Smithsonian Tropical Research Institute, Panama and Department of Zoology,
University of the Witwatersrand, Johannesburg

Female Choice in the Synchronously Waving Fiddler Crab *Uca annulipes*

P. R. Y. Backwell, M. D. Jennions, J. H. Christy & N. I. Passmore

Abstract

In the fiddler crab, *Uca annulipes*, males attract receptive females into their burrows by waving their greatly enlarged major claw. We have previously shown that males clustered around a female wave in close synchrony. Females may have a preference for leading signals and synchronised waving may arise as an epiphenomenon of competition between males to signal first. Indeed, the males in clusters that females approach and visit in their burrows are more likely to produce leading waves than are their neighbours. Here we document two other differences in the waving behaviour of visited males and their neighbours. First, visited males complete the downward component of the wave more rapidly than their neighbours. Second, the interval between the end of one wave and the start of the next is shorter for visited males. How can waving be synchronous if visited males wave faster than their neighbours? While only 9% (40/431) of waves by neighbours did not overlap those of the visited male, 22% (110/501) of visited male waves did not overlap the wave of a focal neighbour (111 visited male-neighbour dyads). Hence, while overlapping waves are nearly synchronous, visited males produce additional, 'nonoverlapping' waves that result in a higher wave rate than that of their neighbours.

Corresponding author: P. R. Y. Backwell, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002–0948, USA. E-mail: backwelp@naos.si.edu

Introduction

Synchronous signalling for sexual advertisement has been documented in crickets, grasshoppers, fireflies and frogs (reviewed by Greenfield 1994), all of which use either auditory or bioluminescent signals. Recently, we reported the first case of synchronous production of an ordinary visual courtship signal based on reflected light (Backwell et al. 1998). We showed that male fiddler crabs, *Uca*

annulipes, cluster around a receptive female and wave their greatly enlarged cheliped synchronously. Clusters consist of 2–6 males. The female approaches and enters the burrow ('visits') of one male in the cluster. Her decision to stay in the burrow, mate and breed depends primarily on physical features of the burrow (Backwell & Passmore 1996). In Okinawa, Japan, the closely related species, *U. perplexa*, also waves synchronously in a comparable signalling context (J. Christy, pers. obs.; M. Murai, pers. comm.).

Most hypotheses to explain synchronous signalling are based on by-product mutualism (reviewed by Dugatkin 1997) in which males cooperate to signal synchronously because synchrony benefits each signaller. None of these hypotheses provide a plausible explanation for synchrony in *U. annulipes*. Greenfield & Roizen (1993) provide an alternative explanation based on competition rather than cooperation between signallers. If females prefer leading signals, then game theory analysis shows that synchrony is a by-product of an evolutionary stable strategy in which males compete to signal first. This explanation is consistent with our observations of *U. annulipes*. We found that females visited the male in a cluster that produced more leading waves than his neighbours (Backwell et al. 1998). This correlation between leadership and attractiveness could be the result of a female preference for leading signals or a preference for some other trait that is correlated with leadership.

Here we report that attractiveness is correlated with three other aspects of male courtship behaviour. We review the male traits that correlate with mating success and discuss which are most likely to be used by females during mate choice, and the implications of preferences based on these traits for the evolution of synchronous courtship signalling.

Methods

We studied a population of the fiddler crab, *Uca annulipes* in the Mangrove Conservation Area of Durban Harbour, South Africa during the summer of 1993. We worked on a 60×40 m intertidal mudflat. For additional information on breeding behaviour see Backwell & Passmore (1996) and Jennions & Backwell (1996, 1998). We used a Panasonic M-7 video camera to film wandering females as they moved across the mudflat surface, through the population of courting males. The recording speed was 25 frames per second, giving a measurement accuracy of 0.04 s. We then numbered each frame individually to allow frame-by-frame analysis. We analysed one male visit per female (n = 45).

At rest, a male holds his flexed cheliped in front with its long axis approximately parallel to the ground. When a male waves, he extends the claw laterally while raising it so that the claw tip swings up and the long axis passes through the perpendicular position. He then lowers and flexes the claw to its starting position. For each male within a synchronously waving cluster, we noted the frame number at: (a) the start of a wave, when the claw began the up-swing; (b) the peak, when the claw tip was at its highest point; and (c) the end, when the claw had returned to the resting position. We recorded these values for all waves given by all males

from the time the female initiated movement towards the males, until the final wave by the male she visited before he descended into his burrow. We then calculated: (1) the duration of the wave up-swing (start to peak); (2) the duration of the wave down-swing (peak to end); (3) the interwave interval. Inter-wave or intercall interval is usually defined as the duration between the onset of successive advertisement signals (e.g. Jennions et al. 1995). This value could, however, be confounded with the actual duration of the signal. To ensure statistical independence of our three measurements, we defined the interwave interval as the time between the end of one wave and the start of the next.

Statistical analyses are based on paired tests with each cluster of males providing one comparison (n = 45). We used Wilcoxon's matched-pairs test to compare the mean up-swing duration, down-swing duration and interwave interval of the visited male with the mean value per wave for all the neighbouring, nonvisited males. Differences between visited and nonvisited males might result from changes in signalling by visited males as the female approaches. Such changes would be the result, rather than basis for, female choice. It is not possible to measure waving before the female initiates her approach since males only begin waving synchronously once a female is approaching. We therefore repeated the above analyses only using values from the first wave and first interwave interval of each male. We also tested whether the magnitude of the measured wave variables changed during the female approach by calculating the correlation between each variable and the order of each wave (1, 2, 3, ..., n) for each male separately, but excluding males that gave less than six waves. We tested whether the mean correlation coefficient differed significantly from zero (n = 18 clusters) using one-sample t-tests of Fisher's Z-transformed correlation coefficients. We then tested whether the correlation coefficient of the visited male differed from the mean correlation coefficients of his neighbours using a Wilcoxon's matched-pairs test (n = 18 clusters).

We investigated differences in the timing of wave production by pairing the 45 visited males with each of the nonvisited males in their cluster to create 111 visited male-neighbouring male dyads. For each dyad, we classified waves as either overlapping or nonoverlapping. We defined a pair of waves as overlapping whenever the onset of one wave occurred during wave production (up-swing or down-swing) by the other male. We then tested whether visited and nonvisited males differed in the mean number of nonoverlapping waves they produced per dyad (Wilcoxon matched-pairs test, n = 45 clusters).

In total, we made 10 comparisons between visited and neighbouring male waving behaviour. We therefore corrected these probabilities using the Bonferroni correction (p critical = 0.05/10 = 0.005). We also carried out six one-sample t-tests, and therefore corrected the associated probabilities so that p critical = 0.0083 (0.05/6). Unless otherwise stated, all tests are two-tailed, and the alpha level of significance is set at p = 0.05.

Results

For the purpose of our analysis, the 45 visited males produced a total of 501 waves and the 111 neighbouring males produced 431 waves. There was no difference

in the duration of the wave up-swing between visited and nonvisited males. Visited males, however, produced waves with significantly shorter down-swings as well as significantly shorter interwave intervals. The results were almost identical regardless of whether only the value for the first wave or the mean value for all waves per male were used (Table 1).

Based on counts from the 111 male dyads, there were 782 overlapping waves (391 wave-pairs) by visited and nonvisited males. There were also 150 non-overlapping waves. Of these, 110 were produced by the 45 visited males and only 40 by the 111 nonvisited males. Visited males gave significantly more nonoverlapping waves than their neighbours (Table 1). In sum, 91% of neighbours' waves overlapped with those of the visited male (n = 391 of 431 neighbours' waves); while only 78% of the visited males waves overlapped with that of a given neighbour, when tallied on a dyad by dyad basis (n = 391 of 501).

Analysis of the temporal sequence of waving showed that none of the temporal correlations for the three wave parameters had a mean significantly different from zero for either visited or neighbouring males (one-sample t-tests, all n = 18, all p > 0.05). The single exception was the wave up-swing of visited males (t = 2.93, n = 18, p = 0.009) which decreased with time. However, this result is not significant when the Bonferroni correction for multiple comparisons is made. Examination of the magnitude of the temporal correlations for visited and neighbouring males showed that only interwave interval differed (p = 0.020, Table 1). Again, however, this result is not significant if the necessary Bonferoni correction is made.

Discussion

Temporal Trends

Differences in the wave parameters between visited and nonvisited males might result from changes in signalling by visited males as the female approaches. Such changes would be a result, rather than a basis for, female choice. Studies of other species have shown that males sometimes alter their signalling during or following female approaches (Collins 1994; reed frogs, *Hyperolius marmoratus*, Backwell, pers. obs.). We found that male *Uca annulipes* do not substantially change their waving behaviour during female approaches.

There was a tendency for visited males to decrease their wave up-swing duration as the female approached. However, neither the temporal correlations nor the absolute values of up-swing duration differed significantly between visited and neighbouring males. We therefore conclude that wave up-swing duration (the only parameter which may be affected by the female approach) is unlikely to be a cue for female choice in *U. annulipes*. Even so, to be conservative, we subsequently controlled for slight differences in the rate of temporal change in courtship between visited and neighbouring males by repeating our analyses using only the first wave of each male.

Differences between Visited and Neighbouring Males

Visited males produced waves with faster down-swings than the waves of neighbouring males. The interval between successive waves of visited males was

Table 1: Wave characteristics of visited and neighbouring males (n = 45 clusters of males). Temporal correlations (n = 18 clusters) All values are presented as $\bar{x} \pm$ SD, p-values are from Wilcoxon's matched-pairs tests

Characteristic	Using all waves				First wave only			
	Visited male	Neighbours	Z	p	Visited male	Neighbours	Z	p
Wave up-swing (s)	0.29 ± 0.07	0.30 ± 0.06	1.60	0.11	0.30 ± 0.10	0.29 ± 0.08	0.15	0.88
Wave down swing (s)	0.30 ± 0.07	0.35 ± 0.10	3.75	<0.001*	0.33 ± 0.14	0.38 ± 0.13	2.85	0.004
Inter-wave interval (s)	0.94 ± 0.24	1.47 ± 0.67	5.19	<0.001*	1.05 ± 0.50	1.54 ± 0.74	3.77	<0.001*
No. of non-overlapping waves (per dyad)	0.97 ± 1.00	0.37 ± 0.78	3.77	<0.001*				
Temporal correlation for wave up-swing (r_s)	−0.28 ± 0.41	−0.02 ± 0.35	1.68	0.094				
Temporal correlation for wave down-swing (r_s)	−0.20 ± 0.50	0.11 ± 0.41	1.85	0.064				
Temporal correlation for interwave interval (r_s)	−0.21 ± 0.49	0.10 ± 0.46	2.33	0.020				

* p < 0.05 with Bonferroni correction.

also less than that for neighbouring males. These differences were detected in the analysis based only on first waves and using the mean values from all waves in the sequence (Table 1). Previous work indicates that mate choice in *U. annulipes* results from responses to several cues. Mate choice is a two-stage process in which a female's decision to stay or leave a visited burrow depends primarily on its physical features (Backwell & Passmore 1996). Additionally, at least five male traits potentially increase the initial probability that a male is visited by a female: (1) larger male claw size (Backwell & Passmore 1996); (2) greater production of leading waves (Backwell et al. 1998); (3) faster down-sweeps (this study); (4) shorter interwave interval (this study); and (5) more 'asynchronous', nonoverlapping waves (this study). We can not conclusively state which of these traits are actual cues used during female mate choice because the evidence is purely correlational. As currently understood, however, only a preference for leading signals can lead to the evolution of synchronous signalling. Hence, it seems likely that wave leadership *is* one of the traits by which females choose mates.

There is no general explanation why females might prefer leading signals. For sound or bioluminescent signals, proximate explanations are based on sensory and neurological constraints that make it difficult or impossible to perceive the second of two successive signals if this is emitted during the refractory period following the first (Greenfield 1994). Whether the same explanation can also account for a preference for leading signals in ordinary visual systems remains to be seen. At the adaptive, functional level of explanation, however, it is intriguing that leadership correlates with several male phenotypic traits that are usually taken to be indicators of quality (male size, speed of movement and display rate). This fits with the prediction by Sheridan et al. (1994) that a preference for leading signals will result in a preference for males that maintain higher signalling rates. Even if a preference for leading signals originated in a perceptual bias that did not specifically evolve for adaptive mate choice, the fitness effects on females or offspring of choice of a high quality mate may now maintain the preference (Backwell et al. 1995).

Finally, one misunderstanding that may arise from these results is how waves can be produced with such a high degree of synchrony when the visited male has a higher wave rate than his neighbours. In our earlier study, synchrony was measured in relation to waving by the visited male (Backwell et al. 1998). We showed that neighbouring males mainly produce waves in very close synchrony with those of the visited male. From the visited male's perspective, the situation is slightly different. Although the majority of his waves are synchronised with those of neighbours, he also produces 'extra' waves that either do not overlap any of his neighbours' waves, or are in synchrony with only some of his neighbours' waves. These 'extra' waves result in a shorter mean interwave interval for visited males, hence a higher wave rate, as well as the production of a greater number of non-overlapping, and therefore asynchronous, waves. Although the production of extra waves can not explain the evolution of synchrony, it does provide a cue that may be particularly conspicuous to females approaching a cluster of males. Solitary, nonoverlapping waves may stand out prominently against a general background of synchronous signalling. Once males had evolved a mechanism that generated

synchronous waving, females could use nonoverlapping waves as a cue for mate choice rather than simultaneously assessing the wave rates of several males.

Acknowledgements

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