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Social cues affect synchronization of male waving displays in a fiddler crab (Crustacea: Ocypodidae)

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The influence of social context in animal signals can lead to complex communicational patterns. In particular, the interaction between individuals can lead to intriguing collective dynamics, such as the temporal synchronization of signals. A fascinating example of such temporal synchronization involves the waving displays of fiddler crabs, in which males raise and lower their enlarged claws in species-specific rhythms. The adaptive significance of this phenomenon is still obscure, but possibly involves female preference for leading waving displays. However, waving displays are highly complex social signals that might be involved in a variety of forms of communication other than simply attracting females, but little is known about the influence of social context on wave synchronization. In this study we carried out field experiments to investigate the effect of two social factors, male density and female presence, on the level of waving synchronization in the fiddler crab *Uca leptodactyla*. Groups of males at varying densities were established in enclosures and recorded either in the presence or absence of a female. Our results indicate that the main factor driving synchronization is the presence of the female, with males not only changing the timing of their waving displays, but also altering their spatial distribution in the arenas. On the other hand, male density had a negligible effect on synchronization (despite significantly increasing waving rate), suggesting that male–male communication plays a minor role in the emergence of waving synchronization in this species.

Temporal synchrony can be observed in a variety of contexts in natural phenomena, occurring at many different levels of biological organization (Greenfield, 1994a; Pikovsky, Rosenblum, & Kurths, 2001; Strogatz, 2003; Strogatz, Abrams, McRobie, Eckhardt, & Ott, 2005; Sumpter, 2010). Examples range from the cellular level, in sperm cells swimming towards an egg (Gray, 1928; Machin, 1963; Yang, Elgeti, & Gompper, 2008), the activity of pacemaker cells of the heart (Michaels, Matyas, & Jalife, 1987; Peskin, 1975) and neural activation (Diesmann, Gewaltig, & Aertsen, 1999; Varela, Lachaux, Rodriguez, & Martinerie, 2001), up to the level of interactions among individuals, such as the synchronous displacement in bird flocks and fish shoals as a predator defence strategy (Brock & Riffenburgh, 1960; Caro, 2005; Goldman, 1980; Partridge, 1982). All of these phenomena share a common characteristic: the units of the system interact and adjust their rhythms (Pikovsky et al., 2001).

Behavioural synchronization of courtship displays evolved repeatedly in a variety of animal taxa, including the bioluminescent signals of fireflies (Buck, 1988; Buck & Buck, 1978; Lloyd, 1973), sound signals in anurans (Greenfield, 1994a; Tuttle & Ryan, 1982) and katydids (Greenfield & Roizen, 1993; Sismondo, 1990), and visual signals in fiddler crabs (Backwell, Jennions, Passmore, & Christy, 1998; Backwell, Jennions, Wada, Murai, & Christy, 2006; Gordon, 1958; Reaney, Sims, Sims, Jennions, & Backwell, 2008). The adjustment of signal production rhythms involved in synchronization can be produced by two (nonmutually exclusive) main mechanisms. First, a phase delay mechanism in which a male adjusts the timing of his courtship signal upon perceiving a neighbour's signal but resumes immediately to his free-running rhythm after each advanced signal. The outcome of this mechanism is an

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unclear synchrony, with some individuals frequently dropping out of the collective activity for a cycle and then re-entering, in phase, two cycles later. On the other hand, the free-running rhythm can be adjusted even when neighbours do not have equivalent free-running rhythms. For example, slow males gradually speed up their signalling and fast males slow down. Because of this feature and the precision of the interaction, this type of mechanism results in more precise synchrony (Greenfield, 1994a, 1994b). Several hypotheses have been proposed for the adaptive significance of synchronous courtship in animals (Buck & Buck, 1978; Greenfield, 1994b; Nityananda & Balakrishnan, 2009; Tuttle & Ryan, 1982). Two influential ideas have been called the 'cooperation hypothesis' and the 'precedence effect'. Under the cooperation hypothesis, the synchronous activity would allow animals to benefit from being in a group (Dugatkin, 1997; Greenfield, 1994b; Sumpter, 2010) through the intensification of the courtship signal sent from long distances (Buck & Buck, 1978), the assessment of the rival's competitive potential (Backwell et al., 2006; Berglund, 1996; Pope, 2005) and/or predation avoidance, in a phenomenon analogous to the selfish herd (Hamilton, 1971; Tuttle & Ryan, 1982; Viscido & Wethey, 2002). According to the precedence effect hypothesis, however, synchrony is an epiphenomenon of competition to produce leading signals, a trait selected by females that may simply be more highly stimulated by the first and more conspicuous signal in a series (Greenfield & Roizen, 1993; Greenfield, Tourtellot, & Snedden, 1997; Litovsky, Colburn, Yost, & Guzman, 1999; Reaney et al., 2008).

Fiddler crabs (*Uca* spp., Decapoda: Ocypodidae) are an unusual example of courtship synchrony given that they are the only case known and studied to use reflected light and the movement of conspicuous parts of the body (Backwell et al., 1998). These movements are the conspicuous and characteristic male waving displays produced by raising and lowering the enlarged claw above the level of the eye-base (How, Zeil, & Hemmi, 2007; Rosenberg, 2002; Zeil & Hemmi, 2006). There are a wide range of stereotyped species-specific waving displays that vary in complexity and involve differences in shape, duration and periodicity of the trajectory of the claw (How, Zeil, & Hemmi, 2009; Perez, Rosenberg, & Pie, 2012).

Relatively little is known about how social cues affect the level of synchronization of waving displays. Previous investigations have mainly focused on the influence of female presence on stimulating synchronous courtship (Backwell et al., 1998, 2006). Synchronous waving has been confirmed in four species of fiddler crabs. It occurs in *Uca annulipes* and *Uca mjoebergi* when mate-searching females are present (Backwell et al., 1998; Gordon, 1958; Reaney et al., 2008), and it occurs in *Uca perplexa* and *Uca saltitanta* regardless of whether a female is present or not (Backwell et al., 2006). Female preference for leading signals was initially verified in *U. perplexa* and *U. annulipes* and, in the latter, was associated with the selection of other male traits such as claw size, waving speed and waving rate (Backwell, Jennions, Christy, & Passmore, 1999; Backwell et al., 2006). Additionally, *U. saltitanta* and *U. perplexa* females show preference for higher waving rates and nonoverlapping waving displays (Backwell et al., 2006). Males seemingly become more distinctive from their group by intensifying their signal in relation to their opponents, but it is still not clear whether female preferences are for waving leadership or for high waving rates (Pope, 2005). Interestingly, two-choice experimental studies on female mate preference in *U. mjoebergi* showed that females prefer the leader male in an asynchronous pair rather than a male in a synchronous pair (Reaney et al., 2008), and that females prefer males with higher waving rate and males whose waves immediately precede or are in opposite phase to a synchronous group (Kahn, Holman, & Backwell, 2014).

The level of synchrony varies among fiddler crab species, and this might be linked to the species-specific waving complexity (Araujo, Rorato, Perez, & Pie, 2013; Perez et al., 2012). Females influence waving complexity by triggering the addition or deletion of components of the display, often resulting in an adjustment of waving rate (Pope, 2005), a trend that has also been reported in some nonsynchronous species (Pope, 2000). For synchronous species, such as *U. perplexa*, female presence stimulates higher waving rate. This can be reflected in lower levels of synchrony, as some males are unable to keep up with the group. However, in *U. saltitanta* there is no difference in the level of synchrony when females are present or absent since waving rate decreases in the presence of a female, allowing all males to keep up (Backwell et al., 2006).

Fiddler crab waving displays are highly complex social signals used in a variety of communication contexts, and not simply to attract females (Backwell & Jennions, 2004; Booksmythe, Jennions, & Backwell, 2010; Crane, 1975; Milner, Jennions, & Backwell, 2010; Salmon, 1984). In an attempt to explore the origins of synchrony, we previously conducted a theoretical study with spatially explicit models simulating the synchrony of waving displays (Araujo et al., 2013). The waving was modelled by coupling logistic map equations (May, 1976; Ott, 1993), where one of the parameters controlled waving complexity by changing the waving periodicity or even allowing for chaos. The model also explored the male's attention of visual orientation in relation to its neighbours as well as the effect of male density. The model predicts that synchronization is more likely to occur at low or extremely high densities if the wave is simple (when the logistic map has period two asymptotic solution). As the wave becomes more elaborate (increasing periodicity or even being chaotic), synchrony is restricted to low densities. The model also predicts that synchronization is favoured if we assume that fiddler crabs have a selective field of attention, despite their 360° visual field (Zeil, Nalbach, & Nalbach, 1986), and that it is pointed towards the direction where male density is highest. None of these predictions have been explored empirically.

Experiments controlling the social context, such as the presence of females and/or the density of males with whom they can engage in synchronous waving, can be a valuable approach to understand the adaptive significance of synchrony in fiddler crabs (Galeotti, Saino, Sacchi, & Møller, 1997; How et al., 2007; Pope, 2000, 2005). Here, we investigate the occurrence of synchronous waves in males of *Uca leptodactyla* by manipulating and exploring the effects of female presence and male density. This is the first attempt to test the prediction of Araujo et al. (2013) regarding the influence of density on waving synchronization with empirical data in an attempt to better understand the mechanisms that drive elaborate synchronization of courtship signals.

METHODS

This study was carried out between February and March of 2012 in Baixio Mirim, Guaratuba bay, Brazil (48°36.4′W, 25°52.4′S). This tidal area is composed of a mosaic of microhabitats varying from sandy to muddy substrates, in which *U. leptodactyla* is the most numerous fiddler crab species, with an estimated average ± SD density of 141.83 ± 50.26 individuals/m^2 (Masunari, 2006). The study period corresponds to the peak of the reproductive season (Masunari, 2006). Under natural conditions, fiddler crabs wave in open areas in densely aggregated populations, making it hard to detect and delimit the individuals that are engaged in synchronous waving groups, as well as to manipulate their densities. Thus, we isolated groups of male fiddler crabs using 12 wooden enclosures (30×40 cm and 6 cm tall). These enclosures were fixed on the