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A conspicuous courtship signal in the fiddler crab *Uca perplexa*: female choice based on display structure

Abstract The fiddler crab *Uca perplexa* has a conspicuous male courtship signal that is directed at females to attract them to the male's burrow for mating. The signal involves waving the unflexed large claw up and down. To determine whether the spatiotemporal structure of the wave is under selection by female choice, we examined whether females had a preference for any particular features of the wave. Females respond to a waving display by either visiting the male's burrow entrance or by electing to pass without visiting the burrow. We filmed mate-searching females and the waving males that they visited or passed. We documented the wave structure of these males using frame-by-frame analysis. Males produce a two-part wave with component A preceding component B. Both components have an upstroke, a pause at the apex and a downstroke. The tip of the claw was raised much higher in B than in A. Visited males had a shorter delay between the two wave components than did males that the females passed without visiting. Visited males also produced component B waves that had a slower upstroke than those of passed males. There was a significant correlation between the relative height of the raised claw and the duration of the upstroke of component B. Females were selecting males that raised their major claw to the highest position (two to three times as high as the carapace width). Passed males brought down their major claw earlier and from a lower position than did visited males. The data suggests that wave structure has evolved through female choice. Male display rate and body size were not female choice cues. An earlier study showed that display duration was also not used by females in selecting mates.

Keywords Courtship signal · Claw waving · Female choice · Fiddler crab

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Introduction

Based on sexual conflict and signal evolution theory, large conspicuous signals will evolve when the degree of conflict of interest between a signaler and a receiver is large (Krebs and Dawkins 1984). Between prey and predator, among sexual rivals or between a parasite and its host, individuals face conflicting interests (Zahavi 1977). Warning signals given by a prey species toward a predator or threat displays exchanged among rivals are some examples of conspicuous signal exchanges (Clutton-Brock et al. 1982; FitzGibbon and Fanshawe 1988; Cresswell 1994). Clutton-Brock et al. (1982) argued that the roaring signal by red deer stags provides a sensitive criterion for assessing each other's fighting ability. Stotting is an honest signal that informs predators of a Thomson's gazelle's ability to outrun them (FitzGibbon and Fanshawe 1988). The ability to sing while being chased is a measure of the stamina of the skylark (Cresswell 1994).

Visual displays of birds of paradise (Frith and Beehler 1998) and peacocks (Petrie et al. 1991) and claw waving displays of fiddler crabs (Crane 1975) are also large and conspicuous signals that function in courtship or mate attraction. These signals are combined with structures like plumes or crests that affect the behavior of another animal (Manning and Dawkins 1998). Male ornamentation of visually displaying species supports its role as an amplifier of a visual display (McClintock and Uetz 1996; Hebets and Uetz 1999).

Females use courtship for mate assessment (Bradbury and Vehrencamp 1998). In visual courtship behaviors, male display rate (Bischoff et al. 1985; Gibson and Bradbury 1985; Kennedy et al. 1987; Knapp and Kovach 1991;

Karino 1995; Vinnedge and Verrell 1998; Backwell et al. 1999; Kodric-Brown and Nicoletto 2001) and duration (McDonald 1989) are the most common sexual traits that are selected by female choice (Andersson 1994) and were well studied. More subtle spatiotemporal aspects of the courtship displays, such as the zigzag dance in three-spined stickleback, *Gasterosteus aculeatus* (Tinbergen 1951), and the alternate wing clap in Victoria's riflebirds, *Ptiloris victoriae* (Frith and Beehler 1998), have received less attention. Studies focusing on shapes or forms of body part movement performed by males in front of females are needed. In most cases, we do not even know whether they have evolved through female choice. In fiddler crabs, studies of waving display were focused on the differences between species (Salmon 1965, 1967; Salmon et al. 1979; von Hagen 1983) and on other course-scale features such as wave rate and leadership (Backwell et al. 1998, 1999). There are no studies that examine the finer-scaled spatiotemporal wave structure to determine whether female choice shapes these aspects of the signal design.

Fiddler crabs live in individual burrows in mixed sex colonies on intertidal mudflats. They are surface active for 6–8 h around the diurnal low tide. During this time they feed, court, and mate. Males have one greatly enlarged major claw and one small feeding claw. They wave their major claw to attract females for mating and to threaten and fight other males. Mate-searching females move through the population of displaying males, responding to some of the waving males by approaching them. When a male is approached, he starts high intensity waving in which he unflexes his major claw and raises and lowers it several times. The major claw, at its maximum relative weight, reaches almost half the total weight of the crab (Crane 1975). When the major claw is raised during a waving display, it appears above the receiver crab's visual horizon (Land and Layne 1995). This makes it a very conspicuous signal for female crabs. As the female nears him, the male flexes his claw and descends into his burrow. The female follows him underground and the male plugs the burrow entrance with sand. Mating occurs underground. After copulation, the pair spends 1–5 days underground until the female ovulates (Nakasone and Murai 1998).

Courtship claw waving of male fiddler crabs is a conspicuous signal and is more flamboyant than the courtship signals of many other species (Manning and Dawkins 1998). Our objective was to determine if female choice has played a part in shaping this conspicuous signal both in the course-scale aspects, such as wave rate and duration, and in the finer-scaled spatiotemporal structure of the waves.

Materials and methods

We studied *Uca perplexa* on an intertidal mudflat on the Okukubi River, Okinawa, Japan. Males of this species produce background waving when they attract females from a distance and courtship waving at closely approaching females. Observations of courtship waving were made from May to August 2000–2002. We studied medium brachychelous (original clawed) males of 14–16 mm carapace width (CW) and medium females of 11.5–13.5 mm CW in the size range of mated males and females (male CW 11.8–18.6 mm and female CW 9.7–15.0 mm; Nakasone and Murai 1998). We carefully followed mate-searching females as they moved between courting and synchronously waving males. By moving slowly it is possible to avoid startling the female or surrounding males (see Backwell and Passmore 1996). When an approaching female to a male is at a mean distance of 8.9±0.45 cm from his burrow, he descends into his burrow (Nakasone and Murai 1998). The female then either followed the male and touched his burrow entrance with her walking legs (visited him) or passed by the male without touching his burrow entrance (passed him). Once the female made the decision to accept a male as her mate, she followed the selected male into his burrow and remained underground where mating and incubation took place. We used a video camera with 16× zoom lens and 1.6× extender set on a tripod to film waving of visited and passed males. We filmed the entire sequence of a female approach and the associated male waving from before to after the female visited or passed the focal male. Active courtship waving occurs for a relatively short period (up to 3.5 s) from the time that the female starts to approach the male to the time at which he descends into his burrow. This brief but intense period of active courtship occurs when the female is extremely close to the male, eliminating the need to control for differences in the distance between the signaler and receiver. The camera lens was 20 cm above the sediment because this is the lowest we could position it without having to bury it in the sediment. Although it would be preferable to position the camera at the height of the crab's eyes, the disturbance caused by excavating the sediment precludes this option. We moved the camera to track the female as she moved between courting males. Due to the relatively predictable path of the female, it is often possible to position the camera behind the female and to film the focal male directly from the front. The camera was usually 1.5 m from the crabs. The recording speed was 30 frames/s, giving a measurement accuracy of 33 ms. The shutter speed was 1/1,000 s. We measured the CW of live males captured after filming. The major claw length was also measured in the year 2002 field season to calculate the relative size of the claw to the CW. We numbered each video frame individually to allow frame-by-frame analysis. We analyzed one visited or passed male per female (the first male in her path). Although males were not marked, we rereleased them into their own territories. We avoided recording the same males by filming at different sites for each new female.

When a male waves, he usually produces a two-part wave with an A and a B component (A-plus-B wave). Component A precedes component B. While there are some similarities in the two components (both have an upstroke, a pause at the apex, and a downstroke), they are obviously distinctive. In B waves, the tip of the major claw was raised much higher than in A and they differed in the duration of the upstroke, the pause, and the downstroke

(see Fig. 2). For each male, we noted the frame number at (1) the start of each component when the claw began the upstroke, (2) the start and end of the apical pause, and (3) the end when the claw had returned to the lower position. These values were recorded for both components of each of the subject's wave for 2–3 s during an interval from the time that he initiated waving toward the female until he descended into his burrow (males wave at approaching females for only 1.9–3.5 s; Murai and Backwell 2005). We then calculated: (1) the duration of the upstroke, (2) the duration of the apical pause, (3) the duration of the downstroke, and (4) the interval between A and B components (from the end of A to the start of B).

The interwave interval (the time from the end of one wave to the start of the next) was calculated. Males sometimes omitted component B following a component A (termed A-only wave). In such cases, the interwave intervals between A-only and the following A-plus-B waves, between A-plus-B and the following A-only waves, and between successive A-only waves were calculated.

We compared the waves of visited and passed males. The A-plus-B wave data that was used for the analysis was from 39 visited males (65 waves in total) and 31 passed males (52 waves in total). We used A-only wave data from 57 visited males (149 waves in total) and 39 passed males (112 waves in total). Waving males flexed their claws producing the B component when the female temporarily stopped moving. They resumed normal waving when the female moved again. We used data for normal waving only, decreasing the sample sizes for the wave category of A-plus-B rather than that of A-only waves.

We measured the relative height of the highest reach of the dactyl tip of the major claw from the surface of the sediment for the B component of A-plus-B waves. We also measured the relative height of the anterolateral angle (the horn-like tip on the front edge of the carapace) on the major claw side of the carapace when the dactyl tip was at the highest reach. The measurement was made by printing a frame in which the dactyl tip reached at highest point in B on a sheet of 210×297-mm print paper. Two vertical lines were drawn from the dactyl tip and the anterolateral angle against a reference line connecting the tips of the front legs of both sides. We measured the distance (H or H') between the intersection of the vertical line and the reference line and the dactyl tip or the anterolateral angle. We also measured the CW on the printed image (W). We calculated the relative height of major claw (H/W) and that of anterolateral angle (H'/W) (Fig. 1). We used data sets from 35 visited and 24 passed males and analyzed one or two measurements for each male (52 and 37 waves in total, respectively).

Durations of upstrokes, apical pauses and downstrokes in the A components of waves and the durations of apical pauses and downstrokes in the B components of A-plus-B waves were not normally distributed. We could not transform them to fit a normal distribution. We therefore used standard nonparametric tests (Kolmogorov–Smirnov tests) to compare durations of upstrokes, apical pauses, and downstrokes of both components and intervals between A
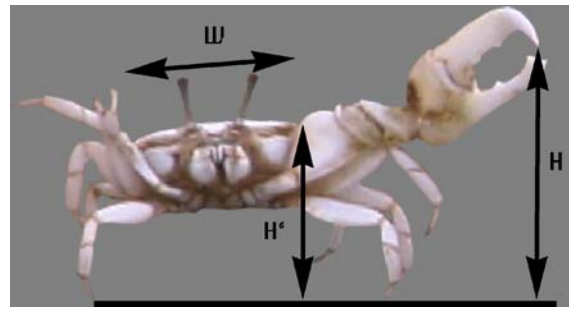

Fig. 1 Method used to measure the height of dactyl tip and anterolateral angle from the ground (H and H'). The height was measured relative to the CW (W). A *straight line* connecting the tips of both front legs shows the reference line

and B components, between visited and passed males. Log transformed values on interwave intervals were normally distributed and had equal variances. We used F tests for comparison of interwave intervals between visited and passed males and Fisher's protected least significant difference (PLSD) for comparison among interwave intervals of each group of males. All values are given as means±SE.

Results

The separate regressions of claw length on CW for 35 visited and 25 passed males do not differ in slope [analysis of covariance (ANCOVA) $F_{1, 56}=0.84$ and $P=0.36$]. The claw length did not differ between visited and passed males when CW is kept constant (ANCOVA $F_{1, 57}=0.05$ and $P=0.83$) and the pooled regression was significant (ANCOVA $F_{1, 57}=285.3$ and $P<0.01$).

Visited ($N=39$) and passed males ($N=31$) did not differ in the duration of the upstroke ($\chi^2=0.37$ and $P>0.99$), apical pause ($\chi^2=3.60$ and $P=0.33$), and downstroke ($\chi^2=2.03$ and $P=0.73$) of the A component of A-plus-B waves (Kolmogorov–Smirnov test). Visited males, however, produced A-plus-B waves with significantly longer upstrokes of the B component than did passed males ($\chi^2=31.16$ and $P<0.01$), although there were no differences in the durations of the apical pauses ($\chi^2=1.02$ and $P>0.99$) and downstrokes ($\chi^2=0.36$ and $P>0.99$) of B components. The interval between A and B components of the wave by visited males was significantly shorter than those for passed males ($\chi^2=7.53$ and $P=0.05$; Fig. 2). Regression of the duration of upstroke of B on CW of visited males was not significant ($F_{1, 35}=0.31$ and $P=0.58$).

There was no significant difference in the duration (ms) of the upstroke, apical pause, and downstroke of A-only waves between visited ($N=57$) and passed ($N=39$) males (upstroke 43.6±1.7 and 42.7±1.8, respectively, $\chi^2=1.08$, and $P>0.99$; apical pause 19.6±1.8 and 21.3±2.1, respectively, $\chi^2=0.97$, and $P>0.99$; and downstroke 53.8±1.9 and 55.1±1.9, respectively, $\chi^2=2.15$, and $P=0.68$).

The interwave interval between successive A-plus-B waves was not different between visited and passed males. When A-only waves were involved, the interwave
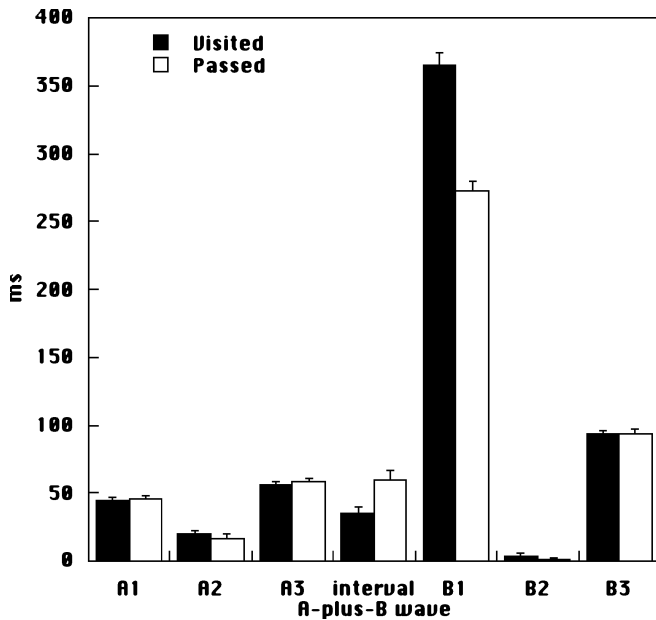
Fig. 2 Durations in millisecond (*X*+SE) of upstroke, apical pause, and downstroke measured in components A and B and the duration of the interval from the end of A to the start of B (A-plus-B wave). Upstroke, apical pause, and downstroke are shown by A1, A2, and A3 for component A and by B1, B2, and B3 for component B, respectively

interval between A-plus-B and the following A-only waves, between A-only and the following A-plus-B waves, and between successive A-only waves were not different between visited and passed males (Table 1).

The interwave interval when one wave was followed by A-only wave was shorter than when followed by A-plus-B wave (Fisher's PLSD *P*=0.01). The interval between successive A-only waves was significantly shorter than the interwave interval when A-plus-B wave was followed by A-only wave (*P*=0.01). The same results were obtained in both visited and passed males (Table 1).

Separate regressions of relative height of the major claw tip on duration of upstroke (B1) of the B component for visited and passed males do not differ in slope (ANCOVA $F_{1, 85}$=0.23 and *P*=0.64). The relative height of the claw tip did not differ between both groups of males when the duration of B1 is kept constant (ANCOVA $F_{1, 86}$=1.90 and *P*=0.17). The pooled regression was significant (ANCOVA $F_{1, 86}$=39.02 and *P*<0.01). Combining the two data sets showed that there was a significant correlation between the relative height and the duration of B1 (*r*=0.68, t_{88}=40.72, and *P*<0.01). This indicated that the males took longer to

raise the major claw relatively higher (Fig. 3). Regression of the relative height of major claw (*H/W*) on CW of visited males was not significant ($F_{1, 50}$=0.02 and *P*=0.89).

The relative heights of the anterolateral angles on the major claw side of the carapace (*H′/W*) were significantly different between visited males and passed males (1.288± 0.018 and 1.203±0.018, respectively, $F_{1, 57}$=10.54, and *P*=0.002). This indicated that visited males raised their body higher than did passed males. The distances between the anterolateral angle and the major claw tip (*H/W−H′/W*) were also significantly different (0.820±0.044 and 0.567± 0.052, respectively, $F_{1, 57}$=13.83, and *P*=0.0005). Therefore, the claw tip (*H/W*) of visited males was raised higher than that of passed males (2.108±0.044 and 1.770±0.048, respectively, $F_{1, 57}$=25.47, and *P*<0.0001). These results were significant at 0.01 when Bonferroni corrections were made.

Discussion

Males that were visited by mate-searching females produced waves that were distinct from those given by males that the females passed without visiting. Visited
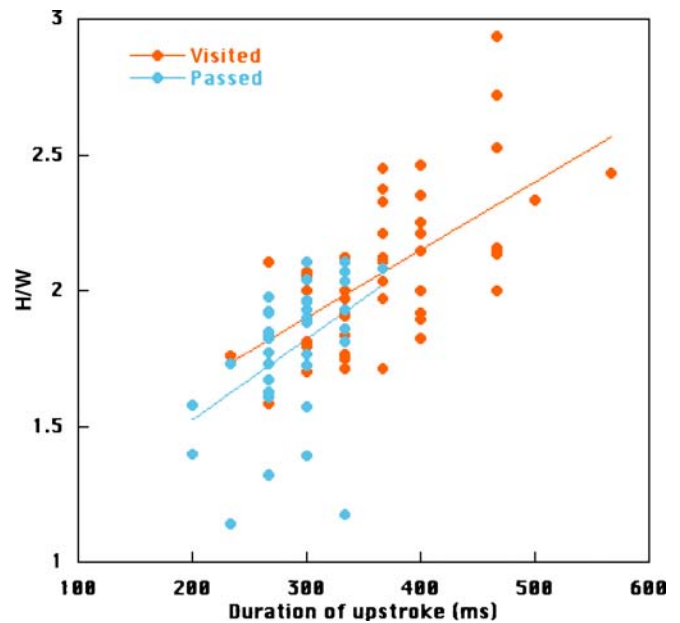

Fig. 3 Relationship between the duration of upstroke (*B1*) of A-plus-B wave in millisecond and the relative height (*H/W*) of the elevated dactyl tip

Table 1 Comparison of interwave interval (IWI) of *X*±SE in millisecond between visited and passed males

IWI between	Visited	Passed	F	df_1, df_2	P value
AB and AB	1,231.4±124.5 (*N*=17)	1,208.9±74.4 (*N*=15)	0.05	1, 30	0.83
A and A	515.4±52.8 (*N*=26)	516.3±48.6 (*N*=21)	0.00	1, 45	0.99
A and AB	1,186.0±152.2 (*N*=19)	1,176.5±100.8 (*N*=17)	0.17	1, 34	0.68
AB and A	834.8±97.4 (*N*=23)	727.8±73.6 (*N*=15)	0.32	1, 36	0.57

AB A-plus-B wave, *A* A-only wave, *N* number of males

males produced waves with shorter intervals between A and B components of A-plus-B waves than did passed males. Visited males also produced waves with slower upstrokes than those of passed males, which means that females visited males that had their claws elevated for longer periods. Females' decisions to visit or pass a male's burrow depended on the form of the B component but not on the form of the A component in A-plus-B waves or A-only waves.

There was a clear relationship between the relative height of elevated claw and the duration of upstroke of B components in the A-plus-B wave. As the female selected longer upstrokes, they were selecting males that raised their major claw to the highest position (two to three times as high as CW). It also suggests that it takes more time to raise the major claw to that position and that passed males bring down their major claw before reaching it.

The duration of the upstroke (B1) and the relative height (H/W) of component B did not increase with CW. This suggests that the body size is not an important female choice cue. Relative major claw size to CW did not differ between visited and passed males. This eliminated the possibility that males with larger relative claw size can raise their claws to higher position relative to CW than can males with smaller relative claw size and/or that they take more time to raise the major claw.

The interwave interval was not different between visited and passed males. This suggests that the male display rates were not important female choice cue. However, waving in *U. perplexa* is a costly signal (Matsumasa and Murai 2005). Males took a longer time to produce A-plus-B waves than A-only wave. Males that produced A-plus-B waves spent a longer time initiating the next wave (A-only wave) than males that had produced A-only wave. It is possible that B components are more costly to produce than are A components. Visited males took more time to produce B components and raised their major claws to a higher position than did passed males. Males probably varied in their ability to sustain the weight of their major claw in the air. This suggests that more viable males may pay a smaller cost to produce the wave upstroke. If costly signals are reliable with respect to the male quality (Zahavi 1977), the female may preferentially select these signals.

Many animal courtship displays involve the repetition of some specific behavioral action. Why do animals perform an action more than once? The signaler should carry out repetitive display actions for the receiver to estimate the signaler's quality (Payne and Pagel 1997). According to Kruijt and de Vos (1988) who studied the black grouse, *Tetrao tetrix*, females usually require prolonged periods of courtship before they are willing to copulate. Consequently, nonterritorial males have little success in copulating. Signaling by *U. perplexa* was repeated during the amount of time that the female needs for her assessment, according to changing levels of female responsiveness to courtship, but the signaling duration was not a female choice cue (Murai and Backwell 2005).

In *Uca annulipes*, at the start of the mating cycle females selected the larger males of those sampled as mate and they also decided whether to mate with a male based on burrow features (Backwell and Passmore 1996). In another fiddler crab species (*Uca crenulata*) females use burrow diameter as a final mate choice criterion (deRivera 2005). Male size was not a female choice cue in this study. Females use fine-scaled spatiotemporal wave characteristics to decide whether they visit males (Backwell et al. 1999; this study). They may use additional cues (either aspects of the wave or nonwave-related cues) to decide whether they mate with the male. It is evident that multiple criteria are employed for female choice in fiddler crab species.

The flash of a red dewlap of *Anolis* lizards against a green background attracts females from a distance and, at closer range, females select males based on a head bobbing display (Sigmund 1983). In Jackson's widowbird the jump acted as a signal to draw females in from a distance and when she landed in a male's small display court, he stopped jumping and performed tail-quivering displays (Andersson 1989). When males and females are in close proximity, the conspicuousness of courtship signals can be reduced to prevent eavesdropping by predators or mate competitors (Bradbury and Vehrencamp 1998). In fiddler crabs, vision is poor below the crab's horizon (Land and Layne 1995; Zeil and Al-Mutairi 1996). Vision is very good, however, if the object penetrates the horizon line (Land and Layne 1995; Zeil and Al-Mutairi 1996; Christy et al. 2002). A variety of fiddler crab signals such as sand hoods that advertise their burrow entrances, dark styli extending vertically upward from the eyes, and enlarged claw waving are examples of vertical objects that penetrate the crab's horizon line (Zeil and Al-Mutairi 1996). Conspicuous upstroke may be more stimulatory to females because they penetrate the horizon and therefore activate more ommatidia.

Male *U. perplexa* wave at approaching females (courtship signals) and they also produce background waving when they attract females from a distance (mate attraction signals). They produce circular waves for mate attraction. The claw starts from the flexed position and is unflexed outward, then raised and flexed again, and returns to the starting position (Crane 1975). During courtship waving, males always bring down their major claw suddenly from the highest position without flexing. Courtship signals have a shorter downstroke than mate attraction signals (unpublished data). Males may shorten the time spent holding their major claw near the wave apex to decrease the predation risk to themselves and females. Males may, in fact, face a trade-off between female and predator attraction.

Mate-quality signals vary among males, therefore signaling high quality could also be selected (Pfennig 1998). Component B of A-plus-B wave that were produced by visited males were different to those produced by passed males. A components, however, did not differ. This suggests that females use the variation associated with B components for assessing mate quality. Species recognition signals are often highly stereotyped compared with other

signals (Gerhardt 1991). If species recognition signals are given in the mate attraction process (Bradbury and Vehrencamp 1998), it is unlikely that they work in the courtship process. Future research will be needed to determine the function of the A components of the courtship waves.

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