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Original Article

Why signal if you are not attractive? Courtship synchrony in a fiddler crab

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Synchronized male courtship signals are puzzling because males generally compete with each other for females. Male *Austruca mjoebergi* fiddler crabs wave in synchrony to attract females, but, all else being equal, females have a strong preference for "leader" males that can produce waves before other males ("followers"). So why do followers participate in synchrony? Here, we experimentally investigate three explanations for why followers might wave in synchrony: 1) followers obtain a small proportion of matings, 2) followers are more likely than a leader to attract females if they are positioned closer to her than is the leader, and 3) synchrony functions as a long-distance visual signal that attracts females so there is a net benefit to synchrony for all males. Using robotic male crabs, we found that females show a strong preference for leading males, but followers obtain a "better-than-nothing" proportion of mates. We also showed that closer proximity of a follower to the female did not affect her preference for leaders, although being a leader increased a male's success when he was further from the female than were rival males. Finally, females were more likely to approach a distant group if there was a leader present, suggesting that followers do benefit from participating in synchrony.

Key words: **fiddler crab, lek, mate choice, sexual selection, signal, synchrony, visual courtship.**

INTRODUCTION

Group living animals often interact with each other in complex ways that appear highly coordinated to observers. Such collective behavior can range from schools of fish or flocks of birds simultaneously moving together, to the precise timing of mate attraction signals so that they overlap to create a strong, unified signal (Greenfield 1994). The synchrony of male courtship signals is particularly interesting because it seems counterintuitive for males to cooperate when they are competing with each other for access to females. In many species, however, all males in a group benefit from cooperating to signal in synchrony. For example, male fireflies (*Photinus carolinus*) often flash together as a group with near perfect synchrony. Each individual male benefits from signaling synchronously because the group signal is more detectable to females from a distance (Moiseff and Copeland 2010), and because synchrony confuses predators reducing each individual's risk of predation (Nityananda and Balakrishnan 2009).

Yet synchrony can also evolve when there are no obvious benefits to certain group members. This seemingly occurs if females have a preference for males that produce leading signals (i.e., slightly in advance of rival signals). In auditory communication, females are thought to prefer leaders because their signals are easier to perceive and localize as they are not masked by the calls of other males (Greenfield 1994). Males therefore compete to produce leading calls, resulting in incidental synchrony purely as a byproduct (Greenfield and Roizen 1993; Greenfield et al. 1997; Party et al. 2015).

In visually signaling species, females can also prefer leading signals. This has been shown in several species of synchronously waving fiddler crabs (Backwell 2018). In *Austruca mjoebergi* and *A. annulipes*, males wave in close synchrony and females preferentially approach the male whose wave starts shortly before the others ("leader") (Backwell et al. 1998; Backwell et al. 1999; Reaney et al. 2008).

If females have a strong preference for leaders, why do "followers" signal at all? This question is not limited to synchronously waving species; in any signaling species where females have a strong preference for a particular trait, why do males without that trait attempt to compete? For example, in lekking species where males display to females simultaneously, dominant males attract more females than subdominant or subordinate males (Höglund and Alatalo 1995). Yet female mate choice is nonrandom;

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therefore subdominant and subordinate males continue to display to females even though they are comparatively less attractive (e.g., Mediterranean fruit flies *Ceratitis capitata*; Whittier et al. 1994). This is especially puzzling when signaling is expensive in terms of lost time, expended energy, predation risk, or thermal stress.

Here, we studied female preference for leaders in synchronously signaling groups of male *Austruca mjoebergi* fiddler crabs. We know from previous work that females have a strong preference for leading waves (Reaney et al. 2008; Kahn et al. 2014), but it is unknown why "follower" males wave in synchrony (or wave at all). We address three possible explanations:

(i) Female preference for leaders may be strong, but is not absolute. Followers may still be able to attract a small, better-than-nothing, proportion of females as mates.
(ii) The relative proximity of males to a mate-searching female is likely random since it depends on the direction of her approach. If a follower is closer to the approaching female, he may be able to attract her to his burrow even though there is a leader within the group.
(iii) Synchrony may, on average, benefit all males (both leaders and followers) if a synchronous group can attract more females due to its increased detectability and locatability.

METHODS

Study species

We studied wild *Austruca mjoebergi* from a population in East Point Reserve, Darwin, Australia (12° 24′ 032″ S; 130° 49′ 050″ E) in October-November 2019 (data for Experiment 1 were collected during spring 2015 and 2016) during the low neap tide.

This species lives in dense, mixed-sex populations on inter-tidal mudflats where males court mate-searching females by waving their enlarged claw in synchrony with other males. The synchrony produced by waving males is strong and precise (α of 5° where an α of 0° or 360° indicates precise synchrony; Reaney et al. 2008; Backwell 2018), but ceases once females are absent (Backwell 2018).

Male waves increase in intensity once females are close enough to their burrow (Milner et al. 2012), and receptive females visit multiple males and assess their burrows before choosing a mate. Mating occurs in the male's burrow, where females will then incubate their eggs until they release larvae about 20 days later.

Animal collection

We caught wandering females on the mudflat, and individually placed them in plastic cups filled with ~50 mL seawater. All females were kept in the shade to prevent thermal stress. After testing, females were measured using dial callipers (carapace width, mm) and released back onto the mudflats to continue mate-searching.

We conducted female choice trials in the field using custom-built robotic crabs that mimic *A. mjoebergi* male waving behavior (Figure 1). Each robotic crab unit consisted of a small metal arm driven by a motor and fitted with a plaster replica claw (24 mm long), painted to match male *A. mjoebergi* claws (Detto and Backwell 2009). Trials were run on an elevated arena covered in a smooth, flat layer of mangrove sediment, with only the metal arm of the robotic crab protruding above the arena surface (Reaney et al. 2008; see Figure 1).

In each experiment, females were presented with a choice between robotic crab units that differed only in the timing of their waves (Figure 2). All units waved at a rate of 16.8 waves/min, with a single claw wave taking ~3.58 s to complete (Reaney et al. 2008). The number of robotic units presented to females varied across the three experiments (from two units up to four units, see Experiment descriptions). The roles and positions of the robots in the arena were randomly switched between trials to avoid any directional biases.

Figure 1
Photograph of the robotic units used to mimic male *A. mjoebergi* fiddler crabs in Experiment 1. Both units have their claws at the lowest wave position (start/end position). The motor driving the metal arm and claw is hidden beneath the mangrove sediment covering the arena. Image credit: D. Perez.

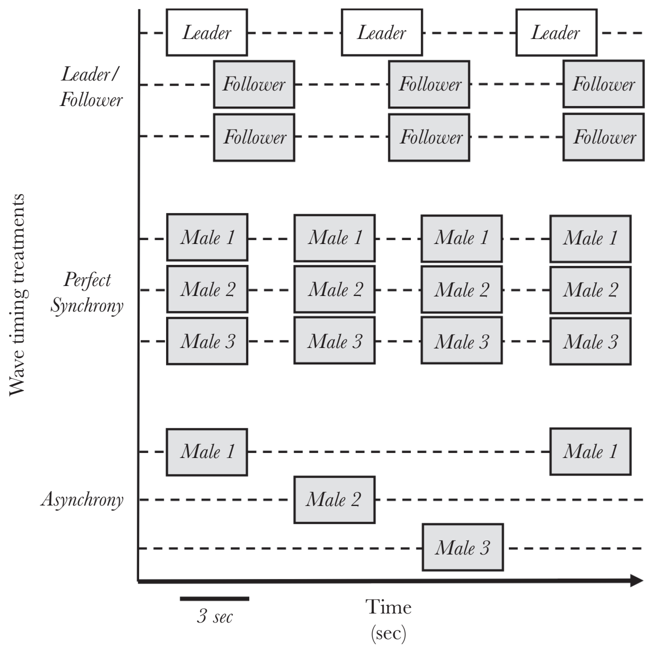

Figure 2
Graphical representation of wave timing for the three waving treatments used in Experiment 3. Experiments 1 and 2 used the same wave timings with the exception of fewer robotic units in Experiment 1, and more units in Experiment 2. For leader-follower wave timing, white rectangles represent the waving period for the leader performing a single claw wave (ending their wave 1.8 sec before the followers; shaded rectangles). Robotic male units waved at a rate of 16.8 waves/minute, with a single claw wave taking ~3.58 seconds to complete.

At the beginning of each trial, the female was placed under a clear plastic container and was allowed to watch three complete wave cycles of the group before being released remotely. Female choice was recorded if she touched a robotic unit. If a female did not move for 2 min, or touched the outer edge of the arena, the trial was rerun. This was done a maximum of three times before deeming the female unresponsive.

Experiment 1: strength of female preference for leaders

For Experiment 1, we aimed to determine the strength of female preferences for males that produce leading waves. We conducted a two-choice trial in which females (n = 30) were presented with a leading and a following robotic unit (Figure 2). The test arena was 60 × 60 cm and the robots were placed 5 cm apart at one end of the arena, 20 cm away from the female release point (Reaney et al. 2008; Kahn et al. 2014; Figure 3a).

Experiment 2: effect of proximity on female preference for leaders

For Experiment 2, we aimed to determine whether females would preferentially choose followers that were closer to her than was the leader. We conducted three mate choice trials (Figure 3b) that simulated the natural mate-choice context in which the female is surrounded by a small group of synchronously waving males (in nature: two to six males per cluster; Reaney and Backwell 2007). Each trial consisted of four robotic crab units placed on a 60 × 60 cm arena. We tested 40 responsive females in each of the three trials (n = 120 females tested in total).

In trial 1, the units were evenly spaced around a central female release point, where the distance between each robot and the female release point was 10 cm. One of the robots was a leader and the other three were followers that waved at the same time (Figure 2).

For trial 2, we presented the female with the same choice as trial 1, but the leading unit was now 15 cm away from the female release point while the three followers remained 10 cm away from the female release point.

In trial 3, all four units waved in exact synchrony (started and ended at the same time, see Figure 2); three units were 10 cm away from the female release point and one unit was 15 cm away from the female release point.

Experiment 3: long-distance attraction

For Experiment 3, we aimed to determine whether females were more likely to approach a group of males that waved in perfect synchrony, a group that waved asynchronously (alternating waves), or a synchronous group that had a leader (Figure 2). If perfect synchrony is an attractive signal to females, then we expected that

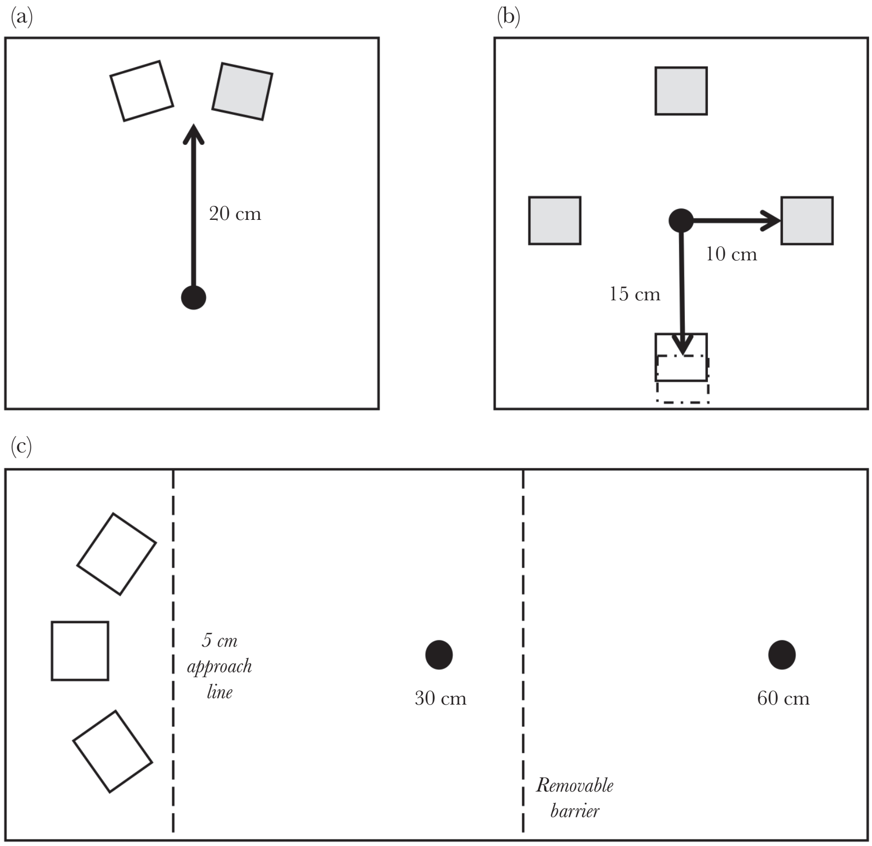

Figure 3
Experimental arenas for testing female preferences using robotic crabs. In Experiment 1 (a), females (black circle) are given a choice between two robotic males; a leader (white square) and a follower (grey square). In Experiment 2 (b), a female is placed in the centre of the arena and chooses among four robotic males that are equidistant from her at 10 cm (trial 1), or when one unit has been moved 15 cm away (dashed square; trials 3 & 4). In Experiment 3 (c), females start their approach at either 30 or 60 cm. An approach was counted when females moved to within 5 cm of the waving robotic males.

asynchronous and leader-follower groups would receive fewer female approaches because these groups do not produce a strong, unified signal.

We conducted six different trials in which we simulated a female approaching a group of males from a distance of either 30 cm or 60 cm (n = 30 females for each trial) in a 60 × 100 cm test arena. We were not interested in which specific units she approached, but rather whether or not she approached the group. For the three trials at each distance, we presented females with a trio of robots that: 1) waved in perfect synchrony; 2) waved asynchronously; 3) had a leader and two followers. Females were randomly assigned an approach distance of either 30 cm or 60 cm. A removable barrier was placed 10 cm behind the female starting position to keep conditions consistent between distance treatments. The females were presented with an array of three robotic crab units placed 5 cm apart at one end of the arena (Figure 3c). We initially included a third set of trials with a release point 90 cm away, but no females (n = 10) responded so we dropped the trial.

Statistical analysis

All statistical analysis was conducted in R version 3.5.1 (R Core Team 2019). To compare the proportion of females approaching a given robot type in Experiments 1 and 2, we ran Exact binomial tests (null = P = q = 0.5 in Experiment 1; P = 0.25, q = 0.75 in Experiment 2). In Experiment 2, we then ran a log-likelihood ratio test to see if the proportion of females approaching the unique robot in each of the three trials differed. In Experiment 3, we initially ran separate log-likelihood ratio tests at each distance to test if the proportion of female responses differed between the three types of groups. If there was a difference, we then ran Fisher's exact tests to see which pairs of groups differed in the proportion of females that responded. Summaries of female body sizes, all female preferences (Experiments 1 and 2) and approaches (Experiment 3) are presented in Table 1.

RESULTS

Experiment 1: strength of female preference for leaders

Females preferred to approach male robots producing leading waves: 26 of 30 approached the leader rather than the follower (Binomial test: $P < 0.001$). Although this is a strong preference for leaders, 13% of the females still chose the follower.

Experiment 2: effect of proximity on female preference for leaders

In trial 1, females had a choice between four robotic crabs; one leader and three synchronous followers (all four units were 10 cm from the female). Fifteen of the 40 females approached the leader and 25 approached a follower (an average of 8.3 approaches to each follower). Females tended to prefer to approach the leader (Binomial test: $P = 0.054$).

In trial 2, females had a choice between four robotic crabs, three were 10 cm away and waved in perfect synchrony, one was 15 cm away and produced leading waves. Thirteen of the 40 females approached the more distant leader and 27 approached one of the closer followers (an average of 9 approaches to each follower; Binomial test: $P = 0.179$).

In trial 3, females had a choice between four robotic crabs waving in synchrony (no leader). Three robots were 10 cm from

Table 1.
Summary of female approaches (Experiments 1 and 2) for robotic male units that produced leading waves (leader) and/or were more distant from the females; and of female approaches for each of the six distance/waving treatments in Experiment 3

Experiments 1 & 2 – female preferences	Chose unique unit (Leader and/or more distant unit)	Chose one of the three other units	Total females tested	Mean carapace width ± SD (mm)
Experiment 1				
Leader – Follower (2 choice)	26	4	30	8.56 ± 1.08
Experiment 2				
Trial 1				
Leader – 3 Followers (4 choice)	15	25	40	9.32 ± 0.96
Trial 2				
Leader – 3 Followers (leader away from group)	13	27	40	9.50 ± 1.01
Trial 3				
Synchrony (synchrony, 1 unit away from group)	5	35	40	9.19 ± 0.87
Experiment 3 – long distance approaches	Approached	Did not approach	Total females tested	Mean carapace width ± SD (mm)
Distance 1–30 cm				
Synchrony	10	20	30	9.28 ± 0.87
Asynchrony	10	20	30	9.15 ± 0.85
Leader-Followers	12	18	30	9.59 ± 0.63
Distance 2–60 cm				
Synchrony	3	27	30	9.02 ± 0.94
Asynchrony	0	30	30	9.00 ± 1.15
Leader-Followers	10	20	30	8.93 ± 1.19

Mean (± SD) female body sizes for females within each of the experimental trials are also presented.

the female and one was more distant (15 cm away). Five of the 40 females approached the distant robot and 35 approached a nearer robot (an average of 11.67 approaches per near robot). Females were significantly less likely to approach the more distant robot (Binomial test: $P = 0.043$).

The proportion of females approaching the unique robot in each trial (the leader in trials 1 and 2, and the more distant robot in trial 3) differed significantly between the three trials ($G = 32.54$, df = 2, $P < 0.001$). There was no significant difference in the proportion of responses to the leader in trials 1 and 2, despite him being more distant in trial 2 (Fisher's exact test: $P = 0.815$). However, females were more likely to approach a distant robot when it produced leading waves than when it waved in perfect synchrony with the other three robots (trial 2 vs. 3: Fisher's exact test: $P = 0.059$).

Experiment 3: long distance attraction

Comparing the approach rate of females at 30 cm: 10 of 30 females (33%) approached a synchronous group; 10 of 30 females (33%) approached an asynchronous group; and 12 of 30 females (40%) approached a leader-follower group. There was no significant difference in the female approach rate to the three types of groups ($G = 0.385$, df = 2, $P = 0.83$).

Comparing the approach rate of females at 60 cm: 3 of 30 (10%) approached a synchronous group; 0 of 30 approached an asynchronous group; and 10 of 30 (33%) approached a leader–follower group. There was a significant difference in the female approach rate to the three types of groups ($G = 16.64$, df = 2, $P < 0.001$). Females were not more likely to approach a synchronous than an asynchronous group (Fisher's exact test: $P = 0.237$). However, females were significantly more likely to approach a leader–follower group than an asynchronous group (Fisher's exact test: $P < 0.001$), and were more likely to approach a leader–follower group than a synchronous group (Fisher's exact test: $P = 0.057$).

At both distances, females that did not approach a group of robotic males either showed no response (did not move) or wandered off to the side of the test arena.

DISCUSSION

Females had a strong preference for robots mimicking male *A. mjoebergi* producing leading waves: 87% approached the leader in two-choice trials. This is consistent with previous work on this species (Reaney et al. 2008; Kahn et al. 2014). Although robotic males that produce following waves are less attractive to females, they still had a 13% chance of being chosen by a female. This could explain why less attractive males wave—it is a "best-of-a-bad-situation" for followers.

Proximity to mate-searching females could potentially influence female choice. If a following male is closer to the approaching female than is the leader, it may increase his chances of being chosen (Booksmythe et al. 2008). Here we found that this does not appear to occur. Females preferentially approached the leader in a group of four waving robots that were equidistant from her; and females retained their preference for the leader even when she had to travel past a group of followers to choose him. When all robotic males waved in perfect synchrony (no leader), females were significantly less likely to approach the distant robot when it waved in synchrony than when it produced leading waves. In combination, these results suggest that proximity to the approaching female does not counteract the leadership preference. As such, following males are unlikely to increase their chances of attracting a female by being closer to her.

Is there a benefit to all males (leaders as well as followers) by waving in a synchronous group? When females were 30 cm away from a group of robotic waving males, there was no effect of wave timing on the likelihood that she approached the group. Females were equally likely to approach a group if the robots were waving in synchrony, asynchrony or if there was a leader in the group. At 60 cm, however, females were more likely to approach a group if there was a leader than when the group waved in perfect synchrony or asynchronously. Having a leader appears to increase the chances that a female will approach a group of waving males. We know from previous work on *A. mjoebergi* that leading waves help males to stand out in a crowd, allowing mate-searching females to orientate towards attractive males and reducing her mate searching costs and predation risk (Sanches et al. 2017). Strengthening the overall visual courtship signal would benefit all males in the group, including the followers: the more females that are attracted to the group, the more likely it is that a follower will be able to persuade one of them to mate with him. In many lekking species, less attractive males can improve their chances of being chosen by a female by clustering around the most attractive males (e.g., great snipes *Gallinago media*: Höglund and Robertson 1990), or by choosing locations that attract the most females (e.g., *C. capitata* flies: Niyazi et al. 2008). Therefore proximity to attractive males or resources are one such way less attractive males can make the most of a bad situation. Importantly, in our study, perfectly synchronous waving did not elicit as many female approaches as did a leader–follower waving pattern (10% vs. 33%). This suggests that synchrony itself does not act as a long-distance attraction but rather that the female is attracted to leading waves.

We currently do not know why females have a preference for leading waves. It could be an adaptive preference if producing leading waves correlates with male quality. For example, leading calls produced by male European treefrogs (*Hyla arborea*) are an honest signal used by females to assess male quality (i.e., his energetic investment into calling), so there is strong selection for males to call first (Richardson et al. 2008). An equally likely (and nonmutually exclusive) explanation is that female preference for leaders arose due to a sensory bias (Ryan and Keddy-Hector 1992): the first signal that a female sees might be more likely to elicit a response. This explanation is often given for "precedence effects" in other invertebrate species with synchronized auditory displays, and is thought to be the result of proximate neural mechanisms that help females orientate towards specific auditory signals (i.e., lateral contrast enhancement; Pollack 1988). For example, the leading calls of male bush crickets (*Mecopoda elongata*) inhibit female response to any closely following calls by suppressing her neuronal activity, leading to strong female preferences for leaders (Römer et al. 2002).

Whatever the explanation for a female preference for leaders, it poses a problem for males that do not produce leading waves. Our findings suggest that less attractive male followers can still benefit from the imperfect group synchrony that arises from male–male competition by strengthening the overall visual courtship signal to attract females from a distance. Even so, females are significantly more likely to choose the leader because he stands out from the rest of the group. So why do followers continue to wave if females almost always prefer leaders? In neotropical katydids (*Neoconocephalus spiza*), females avoid males whose calls immediately follow the onset of a leading call (Snedden and Greenfield 1998). To avoid being unattractive, following male katydids reset their call timing by waiting for several chirps before resuming their call (Greenfield and Roizen 1993). This mechanism of male–male competition amongst neighbors helps maintain synchrony (Greenfield and Roizen 1993). Additionally, follower males might compensate by investing in a different call feature. In *M. elongata* bushcrickets, unattractive followers trade-off call timing for sound intensity; followers increase the amplitude of their calls, another attractive call feature for females, which can even reverse the female preference for leaders (Römer et al. 2002; Fertschai et al. 2007). However, it is unlikely that visual courtship signals can compensate in such a manner as any additional increase in waving intensity by followers would presumably disrupt the overall visual synchrony. Furthermore, females receiving multiple, asynchronous signals from waving males might be unable to extract information about male quality based on temporal cues, and might ultimately defer to a different male trait to choose an attractive partner (e.g., claw size (Kahn et al. 2013)). Future work is, however, still needed to investigate whether less attractive males can modify their waves to attract females without losing the overall benefit of synchrony.

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AUTHOR CONTRIBUTIONS

L.M.H. collected and analyzed data, and wrote the first draft of the manuscript. G.C.M. and D.M.P. collected data and provided invaluable field assistance. P.R.Y.B. conceived the study, assisted with data analysis, and critically revised the manuscript. All authors have read and approved the final version submitted for publication.

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Conflict of interest: The authors declare no conflict of interest.

Data availability: Analyses reported in this article can be reproduced using the data and code provided by Harrison et al. (2021).

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