

# Courtship herding in the fiddler crab *Uca elegans*

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**Abstract** Male and female animals are not always complicit during reproduction, giving rise to coercion. One example of a system that is assumed to involve sexual coercion is the mate herding behaviour of fiddler crabs: males push females towards the home burrow with the goal of forcing copulation at the burrow entrance. We recorded and analysed in detail the courtship behaviour of a North Australian species of fiddler crab *Uca elegans*. Courtship was composed of four main phases: *broadcast waving*, *outward run*, *herding* and *at burrow* display. During interactions males produced claw-waving displays which were directed posteriorly towards the female and which varied in timing and structure depending on the courtship phase. We suggest that courtship herding in *U. elegans* is driven primarily by mate choice for the following reasons, (1) females can evade herding, (2) no other reproductive strategies were observed, (3) males broadcast their presence and accompany courtship with conspicuous claw waves, and (4) the behaviour ends with the female leading the male into the home burrow. As an alternative function for herding in *U. elegans* we suggest that the behaviour represents a form of courtship guiding, in which males direct complicit females to the correct home burrow.

**Keywords** Courtship herding · Visual signal · Coercion · Fiddler crab · *Uca elegans*

## Introduction

The process of sexual selection has given rise to a wide variety of reproductive strategies in nature (reviewed by Andersson 1994). The majority of these strategies involve a degree of complicity between males and females, giving rise to the process of mutual sexual selection, guided primarily by mate choice (Andersson 1994; Kokko et al. 2003). However, males and females are not always fully complicit and one or the other (usually the male) may use a degree of force to obtain mating opportunities. This kind of process is termed antagonistic sexual selection and involves forced copulation, harassment or intimidation (Clutton-Brock and Parker 1995). Examples of all three of these sexually coercive behaviours are common in nature (e.g. Smuts and Smuts 1993; Soltis et al. 1997; Sirot and Brockmann 2001; Jaeger et al. 2002; Vahed 2002; Head and Brooks 2006). Such systems may lead to an evolutionary arms race in which males evolve methods of coercing females and females evolve counteractive measures to avoid coercion (Sirot and Brockmann 2001). For example, male water-striders often engage in forced copulation with females, and females have evolved anti-clasper organs to avoid forcible insemination (Rowe et al. 1994; Arnqvist and Rowe 2002).

Mate herding in fiddler crabs is often cited as a clear example of sexual coercion (Crane 1975; Zucker 1983; Salmon 1984; Salmon and Zucker 1988; but see Dyson 2008). The phenomenon is widespread in the genus *Uca*, but remains relatively poorly understood. Herding occurs when resident burrow-owning males attempt to push passing female wanderers towards the entrance of the male's home burrow. Males achieve this, first by moving to the far side of the passing female so that she is positioned between the male and the burrow (How and Hemmi 2008). They

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then move backwards, using the posterior part of the body to push the female towards the home burrow.

In this paper we describe mate herding behaviour in *Uca elegans*, a narrow-fronted species of fiddler crab from the subgenus *Australuca*. Whereas females appear inconspicuous, males of the species are brightly coloured, with blue patterns on their black carapace and bright red and white claws. The species inhabit open, inter-tidal saltpan mudflats at the upper limit of the tide level, such that their habitat is only inundated for a few days over the spring tide and is dry for the remainder of the cycle. During these dry periods males engage in frequent territorial activity and, occasionally, burrowless females wander the mudflat eliciting vigorous courtship behaviour from nearby males.

We describe the four main sequential components of mate herding in *U. elegans*, broadcast signalling, outward run, herding and burrow courtship. Our findings show that the herding behaviour is part of an elaborate courtship sequence that includes extensive signalling. The structure and timing of these signals is fine-tuned to the relative position of the courted female.

## Methods

All observations were conducted in a large, open mudflat (400 × 100 m) at East Point Reserve, Darwin, Australia (12°24'49"S 130°50'09"E) in November 2005. Data were collected over six successive days during spring tide, corresponding to the peak activity phase of the *U. elegans* reproductive cycle.

The claw-waving signal of *U. elegans* was filmed from the viewpoint of a crab using a digital video camcorder (DCR-HC21E MiniDV Handycam) pointing down onto a mirror angled at 45° resting on the mudflat surface. The video films were digitised at a full frame rate of 50 de-interlaced frames per second (20 ms frame interval) using modified open source software (dvgrab) under Linux, and the *x*–*y*-positions of the major claw-tip were determined for each frame using custom-made software (J. M. Hemmi, The Australian National University). The motion signal of the display was extracted using a two-dimensional motion detection array (2DMD) of correlation-based elementary motion detectors developed by Zanker (1996). The mean motion vectors falling within 5° angle bins were determined frame-by-frame and summarised for an entire display in a kinetograph (see How 2007 for details). A kinetograph is a representation of motion strength and direction over time. Motion direction is encoded along the *y*-axis, time along the *x*-axis and motion strength as pixel intensity. Pixel intensity ranged from white (no motion response) to black (maximum motion response).

The interactions between individuals in natural *U. elegans* populations along with their waving displays were recorded from above using digital video cameras (Sony DCR-HC21E MiniDV Handycam) fixed to poles forced into the mud. The cameras were positioned approximately 1.65 m above the ground, which resulted in a recording area of 0.95 × 1.60 m on the mudflat surface. The observation area was left undisturbed for the duration of recording, except for brief interruptions every 1–2 h to change video tapes. All recorded top-view footage was digitised and down-sampled to 12.5 frames per second (80 ms frame interval) to reduce the amount of data to be processed. Camera orientation and position were estimated, and the lens distortion effects were removed by filming a standard checkerboard pattern in situ and applying open-source camera calibration software (Bouguet 2005).

Crab age and sex were not observed to be evenly distributed across the *U. elegans* study group. All data in this study were collected from areas of high adult male density in which all of the open burrows recorded in the field of view of the video cameras were occupied by males at a mean density of  $5.9 \pm 1.6$  individuals per m<sup>2</sup> (range 3.9–7.9 males per m<sup>2</sup>; *n* = 5 recorded areas). In the digitised videos we identified all interactions between burrow-owning males and wandering females in which the males successfully initiated herding. To maintain data independence, only those herding events that were separated over time, and only single herding events for any one individual male or wandering female, were included in the analysis. For such sequences, body orientation and the *x*–*y* position of the centre of the carapace of the female wanderer and of the herding resident male crab were determined frame-by-frame with an accuracy of ±1 mm. Part of the analysis required estimates of inter-crab distances. In these cases we corrected for measuring from the centre of each crab's carapace by subtracting the combined mean carapace width of the two crabs from the distance measurement. We recorded the occurrence of male claw-waving displays, burrow entrances and burrow exits. Carapace width and major claw length for all crabs were estimated from video images with a measurement accuracy of ±1 mm. All mean measurements are accompanied by the standard error of the mean and the sample size (*n*).

## Statistics

All statistical tests in this paper were performed using the R 2.3.1 open-source statistical package (CRAN 2006). Changes in male claw-wave duration and rate, and changes in female movements across the distinct phases of courtship were analysed using a linear mixed effect model (Schall 1991; Maingdonald and Braun 2003). This method was chosen because the data lacked orthogonality (not all crabs

contributed data to each courtship phase), which precluded the use of an ANOVA. 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). For the analysis of female movements, a conservative estimate of the least significant difference between phases was calculated as double the largest between-group variance. Circular data analysis was conducted using Raleigh's test for directionality (Batschelet 1981). Circular mean angles are also provided with the mean vector length ' $R$ ', a measure of concentration that ranges from 0 (random) to 1 (unidirectional).

A time period of 7.9 h of natural behaviour was recorded at five different locations, from which we identified 22 independent herding interactions between different burrow-owning males and wandering females. Average herding male carapace width was  $23.5 \pm 2.0$  mm (range 18.7–26.9 mm;  $n = 22$ ) and female carapace width was  $15.6 \pm 2.6$  mm (range 11.4–20.7;  $n = 22$ ). These size measurements are consistent with those from other studies (males  $26.6 \pm 7.7$  mm,  $n = 117$ ; females  $20.0 \pm 6.4$  mm,  $n = 64$ , George and Jones 1982). It is important to note, however, that our size measurements are likely to underestimate the true carapace width by approximately 1 mm, as the lateral carapace spines usually included in calliper measurements are not always resolved in the video images.

## Results

### Courtship and the claw-waving display

When active on the mudflat surface males produce a conspicuous visual signal, the claw-waving display. The display occurs spontaneously in the absence of signal receivers (broadcast signalling), but is also directed towards

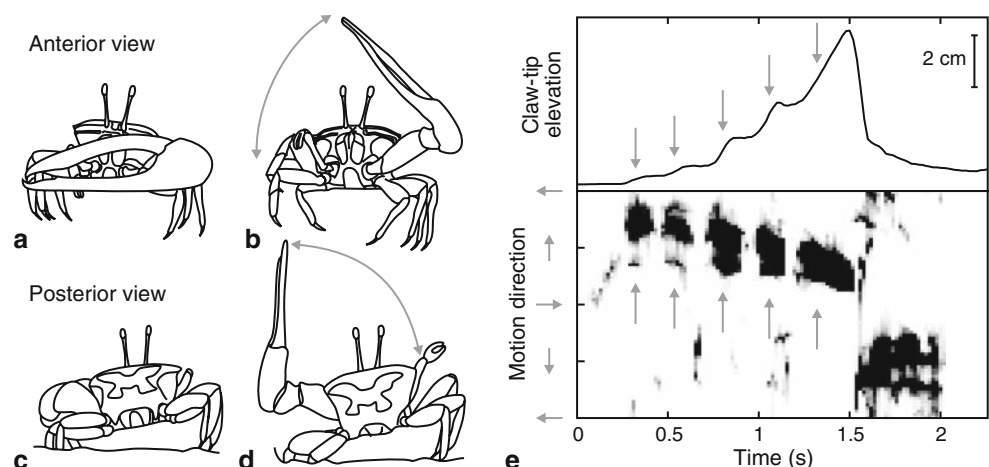
females in courtship contexts. The display consists of a relatively simple vertical waving movement in which the major claw is lifted slowly to a position above eye-level, and then quickly dropped back to resting position (Fig. 1a–d). The uplift of the display is composed of one to five regularly spaced upward jerks of the claw, which are clearly resolved in the kinetograph (five jerks in this example, Fig. 1e, grey arrows). The claw-waving signal is generally produced during the middle to late part of the activity period, when surface activity is dominated by groups of males.

Courtship in *U. elegans* consists of four main sequential components, *broadcast waving*, an *outward run*, *herding* to the burrow, and *burrow display* (Fig. 2a). The duration and frequency of the claw-waving display differed significantly across the four courtship phases [linear mixed effect model: wave duration  $F_{3,17} = 10.7$ ,  $P < 0.001$ ; wave rate (transformed by the square root to maintain normal variance):  $F_{3,36} = 13.2$ ,  $P < 0.001$ ; Fig. 2b].

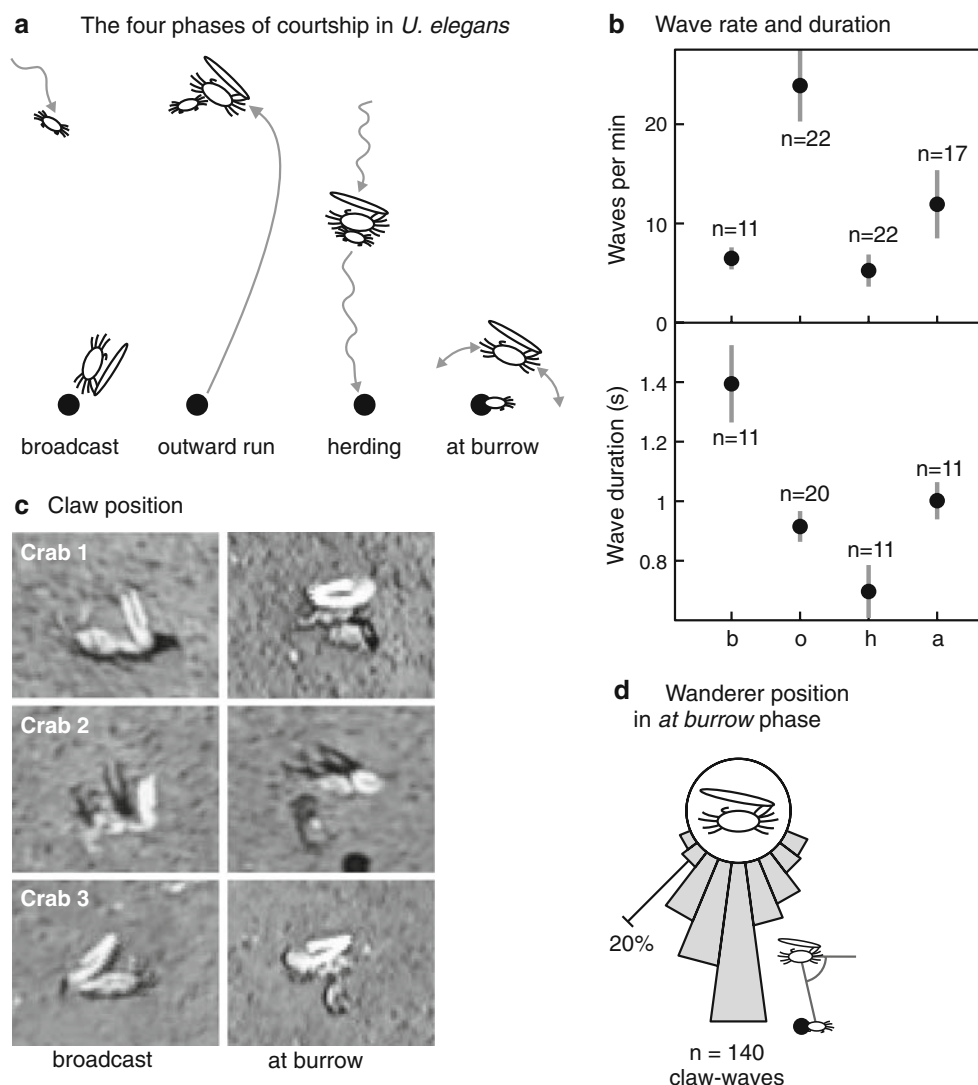
### Broadcast waving

Whilst active on the mudflat surface, male *U. elegans* divided their time between feeding, territorial interactions with nearby males and broadcast waving. Waves were broadcast at a relatively slow rate of  $6.5 \pm 1.1$  waves per minute and with a long signal duration of  $1.4 \pm 0.1$  s ( $n = 11$ ; Fig. 2b). The claw travelled in a diagonal trajectory involving both vertical and lateral movement components, so that, at the peak of the wave, the claw was positioned above and away from the body (e.g. Fig. 2c left: top-down view taken mid-wave shows that the raised claw is held laterally un-flexed away from the body). During the broadcast waving phase, males frequently interacted with other male neighbours on the mudflat surface, often resulting in combat. Individuals were observed using the claw-waving display during territorial interactions (M. J. How,

**Fig. 1** The claw-waving signal of *U. elegans*. Left anterior view (a–b), and posterior view (c–d), of crab posture at rest and midway through the display. **e** Trace of claw-tip elevation (top) and kinetograph (bottom) of a single example display (viewed anteriorly). Vertical grey arrows indicate the position of five jerks during the claw uplift phase



**Fig. 2** Changes in claw-wave characteristics over the four phases of courtship behaviour in *U. elegans*. **a** The four phases of courtship. **b** Wave rate (top) and wave duration (bottom) over the four courtship phases. Each black dot represents the mean of  $n$  individuals and the grey bar indicates  $\pm$  one standard error of the mean. **c** Close-ups from top-down footage of three individual males showing the different claw position at the peak of the claw-waving display during ‘broadcast’ (left) and ‘at burrow’ (right) signalling. **d** Position of the female wanderer relative to the male during ‘at burrow’ claw-waving displays. Each ‘petal’ of the rose plot indicates the proportion of claw-waves falling within  $15^\circ$  bins



personal observation), the appearance of which was indistinguishable from broadcast claw-waves. The involvement of the signal in direct territorial interactions was not quantified in this study.

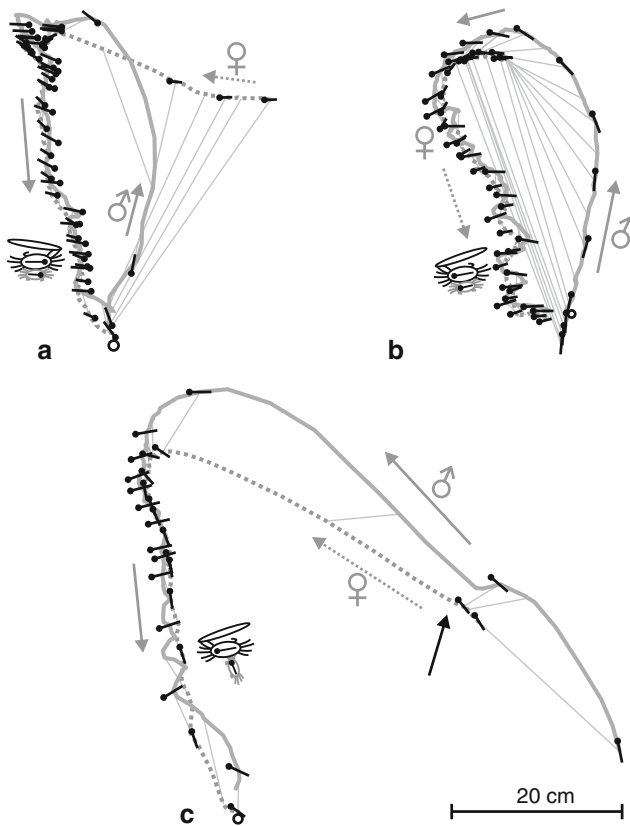
### Outward run

After spotting a wandering female, the burrow-owning male ran in a curved trajectory towards the female's position. When close to the female, the curve of the male's trajectory tightened so that he ended up on the far side of the female's position, presenting his posterior carapace to her (Fig. 2a and examples Fig. 3a–c; see also How and Hemmi 2008). During this initial run, the male signalled vigorously at a rate of  $23.9 \pm 3.6$  waves per minute ( $n = 22$ ) using displays short in duration ( $0.9 \pm 0.1$  s,  $n = 20$ ; Fig. 2b). Note that the sample sizes for wave rate and duration differ for some of the courtship phases (Fig. 2b). This is due to the fact that some individuals did not produce any claw-waves,

resulting in a wave rate of 0 waves per minute and no measure of wave duration.

### Herding to the burrow

The male then proceeded to push or guide the female in a slow, roughly linear trajectory towards the home burrow, maintaining the female and the burrow in a posterior position. Figure 4 presents the movements of males and females during the 22 herding events recorded in this study. In most of the recorded herding interactions, males and females moved relatively slowly in a roughly linear trajectory towards the home burrow (Fig. 4a). In these instances females made no obvious attempts to escape the herding movements of the male. However, on some occasions females made short, fast sideways runs and the herding males countered with quick detouring movements of their own (Fig. 4b). Once the herded female had approached to within approximately 10 cm of a burrow entrance, she



**Fig. 3** Three examples of herding interactions in *U. elegans* viewed from above. In each panel the **black ring** at the **bottom** represents the burrow position, **thick grey line**—male position, **dotted grey line**—female position, **thin grey lines** connect male and female positions at 0.48 s time intervals. The orientation of each crab is represented as a **dot-and-stick**, the orientation of which at a particular point in the interaction is illustrated

tended to run towards it, remaining motionless in the burrow opening. In the cases where this was not the male's home burrow, the herding male would then proceed to prise the female out of the burrow entrance and resume herding towards the correct burrow. The success rate of herding males was relatively high, with 17 of the 22 herding interactions recorded in this study resulting in the female being herded to the entrance of the male's home burrow.

During the *herding* phase, the male and female tended to be in physical contact (mean male–female distance  $0.2 \pm 0.2$  cm, which does not differ significantly from zero  $t = 1.5$ ,  $P = 0.14$ ,  $n = 22$ ). Males produced only short claw-waving displays ( $0.7 \pm 0.1$  s,  $n = 12$ ) at a low rate ( $5.3 \pm 1.6$  waves per minute,  $n = 22$ , Fig. 2b). Only 28 claw-waves were produced by 12 of the 22 individuals during this phase, and these occurred when the male was a short distance away from the female (mean male–female distance  $3.4 \pm 0.8$  cm,  $n = 12$ ). This measure was significantly larger than the overall mean male–female distance for this subset of individuals ( $t = 3.4$ ,  $P = 0.005$ ,  $n = 12$ ), indicating that wave rate was suppressed during male–

female contact, only increasing when a gap appeared between the herding couple.

### Burrow display

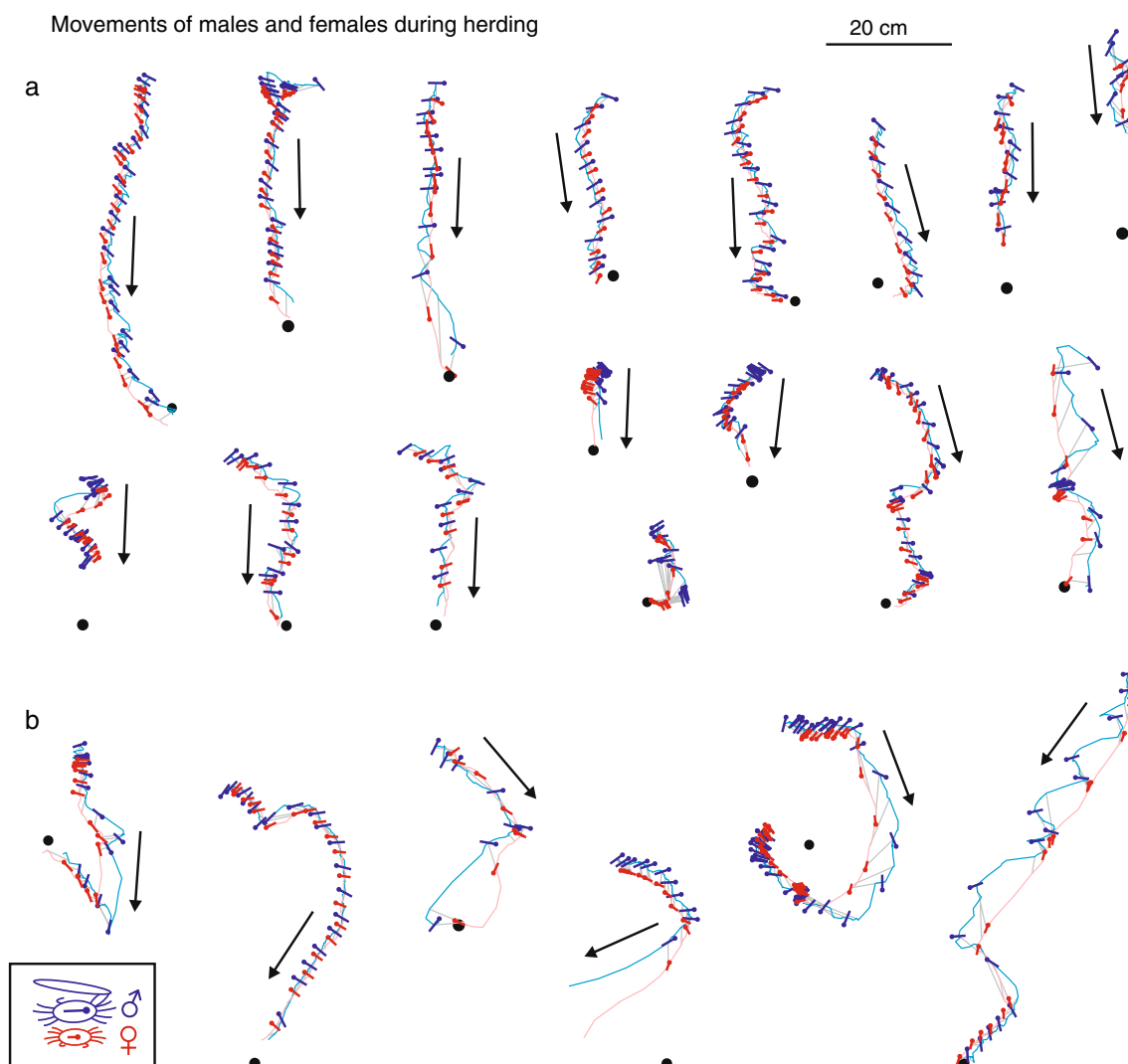
Once herded to the burrow the female remained motionless at the entrance and the male started the final courtship phase, the burrow display. Unusually for fiddler crabs, the male produced posteriorly directed claw-waving displays (mean female position relative to the male =  $-90.4^\circ$ ,  $R = 0.90$ ,  $P < 0.001$ ,  $n = 140$  claw-waves; Fig. 2d). These displays were accompanied by tilting of the body backwards, which lifted the claw directly above the body, resulting in a strong vertical and weak lateral movement component (Fig. 2c, right). These displays were relatively short in length ( $1.00 \pm 0.06$  s,  $n = 11$ ) and repeated at a moderate rate ( $11.9 \pm 3.4$  waves per minute,  $n = 17$ ; Fig. 2b). Claw-wave production was interspersed with low-frequency claw shakes, likely to be involved in short-range seismic signalling (M. J. How, personal observation). Successful burrow displays ended when the female descended into the burrow, followed shortly thereafter by the male. The male later sealed the burrow with a plug of mud collected from the surface, and presumably copulation then followed underground. Unsuccessful burrow displays ended with the female running away from the area. Of the 17 females that were successfully herded back to the burrow entrance, six descended into the burrow, all of which were followed a short time later by the courting male who then sealed the burrow. This suggests that burrow-entry by the female results in underground pair formation. No alternative courtship or mating strategies were observed in the field.

### Female movements

Wandering females generally moved in short intermittent runs and altered their movements depending on the position of courting males. Figure 5a provides an example plot of an individual female's speed over time. In this example, the female moved in relatively quick bursts across the mudflat until a courting male approached (Fig. 5a, 0–9 s). Then, when the outward-running male came near and commenced herding, the female moved slowly, producing an occasional quick burst of speed (Fig. 5a, 9–34 s). Lastly, once at the burrow the female remained almost motionless at the burrow mouth (Fig. 5a, 34–46 s).

Figure 5b presents the proportion of time females spent stationary during the four phases of the courtship cycle. This proportion differed significantly across the four phases of courtship (linear mixed effect model:  $F_{3,38} = 6.9$ ,  $P < 0.001$ ). Outside of courtship interactions (in this case, during the broadcast phase) females spent roughly half their time stationary. This changed during the outward run and





**Fig. 4** Male and female trajectories during the *herding* phase. Crab position and orientation at 0.48 s intervals is provided by blue (male) and red (female) ball and stick models (see insert bottom left), each of which is connected by a thin grey line. Each trace is rotated so that

herding is initiated at the top and proceeds downwards towards the burrow (black circle). **a** Herding events that proceeded relatively linearly towards the home burrow. **b** Interactions involving quick female runs and male counteracting detours

herding phases, when females spent more time moving than standing still. Finally, during the burrow courtship phase, the female spent the majority of the time stationary, consistent with the observation that females remained motionless in the mouth of the male's home burrow for much of the time. According to a conservative estimate of the least significant difference ( $\text{lsd} = 0.18$ ; calculated as double the largest between-group variance), females spent significantly more time stationary during the at-burrow phase than during outward runs and herding.

## Discussion

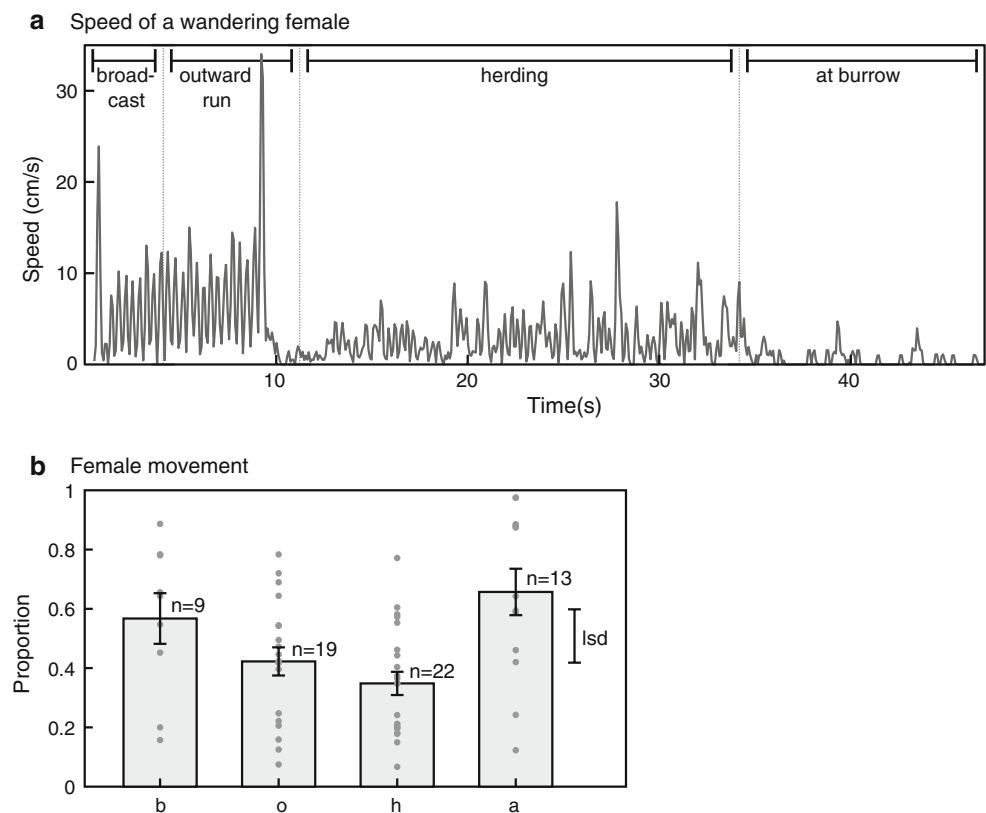
Fiddler crabs of the species *U. elegans* engage in a complex form of courtship, in which burrow-owning males physi-

cally herd wandering females back to the home burrow for pairing underground.

The context dependence and function of the claw-waving display

The variations observed in the male claw-waving display across the four courtship phases of *U. elegans* represents a further example of how fine-scale social context can elicit adjustments in dynamic visual signal structure (How et al. 2008). Claw-waves produced during the pre-courtship *broadcast* phase were long in duration and contained strong lateral, as well as vertical components, making them conspicuous from all directions. The conspicuousness of these signals is further enhanced by large groupings of signalling males. Given the context in which they are produced and

**Fig. 5** Movements of wandering female *U. elegans*. **a** Trace of speed over time for a single wandering female during a courtship interaction. **b** Proportion of time spent stationary by each female across the four phases of courtship. Females were classified as stationary if they were moving at less than 1 cm/s. Grey dots represent the mean for each individual female, and bars represent the mean proportion of all individuals  $\pm$  the standard error



the conspicuous design of these signals, broadcast waves are likely to serve the function of attracting unseen receptive female wanderers from afar (Pope 2005; How et al. 2007, 2008). A second function of the broadcast display may be to signal territorial ownership to surrounding competitors; *U. elegans* males signal in close proximity to neighbouring males and often enter into territorial disputes leading to combat.

During the next phase of courtship, the *outward run*, males substantially increased their claw-waving rate. One reason for increasing signalling behaviour during this phase might be that females may respond to the display by slowing their movement speed and ‘allowing’ the male to approach. It is possible that this signal taps into the first stages of the female’s anti-predator response causing her to ‘freeze’ (Christy 1995; Christy and Backwell 1995; Land and Layne 1995a; Hemmi and Zeil 2005). Alternatively, the signal may at least partly be directed towards surrounding male competitors, potentially advertising the displaying male’s competitive ability and his ‘ownership’ of the target female.

Waving is substantially reduced during the *herding* phase, especially when the male and female are in direct contact. This may be to avoid startling the female at such close range, or because claw-waves may be mechanically difficult to perform while simultaneously manoeuvring the female towards the burrow. Herding males may also reduce

claw-wave rate in an attempt to avoid drawing the attention of other males and entering into territorial interactions. This is also helped by the fact that the close proximity between the female and the male partly shields the female from the attention of competitors.

Finally, after herding, the male starts the *burrow* courtship phase. The displays produced during this phase involve the body being tilted back to bring the claw above the carapace, suggesting that the signal is directed posteriorly towards the courted female. Indeed, such body tilting has been observed in females of other fiddler crab species during posteriorly directed interactions (von Hagen 1993; J. Zeil and M. J. How, personal observation). Burrow claw-waving displays may function to scare the female into remaining still or to descend down into the burrow where copulation can take place. However, the fact that the display is accompanied by additional signal components, such as the presentation of colourful carapace patterns and low-frequency seismic claw shakes, as well as the fact that the claw-waving display contains energetically expensive jerk movements, suggests that the signal is not designed to scare the female, but to provide her with information relevant to mate choice. This may complement information the female may gain from the burrow entrance about the suitability of the burrow for egg development (Christy 1982; Christy and Schober 1994; Backwell and

Passmore 1996; Reaney and Backwell 2007). Interestingly, the observation that claw-wave rate is relatively low during the *at burrow* phase suggests that, in contrast to studies in other species (e.g. Backwell et al. 1999), high wave rate does not seem to be used as a selection criterion by potential female mates. Other cues, such as the ‘jerkiness’ of the claw upstroke or the height of the claw-tip during waving probably play a more important role. An additional effect of posteriorly directed displays is that the intentions of courting males may be less likely to be mistaken as aggressive. Agonistic interactions with males tend to involve presenting the face of the major claw towards the opponent (Land and Layne 1995b), whereas in this courtship system the major claw faces away. Despite all indications that the display is directed towards females in the burrow mouth, the burrow-centred display could act as a competitive signal to warn off other males.

To fully understand the significance of the *U. elegans* claw-waving signal for female choice, a more detailed analysis of female responses to specific signal components in different behavioural contexts will be needed.

#### Courtship herding: coercion or mate choice?

Forced copulation and harassment have been described previously in fiddler crabs and their relatives (Crane 1975; Zucker 1983; Henmi et al. 1993), including examples where herding is used as a mating strategy (Salmon 1984). In these cases it is presumed that herding is coercive due to the observation that the behaviour appears to involve a degree of force (the female is physically pushed towards the burrow) and ends in forced copulation at the mouth of the home burrow (Crane 1975; Salmon 1984; but see Dyson 2008).

Indeed, the herding behaviour of *U. elegans* does seem to involve an element of force: the male and female are in physical contact during herding and the male appears to physically push the female towards the burrow. However, rather than to force females to mate, we propose an alternative function for courtship herding in *U. elegans*: to guide the female past rival males and their burrows back to the home burrow where female choice can take place. We argue this function using the following four pieces of evidence.

Firstly, circumstantial evidence suggests that females were easily able to evade the herding attempts of males, and so must have been behaving with some degree of complicity. Females were able to run at more than 40 cm/s over distances greater than 2 m. Despite the counteractive movements of males, some females were observed evading herding attempts. Females also evaded herding by crouching low and passing underneath the body of larger males (M. J.

How, unpublished data). Furthermore, of the 17 recorded interactions that involved burrow-centred courtship, 11 ended with the female moving away from the burrow mouth, suggesting that the female was able to choose to abort the interaction during this final stage.

Secondly, herding was the only courtship method observed in this species. In general, even in species where coercion is common, forced copulation occurs only as an alternative reproductive strategy (McKinney et al. 1983; Salmon 1984).

Thirdly, courtship in *U. elegans* is generally preceded by broadcast claw-waving displays, often performed simultaneously by multiple individuals in areas of high-male density. This kind of group signalling behaviour strongly suggests an element of mate attraction and mate choice (Backwell et al. 1998, 1999; Burford et al. 1998; Croll and McClintock 1999, 2000). The fact that males adjusted the structure and timing of their claw-waving displays depending on the relative position of the female, suggests that this functions as a sexual signal intended primarily for the courted female.

Fourthly, herding was never observed to end in copulation on the mudflat surface or in the mouth of a burrow, and males were not observed to force females down into the home burrow. Only after the female had first descended into the burrow did the male follow, presumably resulting in pairing underground.

This suggests that rather than being a forceful manipulation of female position, the behaviour represents a form of courtship guiding, in which the female is led to the correct burrow. The behaviour differs markedly from the mate choice strategies employed by other species in which males attempt to attract wandering females to the home burrow using advertisement claw-waves alone (e.g. Crane 1975; Pope 1998; How 2007; How et al. 2008). Instead of attracting females, male *U. elegans* actively collect potential mates from the local area and guide them back to the home burrow where females can make their choice based on the male’s courtship display and burrow quality. In fact, the ability of a male to path integrate whilst herding a female back to his home burrow, passing scores of competing males, may, in itself, provide a useful cue for mate choice.

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