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Claw waving display changes with receiver distance in fiddler crabs, *Uca perplexa*

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Effective communication is critically dependent on the successful transfer of information and, because environmental and social conditions can affect signal transmission, animals should be able to adjust their signals to optimize reliability. We show, apparently for the first time in a movement-based signal, that visual displays are adjusted with respect to the distance of signal receivers. Not only does this show the ability of the fiddler crab to judge distance, but this also shows that signalling is context dependent on surprisingly fine spatial and temporal scales. We elicited courtship behaviour in the crabs with tethered females and simultaneously recorded the displays of males from above and from crab-eye level. As females approached, males increased signal intensity by shortening display duration and altered signal form by reducing the lateral movement component of the waving signal. We suggest that males tune their waving display depending on receiver distance (a) to balance energetic costs with reproductive benefits, (b) to alter the information content of the signal and (c) to avoid signal misinterpretation. Such fine-scale context sensitivity is likely to be far more widespread in animal communication than hitherto recognized from similar signal modifications in auditory communication.

Keywords: claw waving display; communication distance; fiddler crab; movement-based signals; *Uca perplexa*

Animals tune their communication signals according to the levels of environmental noise (e.g. Long & Rosenqvist 1998; Peters et al. 2007) and predation risk (e.g. Manser 2001; Hemmi et al. 2006) and to responses from conspecifics (e.g. Balsby & Dabelsteen 2002; Patricelli et al. 2002). However, relatively little attention has focused on signal modulation relative to receiver distance. Because signals in all sensory modalities attenuate with distance (reviewed in Dusenbery 1992; Bradbury & Vehrencamp 1998), animals may modulate their signals relative to the perceived proximity of the signal receiver. We know that, in everyday life, attracting the attention of a distant person involves gestures and vocalizations different from those used when that person is nearby, yet the few studies on this subject are restricted to changes in the auditory modality. For example, male zebra finches, *Teaniopygia guttata*, increase the amplitude of their courtship vocalizations when communication distance increases (Brumm & Slater 2006), a correlation that is well documented for human speech (e.g. Johnson et al. 1981). Also, several anurans modulate the rate, duration and frequency of vocalizations in a graded manner according to the perceived distance of calling conspecifics (e.g. Wells & Schwartz 1984; Owen & Gordon 2005).

Previous reports have noted and qualitatively described changes in fiddler crab communication displays depending on receiver distance (e.g. Crane 1975; von Hagen 1983; Land & Layne 1995a). However, to our knowledge, the question of how receiver distance affects visual signal design and production has not been addressed in quantitative detail.

Fiddler crabs live in mixed-sex and mixed-age colonies on tropical and temperate mudflats around the world. Males employ conspicuous movement-based visual signals, in which they repeatedly raise and lower their single enlarged claws (Crane 1975). Such displays can be broadcast in the absence of receivers or directed towards individual conspecifics and can function as courtship or territorial signals, depending on the species and context (reviewed in

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Pope 2005). Our study species *Uca perplexa* (Milne Edwards) is an Indo-tropical, broad-fronted species belonging to the subgenus *Celuca* (Rosenberg 2001). Australian populations of *U. perplexa* show predominantly burrow mating; males attract females to their burrows and mating takes place underground. The lateral claw waving display of *U. perplexa* is relatively complex, consisting of the following three sequential stages of movement: a fast lateral unflexing movement, a slow vertical lift and a fast drop of the claw back to resting position (Fig. 1a–c; see also Crane 1975; Murai & Backwell 2006; How et al. 2007). Males broadcast their courtship waving displays in the absence of females and, when a female is present, direct their signals by orienting their front to face the female (*U. pugilator*: Land & Layne 1995b; Nakasone & Murai 1998; *U. perplexa*: Murai & Backwell 2006; How et al. 2007). The choreography of the display is similar to that of many other species of fiddler crab (*U. speciosa* and *U. mordax*: Salmon 1967; *U. pugilator*: Hyatt 1977), but the fine spatio-temporal structure is species specific.

We studied the interaction between visual display structure and receiver distance in *U. perplexa* in the natural environment by inducing courtship interactions between focal males and tethered females while simultaneously recording male lateral claw waving displays and receiver distance.

METHODS

Observations and experiments were conducted in October 2006 in a *U. perplexa* population at Bowling Green Bay, Queensland, Australia (19°23.17′S, 147°06.90′E). The waving behaviour of burrow-owning focal males during experimentally induced courtship interactions was filmed simultaneously from above and from crab-eye level using digital video camcorders (Sony DCR-HC21E PAL MiniDV Handycam). Courtship interactions were induced using a modification of Hemmi & Zeil's (2003a) dummy system consisting of a running line used to drag live tethered female crabs across the mudflat surface towards a focal male's burrow (see also Salmon & Stout 1962; Aspey 1971). The response of the focal male to the approaching tethered female was indistinguishable from courtship responses towards naturally wandering females (Nakasone & Murai 1998; Murai & Backwell 2006; How et al. 2007).

Top-view footage was digitized using modified open-source software (dvgrab) under Linux and down-sampled to 12.5 frames/s (80-ms frame interval) to reduce the amount of data to be processed. The sequences were calibrated and the position of the camera was determined using a checkerboard standard and open-source software developed by Bouguet (2005). We measured carapace width, major claw length and the x–y positions of the focal male and the tethered female frame by frame with an accuracy of ±1 mm using custom-made software (Jan Hemmi, The Australian National University). For the focal male we recorded the following events: the entry into and emergence from the home burrow, the distance from the home burrow, and the frequency and amplitude of lateral claw waves. For each lateral claw wave the maximum extent of the unflexed claw was measured as the angle between claw and body orientation (see Fig. 2c inset).

Crab-eye-level footage was digitized at full temporal resolution of 50 deinterlaced half-frames/s (20-ms frame interval). We determined the x–y positions of the crab's major claw tip, eye closest to the major claw and tips of the walking legs. Data from each sequence were calibrated to a vertical 15-cm ruler at the position of the focal male's home burrow. Crab handedness was normalized by

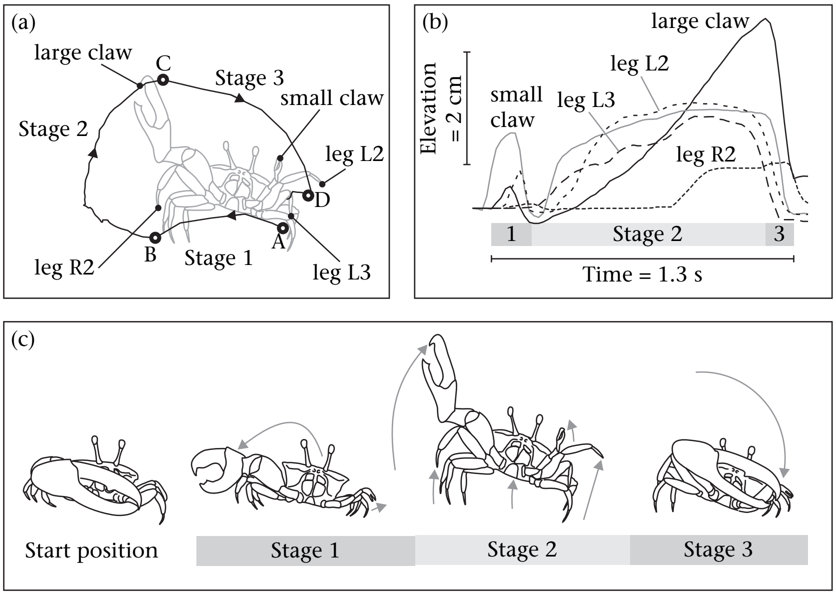

Figure 1. Lateral wave of *Uca perplexa*. (a) Four points used to define the three display stages: A, first movement of the claw; B, end of the initial fast unflexing movement; C, highest point reached by the claw tip; D, end of the fast downward claw sweep. (b) Elevation of five key body parts (illustrated in a) over time during a single lateral wave. (c) Movements during the three stages of the lateral claw waving display: stage 1, both the major and the minor claws are quickly unflexed; stage 2, the major claw is lifted slowly upwards and the body and second ambulatory legs are raised; stage 3, the major claw, body and legs are rapidly dropped back to resting position.

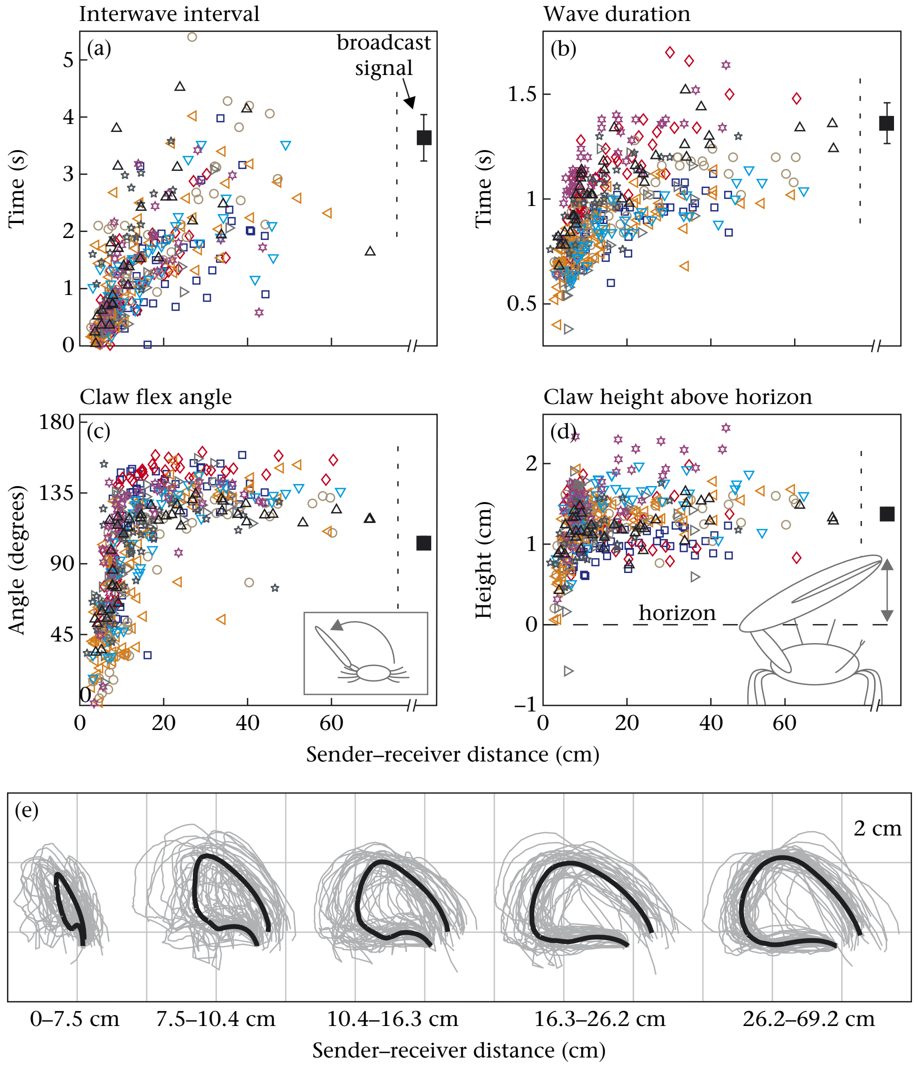

Figure 2. Modulation of signal variables relative to receiver distance. (a) Interwave interval; (b) wave duration; (c) maximum claw flex angle; (d) maximum claw tip height above the horizon. In plots a–d, different symbols identify data from each of the nine focal male crabs. The data point and error bars to the right of the vertical dotted line represent the mean and standard error for broadcast waves. Horizontal dotted line in (d) indicates the visual horizon level, calculated relative to the signaller's eye level at rest. (e) Traces of claw tip paths (grey lines) and the mean shape (black line) for all lateral waves falling within five distance bins ($N = 37$ within each bin). Each claw tip path (grey line) is normalized according to claw size.

horizontally flipping all left-handed crab data. The analysis of claw tip path and speed was restricted to displays performed when the transverse body axis orientation was fronto-parallel to within 10° of the camera's imaging surface. Mean claw tip trajectory was calculated using the eigenshape method (MacLeod 1999). Claw tip speed for the initial phase of the claw waving display (stage 1) was measured as the maximum observed speed, and the speed of the claw uplift phase (stage 2) was measured at a set point three quarters of the way through the phase.

Our analysis was conducted on 1114 lateral waving displays, of which 140 were broadcast (in the absence of a female) and 974 were directed at an approaching tethered female; 208 of these directed signals were performed facing directly towards the crab eye-view camera. Each of nine focal male crabs was subjected to four to nine approaches and produced an average (mean ± SE) of 11.1 ± 3.8 directed lateral waves (range 4–20) during each female approach. Average male carapace width was 11.5 ± 1.1 mm (range 9.7–12.9 mm, $N = 9$) and claw size was 20.1 ± 3.8 mm (range 13.7–24.7 mm, $N = 9$). Average tethered female carapace width was 9.5 ± 0.5 mm (range 8.4–10.2 mm, $N = 9$). These measurements fall well within the size ranges for reproductively active individuals (George & Jones 1982; Nakasone & Murai 1998). Note, however, that our measurements of carapace width are likely to underestimate the true value by around 1 mm because the lateral carapace spines are not always clearly resolved in the video.

Statistics

All statistical tests were conducted in R 2.3.1 (CRAN 2006). Seven display measures (interwave interval, wave duration, claw flex angle, display height, display width, claw tip speed and height above horizon) were analysed with respect to male–female distance, male major claw size and male carapace size (Table 1). Sender–receiver distances were divided into five bins. Bin width was adjusted such that a constant number of data points contributed to each bin. A lack of orthogonality in the data precluded the use of an ANOVA, so we used a mixed-model approach (Schall 1991; Maindonald & Braun 2003). A linear mixed-effect model was used to take into account repeated measures per crab. To adjust for variation between focal males, male identity was entered into the analysis as a random factor (random factors in mixed models are equivalent to the block structure in the analysis of variance). The model was selected by sequentially fitting the parameters of interest, and, in every case, sender–receiver distance was the most dominant, followed by claw size and then body size. Because claw size and body size were correlated (linear model: body size ∼ claw size, $F_{1,7} = 5.7$, $P = 0.049$, $N = 9$) we omitted body size from the results. All mean measurements are accompanied by the standard error of the mean and the sample size (N).

RESULTS

During staged courtship interactions male *U. perplexa* modulated the temporal components of the lateral claw waving display depending on the distance between the male signaller and the female receiver (Fig. 2a, b, Table 1). When broadcast in the absence of receivers the display had a long interwave interval and wave duration (interval: $\mu = 3.7 \pm 0.2$ s, $N = 90$; duration: $\mu = 1.36 \pm 0.03$ s, $N = 118$; Fig. 2a, b, right of dotted line). When females approached from afar (20–70 cm), males changed their waving behaviour from broadcast to long-range directed signalling, during which wave interval decreased ($\mu = 2.3 \pm 0.09$ s, $N = 104$; Fig. 2a) and displays became shorter ($\mu = 1.11 \pm 0.02$ s, $N = 132$; Fig. 2b). At close range (<20 cm), interwave interval and display duration decreased to a minimum.

In addition to temporal variation, male *U. perplexa* modulated various structural components of the waving display depending on receiver distance (Figs 2 and 3, Table 1). Broadcast waves contained a moderate lateral (horizontal) component and an average vertical component (flex angle: $\mu = 105.6 \pm 2.1°$, $N = 140$; height: $\mu = 1.40 \pm 0.04$ cm, $N = 118$; Fig. 2c, d, right of dotted line) and were often accompanied by fully unflexed lifting of several legs (Fig. 3, right of dotted line). Long-range waves directed towards females had an increased lateral component ($\mu = 132.6 \pm 1.3°$, $N = 154$; Fig. 2c) and an average vertical component ($\mu = 1.37 \pm 0.03$ cm, $N = 132$; Fig. 2d), but, as females approached close to the male (<15 cm), the lateral component of the display dropped significantly (Fig. 2c, Table 1) and wave height fell at very close range (Fig. 2d, Table 1). Long-range signalling was also accompanied by two or three unflexed leg lifts, which became flexed during close-range signalling (Fig. 3b, f, g).

The vertical sweep distance of the claw tip, although varying statistically (Table 1) was relatively similar across all sender–receiver distances (close range: 2.2 ± 0.07 cm, $N = 37$; long range: 2.5 ± 0.09 cm, $N = 37$; Fig. 2e). However, the differences in horizontal claw tip sweep distance were quite substantial. This is important because it has a clear impact on display conspicuousness. The horizontal sweep distance for long-range signals (3.3 ± 0.1 cm, $N = 37$; Fig. 2e, right) was almost three times larger than that for short-range signals (1.2 ± 0.1 cm, $N = 37$; Fig. 2e, left). If we assume that, at the eye equator, the fiddler crab eye has a horizontal resolution of 1° (Land & Layne 1995a; Zeil & Al-Mutairi 1996) and that perception of the display requires the signal amplitude at the eye of the receiver to be larger than one interommatidial angle, the maximum perception distance of these displays in the horizontal plane would be 1.88 m for long-range signals and 0.70 m for short-range signals. As well as having a larger effective space, long-range displays are much more omnidirectional than short-range waves: the initial unflexing moves the broadside of the claw through nearly

Table 1. Results of the linear mixed model analysis for the measures in Figs 2 and 4

Measure	Variable	$df_{\text{num,den}}$	*F*	*P* value	*F*	*P* value
Interwave interval (Fig. 2a)	Distance	4,445	**112.3**	**<0.0001**		
	Claw size	1,7	**6.2**	**0.041**		
Wave duration (Fig. 2b)	Distance	4,427	**158.9**	**<0.0001**		
	Claw size	1,7	2.1	0.19		
Claw flex (Fig. 2c)	Distance	4,427	**171.3**	**<0.0001**		
	Claw size	1,7	0.044	0.84		
Display height (Fig. 2e)	Distance	4,173	**9.7**	**<0.0001**		
	Claw size	1,7	**15.5**	**0.0056**		
Display width (Fig. 2e)	Distance	4,173	**101.2**	**<0.0001**		
	Claw size	1,7	**16.0**	**0.0052**		
			Stage 1		Stage 2	
Claw tip speed (Fig. 4a, b)	Distance	4,173	**4.5**	**0.0018**	**7.0**	**<0.0001**
	Claw size	1,7	1.1	0.33	3.1	0.12
Height above horizon (Figs 2d and 4c, d)	Distance	4,427	**84.0**	**<0.0001**	**36.2**	**<0.0001**
	Claw size	1,7	**18.3**	**0.0037**	2.0	0.20

The two explanatory variables (male–female distance and claw size) were tested sequentially in this order. Values in boldface are statistically significant.

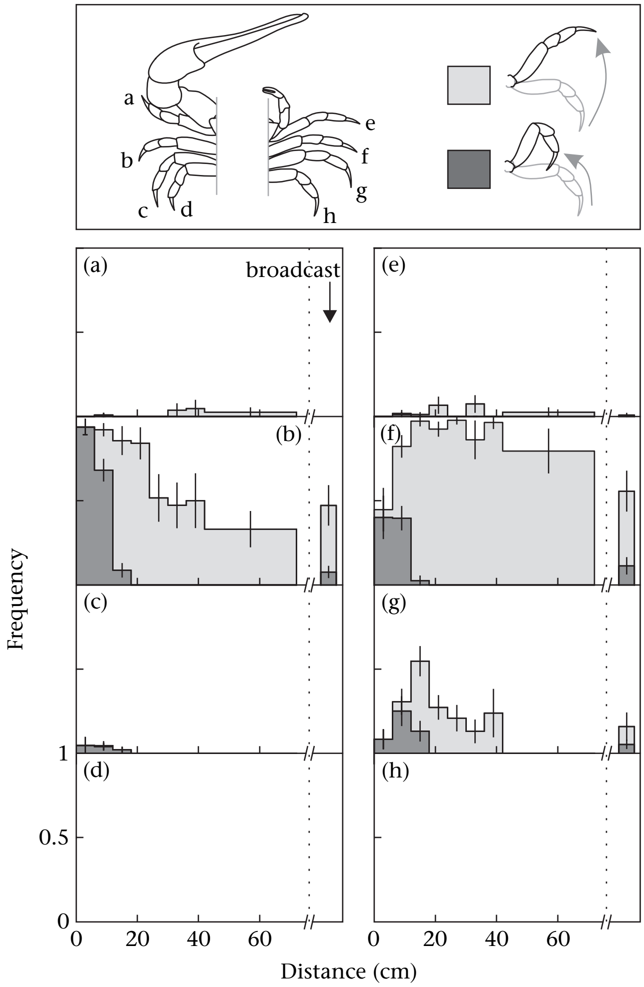

Figure 3. Frequency of walking leg movements with receiver distance. Each panel represents the movements of a single leg (for key see inset). Light grey area, frequency of leg lifts; dark grey area, proportion of flexed leg lifts (see inset for illustration). Data to the right of the dotted lines indicate leg lift frequency during broadcast waving. Error bars represent ± standard error.

140°, which at the same time exposes the inner side of the claw and the bright front of the body. The conspicuousness of long-range waves is further enhanced by the fully unflexed leg lifting behaviour (Fig. 3b, f, g).

During stage 1 of the display, the claw moved at high speed (19.1 ± 0.5 cm/s, $N = 187$; Fig. 4a) and height increased significantly towards the visual horizon as receiver distance decreased (Fig. 4c, Table 1). In contrast, during stage 2 the claw moved slowly (5.6 ± 0.1 cm/s; $N = 187$; Fig. 4b) and height dropped significantly as females approached (Fig. 4d, Table 1). In our analysis, claw speed varied significantly depending on receiver distance (Table 1), tending to decrease at close range (Fig. 4a, b).

Although our data show a clear relationship between signal modulations and receiver distance, such a correlation could theoretically arise as a by-product of a set temporal sequence in courtship behaviour. To test whether this is the case we replotted our data relative to the time from courtship initiation. The observed variance in relation to receiver distance (Fig. 5a) is much lower than that in relation to time (Fig. 5b), suggesting that changes in signal structure depend on the distance over which the signal is transmitted and not on the temporal stage in which it occurs.

DISCUSSION

During staged courtship interactions male *U. perplexa* modulated temporal and structural components of the lateral claw waving display depending on the distance between the male signaller and the female.

Temporal Modulation

For male fiddler crabs, carrying and waving the major claw is energetically costly (Matsumasa & Murai 2005; Allen & Levinton 2007) and males sacrifice valuable feeding time during courtship signalling (M. J. How, personal observation). Temporal adjustments of the visual display may therefore have the effect of balancing physiological costs with the perceived probability of reproductive success. Long interwave intervals during broadcast waving (when the probability of reproductive success is low) suggest relatively low energetic investment in courtship signalling behaviour. In contrast, shorter interwave intervals in the presence of females (when the probability of success is high) suggest high energetic investment. Whether this is also the case during the fine-scale modulation of the display over different receiver distances is more difficult to determine because energy consumption during waving is likely to be dependent on the interaction between multiple structural and temporal features (e.g. claw movement direction, speed and acceleration).

Structural Modulation

In addition to clear temporal changes in the claw waving display, various structural components were also modified depending on receiver distance. These structural modulations may occur as a direct result of changes in wave rate: i.e. to increase signal rate, males may have to delete time-consuming components of the wave display. Indeed, males dropped the lateral component (Fig. 2c) and, to a lesser extent, the vertical component (Figs 2d and 4d) of the claw waving display over close signal—receiver distances while at the same time decreasing the interwave interval (Fig. 2b). However, this association is not necessarily the result of temporal limitations on claw movements because there would still be plenty of scope for reducing overall signal duration by accelerating claw movement in stage 2 of the display (Fig. 4b), which is 3.4 times slower than that in stage 1 (Fig. 4a).

Structural adjustments of the claw waving display depending on receiver distance may reflect attempts to modify the information content of the signal as receiver distance shortens. Animals switch between different courtship signals with different information content depending on the stage in the courtship process in which they occur (Gibson 1996). Animals also alter the structure of

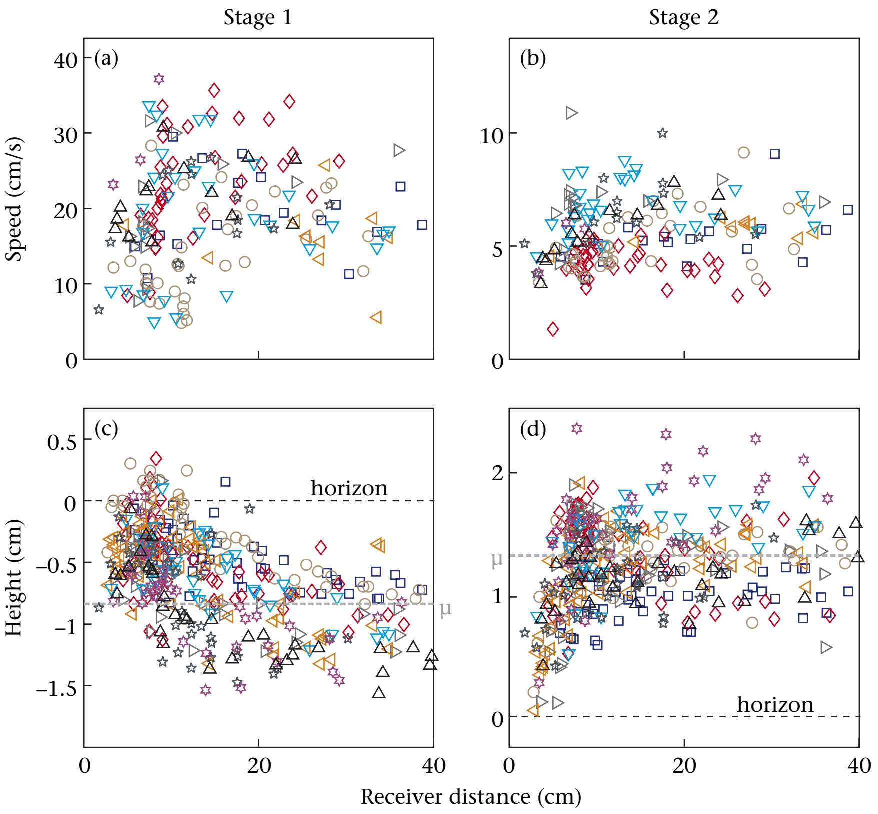

Figure 4. Close-range variation of claw speed and height (a, b). Claw tip speed and (c, d) claw tip height during stages 1 and 2 of the claw waving display. For plots c, d the black dashed line represents the horizon level and the grey dashed line (μ) represents the mean long-range (<20 cm) height. Note that the y axis scale varies between stages.

individual acoustic signals to alter the information they contain according to signalling context (e.g. Manser 2001; Owen & Gordon 2005). Our results suggest that this may also occur for movement-based visual signals. The male fiddler crab's long-range signals are the most visible (Fig. 2e, right), functioning as highly conspicuous beacons to attract females from afar. These signals may serve the additional function of indicating a temporary escape route for wandering females needing protection from potential predators (e.g. Ribeiro et al. 2006). In contrast, short-range signals cover a smaller sweep area (Fig. 2e, left) and are more likely to contain information relevant to mate choice, such as male size or quality. In this instance, performing unflexed leg lifts held close to the carapace and raising the body off the ground could have the effect of exaggerating body size, and male quality could

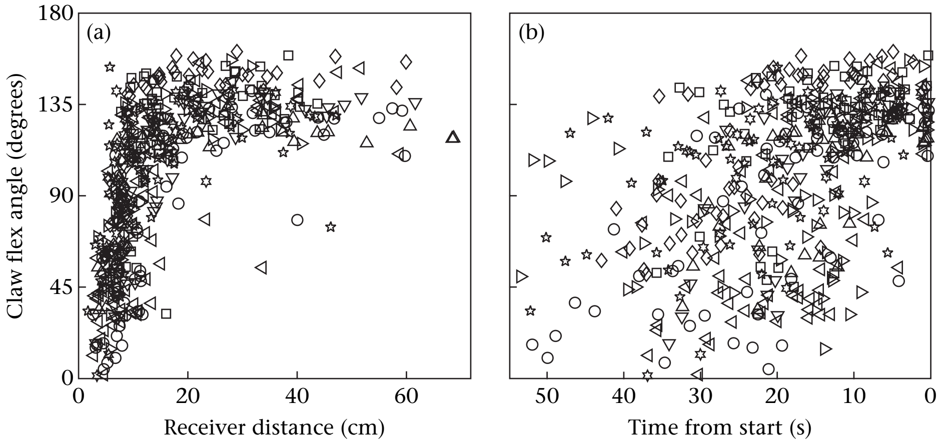

Figure 5. Effect of receiver distance and time from start of interaction on claw flex angle. Claw flex angle plotted against (a) receiver distance (equivalent to Fig. 2c) and (b) time from start of resident–wanderer interaction. The data variance is less in a than in b suggesting that signal modification is not a by-product of a defined temporal courtship sequence but depends on receiver distance.

be indicated from colour signals or display components, such as the slow claw uplift (stage 2). Indeed, previous work has shown a correlation between certain temporal components of stage 2 of the signal and mating success during the final seconds of female approach (Murai & Backwell 2006). To establish a clear link between the observed signal modulations in this study and the changes in information content, a method to analyse the decisions made by courted female *U. perplexa* at fine temporal and spatial scales is needed. One such method would be to construct robotic claw waving machines with variable display characteristics, and to perform pairwise female mate choice experiments similar to those conducted by Detto et al. (2006).

Another reason that males may modify the structure of their displays is to avoid misinterpretation of the signal (e.g. Bradbury & Vehrencamp 1998; Maynard Smith & Harper 2003). This is particularly relevant for signals that have a structure similar to those of other signals with different functions (Mateos & Carranza 1999; Borgia & Coleman 2000; Patricelli et al. 2002, 2006). Two components of the *U. perplexa* claw waving signal have a high potential for misinterpretation. First, at the peak of the claw wave display the male's claw penetrates well above the horizon in the female's field of view (Figs 2d and 4d). Because fiddler crab eyes are on long vertical stalks, their visual environment is conveniently partitioned so that threats appear above the horizon and conspecifics below (Land & Layne 1995a; Layne et al. 1997; Layne 1998). Therefore, the male risks stimulating the female's antipredator escape response (Christy 1995; Land & Layne 1995a), which may grab her attention but may also scare her away. Second, the initial lateral extension of the major claw during long-distance waving is very similar in form to the aggressive movements displayed by males during agonistic interactions. Our results show, as predicted, that male fiddler crabs reduced both of these threatening components during close-range signalling (Figs 2c, d and 4d). Signal misinterpretation can also be avoided by including extra signal components (Møller & Pomiankowski 1993; Hebets & Uetz 1999; Rowe 1999; Hankison & Morris 2003) and the changes in waving display structure observed in this study may be caused by the introduction of a seismic component to the display during close-range signalling (e.g. Salmon 1967; von Hagen 2000).

Judging Distance

Because *U. perplexa* consistently altered the form and intensity of the visual display in response to approaching females at distances of at least 20 cm (Figs 2–4), we have confirmed that resident males are able to judge the distance to conspecifics on the mudflat surface. Previous studies have proposed two simple mechanisms for achieving this (Hemmi & Zeil 2003a, b). First, in a flat world, conspecific distance can be robustly estimated by determining the vertical position of the animal in the visual field of the observer: distant crabs appear close to the horizon, whereas nearby crabs appear lower in the field of view (Zeil et al. 1986; Layne 1998). Second, the apparent size of nearby crabs could be used to estimate their distance: distant crabs appear small, whereas nearby crabs appear large. Manipulating tethered female size and elevation using the experimental system in this study may elucidate the importance of each of these cues for achieving distance estimation.

CONCLUSION

We have demonstrated that male fiddler crabs alter both the intensity and the form of their courtship display with respect to receiver distance. This is the first time that a movement-based visual signal has been shown to change according to communication distance. Our results also extend earlier findings for burrow-centric distance perception (Hemmi & Zeil 2003c) by showing that fiddler crabs are able to accurately judge the distance to conspecifics. Such fine-scale distance-dependent context sensitivity is likely to be much more widespread in animal communication than previously recognized.

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