (S) could be distinguished readily in each trio. Length of the major chela is positively correlated with male weight ( $r_s = 0.66$ ,  $P < 0.001$ ,  $n = 34$ ) and carapace width ( $r_s = 0.37$ ,  $P < 0.05$ ,  $n = 36$ ) in the study population (C. Latruffe, unpublished data). The peak of a wave was taken to be the time at which the tip of the major chela was first raised above the level of the eye stalk. The times at which each male reached the peak of a wave were recorded using an event recorder (Observer v3.0). Interwave intervals (IWIs) were defined as the time from the peak of one wave to the peak of another wave. We will use the notation X-X to refer to IWIs within a trio; for example, L-L is the IWI between two successive waves of the same large-clawed male, and S-M is the IWI between a wave of the small-clawed male and the next wave by the medium-clawed male. IWIs were measured either during the periods in which all three males were out of their burrows together or when each male was out alone. Six trios were analysed for about 1.5 hours each. Trios 1 to 5 were at Cacela-Velha and trio 6 was at Quinta do Marim.

## Results

The interwave intervals (IWIs) of male *U. tangeri* varied considerably; coefficients of variation ranged from 214 - 386%, but were not significantly influenced by the waving male's relative claw size or whether the male was waving alone or in a trio (Table 1).

Table 1. Coefficients of variation (%) of interwave intervals (IWI) between successive waves of the same male (X-X) for the large-, medium- and small-clawed male crabs in a trio when waving alone and when waving with the other two males. (Values are means of medians (minimum - maximum),  $n = 6$ . Non-parametric 2-way analysis of variance: alone vs. trio  $H_{1df} = 2.71$ , ns; IWI  $H_{2df} = 0.65$ , ns; interaction  $H_{2df} = 2.13$ , ns).

IWI	Waving	
	alone	in trio
L-L	286.8 (213.8 - 317.5)	282.4 (259.4 - 377.4)
M-M	257.5 (225.0 - 286.8)	291.8 (270.4 - 385.9)
S-S	280.7 (242.0 - 337.1)	294.2 (246.1 - 315.3)

The timing of waving was affected both by the presence of the other males in a trio and by relative chela size. Large-clawed males significantly lengthened the intervals between their waves when waving in the presence of the medium-clawed and small-clawed males compared with when waving alone (Fig. 1; median L-L IWI in trio =  $2.45 \pm 0.1s$ ; median L-L IWI when alone =  $2.03 \pm 0.07s$ ; mean  $\pm$  SE,  $n=6$ ; Wilcoxon matched-pairs signed ranks test:  $z=2.02$ ,  $P=0.043$ ). Neither of the smaller clawed males showed significant differences in IWI when waving in a trio compared with waving alone (Fig. 1).

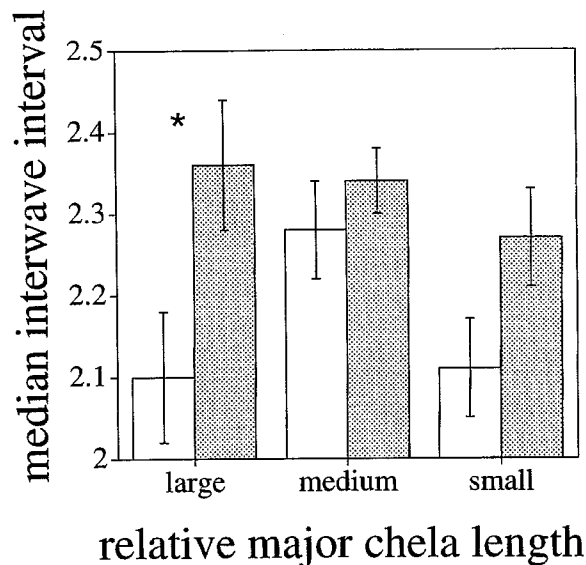


Figure 1. The median interwave interval (IWI) of the three male crabs in a trio (identified by relative length of major chela: large, medium and small) when waving alone (open histograms) and when waving with the other two males present (shaded histograms). Values are means  $\pm$  se (s),  $n=6$ . Wilcoxon matched-pairs signed-ranks test: \* L-L IWI,  $z=2.02$ ,  $P=0.043$ ; M-M IWI,  $z=0.37$ ,  $P=0.72$ ; S-S IWI,  $z=1.89$ ,  $P=0.058$ .

The lengthening of L-L IWI in a trio (Fig. 1) is consistent with the idea that large-clawed males waved after one or both of the other males had done so. The idea can be investigated further by comparing IWIs between waves of the large-clawed crab and the other males. We would predict that these M-L and S-L IWIs (i.e. when L waved after M or S) would be shorter than other between-individual IWIs (L-M, L-S, M-S and S-M). Frequency distributions of these IWIs (Fig. 2) sometimes conformed to our predictions (e.g. trios 1, 2 and 3), but also showed the opposite (trio 4 and 5) or a mix of these patterns (trio 6). This result suggests between- and within-individual variation in whether large-clawed males waved after one or both of the other males in the trio.

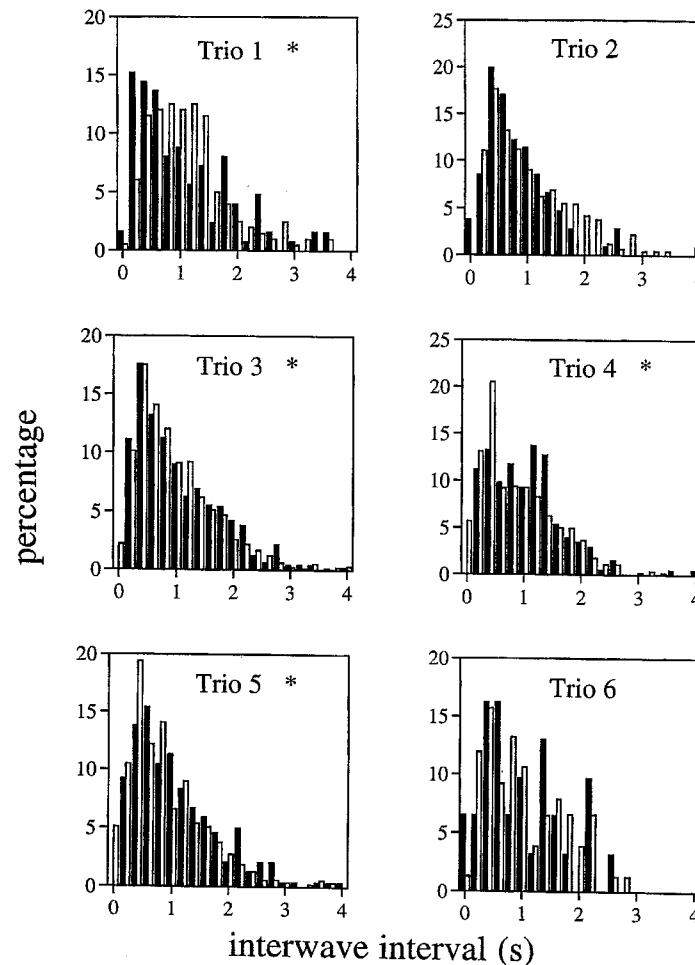


Figure 2. Frequency distribution of IWIs in each of the six trios when the large-clawed male waved after one of the other two males (M-L and S-L IWIs; shaded histograms), IWIs in other waving sequences between different males (L-M, L-S, S-M and M-S) are shown as open histograms. \* shows significant differences ( $P < 0.05$ , 1-tailed Kolmogorov-Smirnov test) between frequency distributions (trio 1:  $z = 1.3$ ,  $n = 125, 199$ ; trio 3:  $z = 1.2$ ,  $n = 493, 856$ ; trio 4:  $z = 1.9$ ,  $n = 205, 545$ ; trio 5:  $z = 1.6$ ,  $n = 240, 469$ ).

## Discussion

Our results showed considerable variation in the timing of the waving signal of male *U. tangeri*. Large-clawed males significantly lengthened the interwave interval (IWI) when two other, smaller-clawed, neighbours were present, and the pattern of change in IWI was sometimes consistent with the idea that the large-clawed male timed his wave to occur soon after one or both of the other males in the trio had waved. These results support the view that groups of waving male fiddler crabs could be considered to constitute a communication network because large-clawed males adjusted their signals in relation to signals from other males in close proximity. Our results also raise two questions of major interest; why were IWIs so variable and why should large-clawed males wave a lower rate if smaller-clawed males were also waving?

The waving patterns of fiddler crabs are described as being stereotyped (e.g. Salmon & Atsides, 1968; Crane, 1975; Hyatt, 1977), yet we found extensive variability in IWI (Table 1). One possible explanation for this level of variability is that *U. tangeri* was the only species of crab waving in our study area and that it is allopatric throughout its distribution. The selection pressures for stereotyped, species-specific patterns of waving might be expected to be strongest where several species of *Uca* are sympatric and to be weakest where each species is allopatric. Therefore, in a communication network in sympatry, the scope to vary signalling strategies based on variation in IWI timing might be expected to be constrained by selection pressures to maintain species-specific aspects of the signal. The extent of such constraints may be best studied by a study similar to ours but conducted on a species of fiddler crab in both allopatry and sympatry.

The second interesting question raised by our results is why, when others in the trio are waving, males with the largest chela increase IWI (i.e. decrease waving rate). Males signalling at higher rates are more successful in attracting females in many species of insect and anuran (e.g. Andersson, 1994) therefore we might expect male *U. tangeri* to wave at a higher rate (i.e. decrease IWI) when other males are also waving. There are two common reasons why signalling at a high rate attracts females more successfully; females are more likely to detect the signal and the signaller may be of higher quality. Both are likely to apply to *U. tangeri*. In fiddler crabs, a male waving at a higher rate will be more conspicuous because his major chela will more frequently enter the most sensitive area of the female's visual field (i.e. above the female's personal horizon; Land & Layne, 1995; Layne et al., 1997). Also waving at a high rate is likely to have a high energetic cost and therefore to be associated with male quality because a male's metabolic requirements are increased by the large amount of striated muscle in the manus necessary for raising and lowering the major chela (Weissburg, 1990). Both of these factors suggest that male *U. tangeri* should wave more frequently (i.e. decrease IWI) when other males are present. However, large-clawed males did exactly the opposite - they decreased waving rate (i.e. increased IWI) when other males were waving.

The decrease in waving rate was probably a consequence of a tendency by large-clawed males in some trios to wave soon after the others in the trio had waved (Fig. 2). This pattern of waving may be related to features of receiver psychology (Guilford & Dawkins, 1991) which, together with a larger major chela, enhance signal attractiveness to females and therefore offset any costs incurred by waving at lower rates. Chela size

is closely correlated with fighting ability in *U. annulipes* (Jennions & Backwell, 1996) and females prefer males with larger major chela in *U. rapax* (Greenspan, 1980) and *U. tangeri* (Oliveira & Custódio, 1998). Thus, the benefit to the large-clawed male in waving shortly after a smaller-clawed male may be that female receivers could more easily assess relative claw size, leading to a mating advantage for the large-clawed male. A second relevant feature of receiver psychology is visual object grouping in which receivers fail to distinguish two visual signals that occur too close together in time (Koffka, 1935). The timing of signals in acoustic communication networks may be constrained by the similar phenomenon of auditory object grouping (Moore, 1997).

To summarise, the benefit to the large-clawed male in waving after the smaller-clawed male had waved may be that the large-clawed male's wave would be perceived separately (i.e. visual object linking does not occur) and its larger chela size would be more easily assessed by the female (i.e. IWI is short enough to allow comparison). If our explanations are correct, then the argument that acoustic signal primacy in a sequence is of overwhelming importance in female attraction in anurans and insects (Greenfield et al., 1997) does not hold for visual signals with qualitative differences (such as relative size of the major chela).

Overall, our results show the advantages of considering the waving displays of male *U. tangeri* in close proximity to be a communication network. For example, our study provides support for the idea that females could use signalling in communication networks to select a mate of the highest relative quality (McGregor & Dabelsteen, 1996; Otter et al., 1998) thereby reducing the risk and the amount of time and energy spent sampling and testing males' burrows (Dyson et al., 1994). Furthermore, although the males could be thought of as a chorus, they did not all adopt the same pattern of waving, either to alternate or to synchronise waves. Rather our study confirms the existence of different male signalling strategies, as some anuran studies have shown (e.g. Klump & Gerhardt, 1992), with some males with the largest major chela enhancing signal effectiveness by waving soon after males with smaller major chelae. Video playback would allow further investigation of signalling strategies in fiddler crab communication networks.

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