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## Faster male displays and less complex choice are more attractive to female fiddler crabs as they reduce search costs



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Keywords: accuracy mate choice robotic crab sexual selection waving display Females that quickly and accurately locate and assess males can reduce their risks of predation, dehydration and heat stress while mate searching. Here we measured the accuracy and time it took female fiddler crabs, *Uca mjoebergi*, to approach robotic claws that simulated males' courtship signals. We ran six experiments: three one-choice experiments varying in waving display rate (fast, medium and slow) and three three-choice experiments with increased number of displays (all with fast wave rate) and complexity (each one at the three different rates; and the three different rates presented at different distances, with the fast wave rate further from the female and the slow wave rate closer to the female). Females approached all waving robots with an accuracy of 9–18°. They approached faster-waving claws more quickly even when they were presented in sets of three claws, but it took females longer to approach a claw in the more complex situation, with claws waving at different rates and distances. Females may approach waving claws more rapidly simply because they present a more continuous and less ambiguous stimulus. The results suggest that high signalling rates may attract females because they reduce female search costs, and they may or may not additionally signal male quality.

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Mate choice is expensive for females. Any increase in searching time will further increase her costs (energy, predation risk, dehydration, overheating). If a male's signal is difficult to localize, a female would take a more circuitous path to the signaller and spend more time exposed to risks. It is not surprising, therefore, that many animals are able to localize signals with great precision. Females usually follow a zigzag path towards displaying males, and the average error of each movement from the target axis is used to estimate the precision of approach. Most female anurans have an approach error angle of  $16-23^\circ$ , but one species has an accuracy of  $1^\circ$  (Rheinlaender, Gerhardt, Yager, & Capranica, 1979; Shen et al., 2008; Ursprung, Ringler, & Hödl, 2009); crickets have an accuracy of  $10-14^\circ$  (Schöneich & Hedwig, 2010); a fly was shown to have an accuracy of  $1-2^\circ$  (Mason, Oshinsky, & Hoy, 2001).

By making his signal stand out, a male can make himself more detectable and more locatable, and this can attract more females (Mowles & Ord, 2012; Ryan & Cummings, 2005; Wilson & Mennill,

\* Correspondence: F. H. C. Sanches, Department of Physiology, Botucatu Biosciences Institute, São Paulo State University (UNESP), Botucatu, SP, Brazil. *E-mail address:* fabiohcsanches@yahoo.com.br (F. H. C. Sanches). 2011). In many species, the same male traits that increase the conspicuousness or locatability of a signaller may also signal his quality or act as a handicap (Mowles & Ord, 2012; Ryan & Cummings, 2005). High signalling rate is one example: it is expensive for males to signal at a high rate (time, energy and predation risk), so display rate is often considered to signal male quality or act as a handicap (Mowles & Ord, 2012; Ryan & Cummings, 2005). In field crickets, males that signal more rapidly accumulate greater energetic costs, and it was suggested that females select mates based on their ability to bear these costs (Mowles, 2014). In chickadees, a slow display rate prevented females from locating the stimulus, and a high display rate caused females to approach the speakers more quickly (Wilson & Mennill, 2011). By increasing the display rate when a female is detected, a male may make himself more visible and more locatable. In a fiddler crab, for example, males increase their wave rate when they detect wandering females (or when they detect the increased wave rate of other males that have seen a female); this increases their conspicuousness and consequently elevates their likelihood of being approached by the female (Milner, Jennions, & Backwell, 2010). If the signal functions entirely to facilitate male localization, it would still be energetically expensive and males would still

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succumb to the energetic costs, but females would approach the more rapidly waving males simply because they are more locatable. There may or may not be additional benefits (e.g. females that mate with more easily detected males may produce sons that are also more easily detected), meaning that the locatability of a signal and its possible role in mate assessment may be closely linked.

Enhanced locatability of complex over simple calls has been suggested as a potential reason why females strongly prefer complex calls in the túngara frog, *Physalaemus pustulosis* (Bonachea & Ryan, 2011). It was shown that females chose more quickly when presented with complex calls than when listening to simple calls, but the accuracy of approach was no different between simple and complex calls (Bonachea & Ryan, 2011). Female tree frogs were also found to approach complex three-component and simpler one-component calls with equal accuracy (Rheinlaender et al., 1979). In the leaf-folding frog, *Afrixalus delicatus*, neither the approach accuracy nor the time to reach the signal were affected by call complexity or number of males present (Backwell & Passmore, 1991).

All the above studies were on acoustically communicating species. This probably reflects the ease with which sound signals can be manipulated and phonotaxis experiments conducted. Visual signals are more difficult since they often require the use of robotic models or video presentations of courtship displays. We know of no study that has examined the accuracy of mate attraction to visual/ movement-based signals that differ in signalling rate, signal complexity or the number of signallers present. Here we use robotics to examine the accuracy and speed of female approaches to signals in the movement-based courtship of a fiddler crab. We test the effect of display rate and choice complexity on the accuracy and speed of female approach. We specifically ask whether the accuracy or duration of female approaches are affected by (1) wave rate, (2) the number of waving claws or (3) the complexity of the choice context (variation in signals and distances).

#### METHODS

We studied a population of the fiddler crab Uca mjoebergi from September to December 2015 at East Point Reserve, Darwin, Australia (12°24'31.89"S, 130°49'49.12"E). Uca mjoebergi is a small fiddler crab (mean  $\pm$  SD carapace width = 10.16  $\pm$  1.43 mm; N = 200) that occurs on the northern coast of Australia. Both males and females defend territories within a large, mixed-sex population. A territory consists of a small area of sediment surface with a central burrow. Males court females from the surface around their burrow by waving their enlarged claw. When a female is ready to mate, she will leave her territory and move through the population of waving males. Males form small clusters (2-6) around the female and, as she moves, males join in or drop out of the cluster. The female visits one of the males in the cluster by walking directly towards him and briefly entering his burrow. She then either leaves the male to continue searching, or she accepts the male and remains underground in his burrow. The chosen male enters the burrow and plugs its entrance with sand; mating occurs within 1 h. The male remains underground with the female, guarding her until she extrudes her eggs onto her pleopods 1–5 days later. The female is then unable to remate, and the male leaves, resealing her in the burrow.

Female preferences were tested using custom-built robotic crabs consisting of a twin-cam motor that moved a small metal arm in a motion exactly mimicking the courtship wave of the species. The motor is remotely controlled to regulate the exact timing of each wave using custom-designed software (for further details of the robotic crabs, see Booksmythe, Detto, & Backwell, 2008; Holman, Kahn, & Backwell, 2014; Reaney, Sims, Sims, Jennions, &

Backwell, 2008). The motor was buried under the testing arena with only the metal arm protruding through the arena floor. The arm had a plaster replica of *U. mjoebergi* claw attached to it. For all trials, we used replicas of the same claw, each measuring 24 mm and painted a yellow that matched the natural claw colour of this species (for details of the claw and paint colour, see Detto, Backwell, Hemmi, & Zeil, 2006). The choice arena was a cleared area of mudflat that was levelled to provide a uniform surface. We placed a video camera (Sony DCR-SR65E) directly above the centre of the arena so that we could film an area of  $45 \times 45$  cm of the choice arena.

Mate-searching females were captured as they wandered through the population of courting males. We housed them individually in shaded cups containing 0.2 cm deep sea water until we used them in the choice trials. For each trial, the female was placed at the release point on one end of the test arena, in a small translucent cup that was remotely lifted once the female had seen three waves of the robotic crabs (for more details, see Booksmythe et al., 2008; Reaney, 2009). A positive response was scored when the female touched (or approached to within 5 cm) a robotic crab arm. Trials were discarded if the female darted, ran to the edge of the area, or remained stationary for >3 min. Each female was retested up to a maximum of three times (each in a different experiment and in a random order), but females were never tested in the same trial more than once. Females were released after they were tested so they could continue mate searching. Females naturally visit numerous males so it is not unreasonable to test them in multiple trials.

We tested 20 females in each of six experiments, and filmed each trial. We analysed the videos using ImageJ (National Institutes of Health, Bethesda, MD, U.S.A.). Trial durations were measured as the time from female release (lifting the translucent cup) until the female reached the robotic claw. We calculated the error angle of each trial by dividing the area between the release point and the robotic crabs into four sections, each 5 cm long. Then, we marked the female's position as she crossed each line and calculated the angle as the difference between (1) the line joining the female with the robotic claw (target axis) and (2) the line joining the female at position *n* with her position at n + 1 (the jump axis between successive lines; Fig. 1). This resulted in three error angles (Fig. 1). To



**Figure 1.** Experimental design with robotic crab (male claw) and female positions (the black circle is the release point and the white circles are the positions when she crossed the lines that divided the arena into four sections of 5 cm). Error angles (1, 2 and 3) were calculated from the angle between (1) a straight line from the female starting position to the robotic crab (dotted connecting lines) and (2) the line between the female starting position and the female position at the next line (solid connecting lines).

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