ORIGINAL ARTICLE

Patricia Backwell · Michael Jennions · Keiji Wada ·
Minoru Murai · John Christy

Synchronous waving in two species of fiddler crabs

Abstract In the fiddler crabs *Uca saltitanta* and *Uca perplexa*, males attract mates by waving their enlarged claws. We show that in both species waving is closely synchronised between neighbouring males in clusters, both in the presence of mate-searching females and in their absence. Wandering females visit those males in the cluster that produce more waves at faster wave rates. In *U. perplexa*, they also selectively visit those males that produce the greatest number of leading waves. Synchronous waving may be the result of a precedence effect causing male competition to produce leading signals.

Introduction

Species with synchronised courtship signals are uncommon yet they occur in at least three phylogenetically distinct groups, each of which uses a different channel of communication: auditory communication in katydids (Greenfield

P. Backwell · M. Jennions · M. Murai
Tropical Biosphere Research Centre,
University of the Ryukyus,
4322 Sesoko, Motobu,
Okinawa 905-02, Japan

P. Backwell (✉) · M. Jennions
School of Botany and Zoology,
Australian National University,
Canberra ACT 0200, Australia
e-mail: pat.backwell@anu.edu.au
Tel.: +61-2-61255481
Fax: +61-2-61255573

K. Wada
Department of Biological Sciences,
Nara Women's University,
Nara 630-8506, Japan

J. Christy
Smithsonian Tropical Research Institute,
Apartado 2072,
Balboa, Republic of Panama

1994), bioluminescent communication in fireflies (Hanson et al. 1971; Hanson 1978) and visual communication in two distantly related species of ocypodid crabs (Aizawa 1998; Backwell et al. 1998). Synchrony must have evolved several times. Early explanations of signal synchrony were based on cooperation between signallers (see Dugatkin 1997), but Greenfield and Roizen (1993) showed that competition was a more likely explanation for the synchrony found in mate attraction contexts. Males may compete to signal first due to the precedence effect: a commonly reported phenomenon in which receivers (females) are more responsive to the leading signal of a pair. The competition between males to signal before their neighbours could lead to synchrony as an epiphenomenon.

In all taxa, synchrony is probably produced by a phase delay mechanism (for a review, see Greenfield 1994; Aizawa 1998; Klump and Gerhard 1992) in which males delay their signal if they perceive a neighbour's signal during a specified period. The delay is slightly shorter than the male's endogenous signalling period, resulting in his following signal being produced simultaneously with or slightly ahead of the next signal of the neighbour (see Greenfield 1994).

The courtship synchrony found in ocypodid crabs is of particular interest because it is unclear why females prefer leading signals. In bioluminescent and auditory channels of communication, simultaneous signals may jam or mask each other (Greenfield 1994), so females may prefer leading signals because they are more easily perceived. In crabs, however, provided that signallers are not aligned with the receiver, simultaneous waves from two or more signallers do not mask or jam each other and are probably both equally perceptible. The precedence effect is likely to have arisen for a different reason in these animals. In the synchronously waving fiddler crab *Uca annulipes*, signal leadership correlates with several male phenotypic traits that are usually taken as indicators of quality: male size, speed of movement and display rate (Backwell et al. 1999). In this species, the female preference for leadership may have evolved for choice of a high quality mate.

Table 1 Comparison of inter-wave intervals (iwi) and synchrony during waving with and without females present in *U. saltitanta* and *U. perplexa*

	U. saltitanta		*U. perplexa*	
	Females present	Females absent	Females present	Females absent
iwi (s) average ±SD (*n*)	1.12±0.58 (608)	1.04±0.54 (561)	1.08±1.31 (978)	1.61±1.10 (2545)
t (P)	2.56 (0.01)		−11.34 (< 0.001)	
Alpha (°) average ±SD (*n*)	16.74±41.72 (33)	17.84±31.65 (25)	36.30±71.32 (50)	3.40±35.45 (67)
Rayleigh (*P*)	<0.001	<0.001	<0.001	<0.001
Watson *F (P)*	0.01 (0.92)		7.90 (0.01)	

We have found two other species of fiddler crab that wave in synchrony: *Uca saltitanta* and *Uca perplexa*. The previously documented synchronous fiddler crab (*U. annulipes*) waved only in response to approaching females. Like *U. annulipes*, these two species wave at approaching females, but they also wave when no female is present. This study examines the synchronous waving in *U. saltitanta* and *U. perplexa*. We compare waving in the two contexts (with and without an approaching female). We also compare the waving behaviour of the male visited by the mate-searching female with that of his non-visited neighbours.

Materials and methods

Study species and study site

Both *U. perplexa* and *U. saltitanta* live on intertidal mudflats. Crabs emerge from their burrows to feed and interact socially for about 6 h daily when their habitat is exposed to the air. Males attempt to attract females by repeatedly waving their enlarged claw. Preliminary observations (K. Wada and M. Murai) showed that small groups of neighbouring males tended to wave in synchrony with each other when attracting females to their burrows for mating. On sighting a female, males of both species move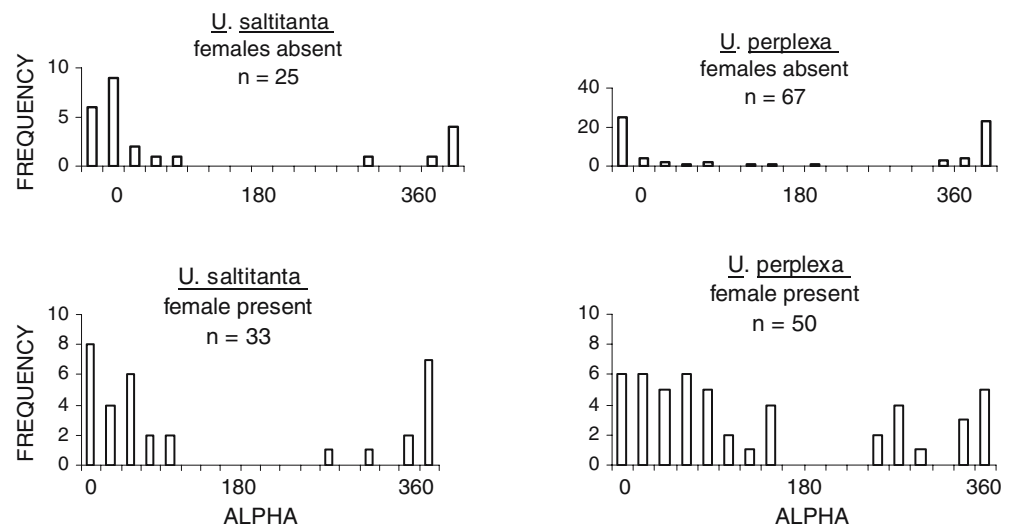 towards her and court vigorously resulting in a loose group of males simultaneously courting a single female. As the female moves across the mud flat, males behind her drop out of the group and males in front of her join in. Females visit several males before selecting a mate. A visit consists of a brief entry into a male's burrow. After re-emerging, the female continues to move across the mudflat. When she eventually selects a mate, she remains in his burrow; the pair mates underground and she incubates her eggs in the male's burrow (Crane 1975).

We studied a population of *U. saltitanta* on the west bank of the Pacific entrance to the Panama Canal in the Republic of Panama and a population of *U. perplexa* at the Okukubi River mouth on the Pacific Coast of Okinawa, Japan. For both species, data were collected during diurnal low tides (*U. saltitanta*, September to November 1999; *U. perplexa*, May to August 2000).

Video recording and analysis

We videotaped groups of males (two to five males per group) waving in the absence of females (*U. saltitanta*, *n*=25; *U. perplexa*, *n*=67). We also followed mate-searching females as they moved through the population and recorded a group of waving males (two to six males per group) during a single visit for each female (*U. saltitanta*, *n*=33; *U. perplexa*, *n*=51). Recordings were made for 2–

Fig. 1 Per group alphas for waving in the presence and absence of females in *U. saltitanta* and *U. perplexa*

Table 2 Comparison between the visited males and their neighbours in *U. saltitanta* and *U. perplexa*

		U. saltitanta		*U. perplexa*	
		Visited male	Neighbours	Visited male	Neighbours
Number of waves	Average±SD (*n*)	8.36±2.10 (33)	7.19±2.52 (59)	7.98±3.97 (51)	5.79±3.36 (130)
	t (P)	2.4 (0.02)		3.49 (<0.001)	
Inter-wave interval (s)	Average±SD (*n*)	1.06±0.56 (243)	1.16±0.59 (365) (361)	0.86±0.87	1.20±1.49 (617)
	t (P)	−2.16 (0.03)		−4.50 (<0.001)	
Wave duration (s)	Average±SD (*n*)	0.28±1.01 (276)	0.28±1.10 (424)	0.42±0.29 (412)	0.44±0.29 (747)
	t (P)	1.06 (0.29)		−1.16 (0.28)	
Number of leading waves	Average±SD (*n*)	2.12±1.34 (59)	2.09±1.57 (59)	2.22±1.44 (130)	1.59±1.39 (130)
	t (P)	0.13 (0.90)		3.61 (<0.001)	
Number of non-overlapping waves	Average±SD (*n*)	3.34±1.62(59)	2.34±1.65 (59)	4.16±3.39 (130)	1.72±1.92 (130)
	t (P)	3.33 (<0.001)		7.24 (<0.001)	

Each synchronous group contributed 6–24 data points

5 min for each group. We documented the timing (start and end) of each wave of each male in each group (0.03-s precision) using frame-by-frame video analysis.

For each group of filmed males (both with and without females present), we calculated the degree of synchrony. To do this, we identified the target male in each group as the one with the fastest wave rate (shortest mean inter-wave interval). We defined a wave cycle as the interval between the onset of successive waves of the target male (wave cycle duration=T_t). Each wave of each of the neighbours was then assigned to the wave cycle of the target male in which it began. We calculated the difference in the onset times of the target male (t_t) and the neighbouring male (t_n) and the phase angle, $\alpha=[(t_n-t_t)/T_t]\times360°$. The phase angle is a measure of synchrony: if $\alpha=0°$ or 360°, the waves of the neighbour and the target male are in perfect synchrony; if $\alpha=180°$, waves are perfectly alternating. Using circular statistics we calculated the mean α per group of waving males and tested whether they were uniformly distributed using Rayleigh's test. We compared the degree of synchrony in the two waving contexts (with and without an approaching female) by comparing the mean α per group using Watson's *F* test. For each species, we also compared the wave rates of males in the two contexts. To eliminate the effect of wave duration, we measured wave rate as the mean interval between the end of one wave and the start of the next.

In the groups with female visits, we compared the waving behaviour of the visited male with that of his non-visited neighbours. We compared the number of waves given, the wave duration and the inter-wave interval (the interval from the end of one wave to the start of the next). We also compared the number of leading waves given by the visited and the neighbouring males. Leadership was determined for overlapping waves only (i.e. those in which the onset of one of the male's waves occurred during the production of a wave by another male). The leader was the male whose wave started earliest. Finally, we compared the number of non-overlapping waves given by visited and neighbouring males.

Results

Comparison of waving with and without a female present

U. saltitanta males waved synchronously whether or not a female was present (Table 1, Fig. 1). There was no difference in the degree of synchrony in these two contexts (Table 1). *U. perplexa* males also waved in synchrony in both contexts (Table 1, Fig. 1). However, synchrony in this species was less precise when a female was present (Table 1). In *U. saltitanta*, males decreased their wave rates when a mate-searching female was present (Table 1). In *U. perplexa*, they dramatically increased their wave rate when a female was present (Table 1).

Comparison between visited and neighbouring males

In both species, the males that were visited by females waved at a faster rate than did their non-visited neighbours in that they produced more waves at a faster wave rate (Table 2). The duration of each wave did not differ between visited and non-visited males in either species. In *U. saltitanta*, visited and neighbouring males did not differ in the number of leading waves they produced; in *U. perplexa*, visited males produced more leading waves than their neighbours. In both species, visited males produced more non-overlapping waves than their neighbours (Table 2).

Discussion

Waving in *U. saltitanta* and *U. perplexa* was synchronous, both when mate-searching females were present and absent. In *U. saltitanta*, there was no difference in the level of synchrony in these two contexts. In *U. perplexa*, however, synchrony became less precise when mate-searching females were present. This may be due to an increase in wave rate. Unlike *U. saltitanta*, male *U. perplexa* sub-

stantially increased their wave rates when they detected a mate-searching female. It is likely that some males were unable to wave at such a high rate and many of their waves were therefore given out of synchrony. In *U. saltitanta*, the slight decrease in wave rate when females were detected may have meant that all males were able to continue waving synchronously.

If synchrony is the result of male–male competition to attract mates (for a review, see Greenfield and Roizen 1993; Sheridan et al. 1994), why do males wave synchronously in the absence of mate-searching females? Waving may be both a long- and short-distance mate attraction signal in these species. If females are attracted to synchronous groups from a distance, males would benefit by waving synchronously even when they do not detect wandering females. Another possible reason is that synchrony functions in inter-male communication as well as mate attraction. A male's ability to produce leading waves may indicate his 'quality' to females as well as to other males (for a review, see Pope 2000). This may result in neighbouring males less often challenging leaders in border disputes or burrowless males less often attempting to usurp the burrows of leading signallers.

In both species, females visited males that produced more waves at faster wave rates than did their non-visited neighbours. Males were able to increase their wave number and wave rate but still stayed synchronous with their neighbours because they gave additional, non-overlapping waves between those given in synchrony with their neighbours. By matching their neighbour's waves with synchronously produced signals and by adding additional waves between successive synchronous signals, preferred males both stayed in synchrony and increased their wave rates. This same effect was found in the synchronous fiddler *U. annulipes* (Backwell et al. 1999). Display rate and intensity are commonly taken as indicators of male quality (Anderson 1994). Females of these species may have a mating preference for signal intensity and display rate.

In *U. perplexa*, visited males produced a greater number of leading waves than did their non-visited neighbours. This result, also found in the synchronous fiddler *U. annulipes* (Backwell et al. 1998), is consistent with a precedence effect in which females have a preference for leading signals. This preference is thought to drive the evolution of synchrony (Greenfield and Roizen 1993). In *U. saltitanta*, visited and non-visited males interestingly did not differ in the number of leading waves they produced. This result, however, is not inconsistent with a precedence effect. If females have a strong preference for leading signals, there would be powerful selection on males

to lead. Strong inter-male competition may result in synchrony that is so precise that no male stands out as a leader or maintains leadership for more than a few waves.

Future research on signal synchrony in fiddler crabs will need to asses whether females do indeed have a preference for leading signals. An alternative explanation of synchrony that does not involve a preference for leadership is call matching (Gerhardt et al. 2000). Synchrony may allow males to adjust their signalling effort so that they are at least as attractive as their rivals. This would effectively prevent females from expressing their preference for faster wave rates.

References

Aizawa N (1998) Synchronous waving in an ocypodid crab, *Ilyoplaxpusilla*: analyses of response patterns to video and real crabs. Mar Biol 131:523–532

Anderson M (1994) Sexual selection. Princeton University Press, Princeton, NJ

Backwell PRY, Jennions MD, Passmore NI, Christy JH (1998) Synchronised courtship in a fiddler crab. Nature 391:31–32

Backwell PRY, Jennions MD, Christy JH, Passmore NI (1999) Female choice in a synchronously waving fiddler crab, *Uca annulipes*. Ethology 10:415–421

Crane J (1975) Fiddler crabs of the world, Ocypodidae, genus *Uca*. Princeton University Press, Princeton

Dugatkin LA (1997) Cooperation in animals. Oxford University Press, Oxford

Gerhardt HG, Roberts JD, Bee MA, Schwartz JJ (2000) Call matching in the quacking frog (*Criniageorgiana*). Behav Ecol Sociobiol 48:243–251

Greenfield MD (1994) Co-operation and conflict in the evolution of signal interactions. Ann Rev Ecol Syst 25:97–126

Greenfield MD, Roizen I (1993) Katydid synchronous chorusing is an evolutionary stable outcome of female choice. Nature 364:618–620

Hanson FE (1978) Comparative studies of firefly pacemakers. Fed Proc 37:2158–2164

Hanson FE, Case JF, Buck J, Buck E (1971) Synchrony and flash entrainment in a New Guinea firefly. Science 174:161–164

Klump GM, Gerhard HC (1992) Mechanisms and function of call timing in male–male interactions in frogs. In: McGregor PK (ed) Playback studies of animal communication. Plenum, NY, pp 153–174

Pope D (2000) Video playback experiments testing the function of claw waving in the sand fiddler crab. Behaviour 137:1349–1360

Sheridan LA, Brookes M, Pomiankowski A (1994) Jamming for sex. Curr Biol 3:896–897