



## Female preferences for timing in a fiddler crab with synchronous courtship waving displays



Andrew T. Kahn<sup>\*</sup>, Luke Holman, Patricia R. Y. Backwell

Evolution, Ecology & Genetics, Research School of Biology, The Australian National University, Canberra, ACT, Australia

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Studies of sexual communication typically focus on the design and information content of a signal of interest, but the timing of signal production relative to nearby competitors can be crucial. Male fiddler crabs, *Uca mjoebergi*, court females with a stereotyped claw-waving display, and males are often observed waving in synchrony with nearby claw-waving males. Using female mate preference experiments with robots that imitate male claw waves, we found evidence that females are more attracted to males whose waves immediately precede a synchronous group of waves (leaders); females also favoured males that waved in opposite phase to a synchronous group (alternators). By contrast, males whose waves lagged behind a group of synchronous wavers (laggards) were no more attractive. We discuss a simple sensory process that could explain how this female preference arises. Our results agree with past findings suggesting that synchrony in fiddler crabs occurs as an epiphenomenon of adaptive male responses to female preferences.

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The synchronous behaviour of many animal species has long fascinated researchers (Buck & Buck, 1968; Carlson, 1985; Gordon, 1958). Of particular interest are the synchronous calls of some anuran and arthropod species with acoustic sexual signals (Greenfield, 1994a). Generally, studies of sexual signalling focus on signal structure (e.g. Doucet, Mennill, & Hill, 2007; How, Zeil, & Hemmi, 2009; Kelley & Endler, 2012) and the information conveyed in these signals (e.g. Backwell, Christy, Telford, Jennions, & Passmore, 2000; Holman, 2012; Searcy & Nowicki, 2005). In comparison, the effect of signal timing relative to competitors on mating preferences has received little attention. But signal timing can have profound effects on mate preferences (Grafe, 1999), which can overcome preferences for other signal traits (Höbel, 2010). To date, synchronous sexual signalling has been investigated in only three channels: acoustic signals in male anurans (e.g. Greenfield & Rand, 2000) and katydids (e.g. Greenfield & Roizen, 1993), bioluminescent flashes in lampyrid beetles (e.g. Moiseff & Copeland, 2010) and claw waving by male ocypodid crabs (e.g. Backwell, Jennions, Passmore, & Christy, 1998).

Generally, synchronicity is thought to have evolved as a product of either cooperation or competition among signallers (Greenfield, 1994b). Cooperative explanations suggest that groups of synchronized males are better able to attract females than nonsynchronized

groups, thereby increasing the average fitness of synchronized males (Lloyd, 1973). This pattern could occur if synchronized, fully overlapping signals create a stronger stimulus, or if non-synchronized, partially overlapping signals create a cluttered, weak stimulus. For example, female fireflies, *Photinus carolinus*, are up to 10 times more likely to respond to synchronous (or near synchronous) simulated male flashes than nonsynchronous stimuli (Moiseff & Copeland, 2010). In this system, male synchrony also appears to maintain species/sex recognition by females against the visual clutter of other bioluminescent signals.

Synchronous sexual signalling could also evolve as an epiphenomenon of competition over signal timing among male rivals (Greenfield, 1994a). For example, in acoustic systems, overlapping signals often 'jam' one another, reducing their efficacy. Males might thus strategically alter the timing of their signals to effectively jam the signal of competitors, or to avoid being jammed by them (Greenfield, Tourtellot, & Snedden, 1997). Similarly, in some synchronously signalling species, female preferences for leading signallers that immediately precede their competitors have been demonstrated (Greenfield & Roizen, 1993; Reaney, Sims, Sims, Jennions, & Backwell, 2008). In these cases, selection should favour males that adjust their signal timing in an attempt to produce leading signals (or to avoid signalling right after a competitor), resulting in more synchronous signals being produced than expected by chance (Greenfield et al., 1997).

Cooperative and competitive explanations of synchrony are not mutually exclusive. For example, in the wolf spider, *Hygrolycosa*

<sup>\*</sup> Correspondence: A. T. Kahn, Evolution, Ecology & Genetics, Research School of Biology, The Australian National University, Canberra 0200, ACT, Australia.

E-mail address: [andrew.kahn@anu.edu.au](mailto:andrew.kahn@anu.edu.au) (A. T. Kahn).

*rubrofasciata*, males actively synchronize their acoustic drumming sexual signals and females prefer tightly synchronized groups (Kotiaho, Alatalo, Mappes, & Parri, 2004), suggesting a cooperative origin of synchrony in this species. However, within loosely synchronized groups, females preferred leading males, whereas within tightly synchronized groups, females showed a preference for the last male to signal. Therefore, both cooperation and competition might play a role in maintaining synchronous signalling in this system.

Here, we studied female preference based on the timing of courtship waving in the synchronous signalling of the fiddler crab, *Uca mjoebergi*. Male fiddler crabs (*Uca* spp., Ocypodidae) possess one enlarged claw, which is used as a weapon during territory acquisition and defence, and is waved in a species-specific fashion to court passing females and deter rivals (How et al., 2009). In several fiddler crab species, groups of courting males wave in close synchrony (Backwell, Jennions, Wada, Murai, & Christy, 2006; Backwell et al., 1998; Gordon, 1958). In the only study experimentally addressing the adaptive function of this synchrony, Reaney et al. (2008) used mechanical imitation males to run a series of female mate preference trials in *U. mjoebergi*. They demonstrated that pairs of synchronous males had no advantage over nonsynchronous pairs, suggesting that synchrony is not a cooperative action in this system. Within nonsynchronous pairs, however, females preferentially approached the male that produced the leading wave. This supported earlier findings from the closely related *Uca annulipes* in which males visited by mate-searching females were found to produce more leading waves than their rivals (Backwell et al., 1998) probably by sneaking in extra, nonoverlapping waves as well as waving in synchrony (Backwell, Jennions, Christy, & Passmore, 1999). Taken together, this suggests that synchrony in fiddler crabs occurs as an epiphenomenon of males competing to produce leading waves.

In this study, we further investigated female preferences in *U. mjoebergi* by using robotic imitation males. By using a cluster of synchronized males and changing the timing of one focal male, we were able to assess the benefit of producing unique wave timing. Specifically, we tested whether focal males were favoured when they were either leading, lagging or waving in alternation with a synchronized group. This design allowed us to test whether the findings of Reaney et al. (2008) were driven by a leader preference or laggard avoidance, and to measure the attractiveness of males waving in alternation.

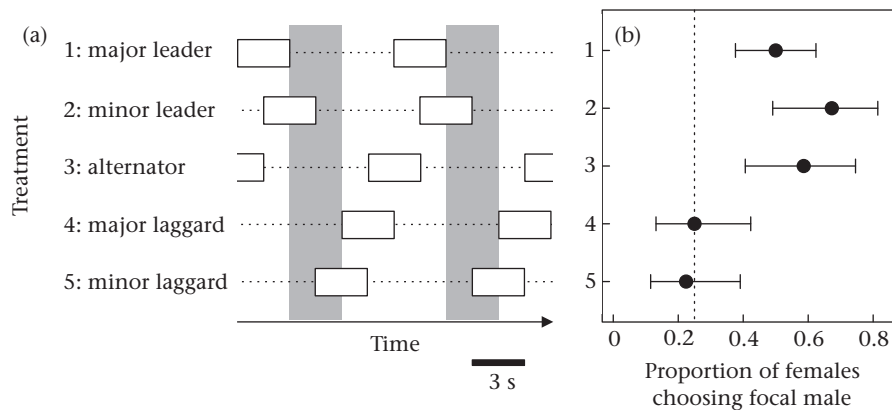
## METHODS

We studied a *U. mjoebergi* population in October 2012 in East Point Reserve, Darwin, Australia (12.41°N, 130.83°E). *Uca mjoebergi* are small crabs (<20 mm carapace), living in very dense, mixed-sex populations on the intertidal mudflats of northern Australia. These crabs spend most of their lives in and around their burrows. In the mating period, receptive females leave their burrows and sequentially sample the burrows of several courting males before choosing a mate. Males court females by waving their enlarged claws. Females tend to prefer larger-clawed males, which wave faster (Kahn, Dolstra, Jennions, & Backwell, 2013; Reaney, 2009). Copulation and oviposition occur in the male's burrow, after which he leaves, with the female remaining to incubate her eggs (Crane, 1975).

We performed female mate preference experiments using custom-built robots, hereafter referred to as males. Each male consisted of a plaster replica claw (20 mm long) attached to a wire arm, which was driven by a motor buried below the claw in a plastic container. The motors were then remotely powered by a central control unit. This system was designed to perfectly imitate the waving action of male *U. mjoebergi* and has been used successfully in several past studies (e.g. Kahn et al., 2013; Reaney et al., 2008). All trials involved four males, and were run on a raised mud-covered arena (60 × 60 cm) in the field with the four males arranged in an arc 5 cm apart. The males waved continuously in a set cycle (see below) from before a female was added to the arena until shortly after the trial finished.

We performed five different treatments in our mate preference experiment (Fig. 1a). In each treatment, three of the mechanical males waved in perfect synchrony at a rate of 6.7 waves/min, with each wave taking 3 s to complete. The fourth male then waved at the same rate, but was either (1) a major leader, completing its wave as the synchronized group began theirs, (2) a minor leader, starting just before the synchronized group, half overlapping, (3) an alternator, waving in alternation with the synchronized group, (4) a major laggard, starting its wave immediately after the synchronized group finished theirs, or (5) a minor laggard, starting half way through the other waves (Fig. 1a). The position of the unique male was randomized and changed every trial, while the positions of the robotic units were randomized and changed every day.

We collected a total of 60 female mate-searching crabs for mate preference trials. Only females that were observed actively sampling signalling males were used. The females were added to the



**Figure 1.** (a) Graphical representation of two full waving cycles for our five treatments (i.e. a snapshot of the waving seen by females). The white rectangles represent time periods in which the focal male is performing a single claw wave (3 s duration), and the shaded bars denote when the other three males are waving in synchrony. (b) Means and 95% CIs for the proportion of female crabs that chose the focal male in each of our five treatments. Shown values are from our generalized linear model. The dashed line represents the proportion of females expected by chance to choose the focal male, under the null hypothesis that all males are equally attractive.

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