

Denise S. Pope

Testing function of fiddler crab claw waving by manipulating social context

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Abstract Many territorial advertisement signals are thought to be dual-function signals, directed to both rival male and receptive female conspecifics. However, few studies have tested this assumption by examining whether in fact both sexes are likely to elicit signaling behavior from territorial males. In this study, I experimentally manipulated the social context of male sand fiddler crabs (*Uca pugilator*) to investigate the effect of different audiences on the performance of the claw-waving display, a territorial signal that is often presumed to be directed to both males and females. To test whether males perform this signal to both audiences, I measured the frequency of waving behavior by focal males when housed in field enclosures alone, with only males, with only females, or with both males and females. Focal males waved at a low frequency when alone, and the presence of males had no effect on their level of waving. However, in the presence of females, focal males showed a significantly higher level of waving, whether or not males were also present. In addition, there was no association between fighting and waving behavior. This experiment provides evidence that from the perspective of the signaling male, the claw-waving display of *U. pugilator* is not a dual-function signal but rather is primarily directed to receptive females.

Key words Fiddler crabs · Territorial signal · Social context

Introduction

Many signals produced by male animals defending territories during the breeding season are assumed to serve a dual function by both repelling rival males and attracting receptive females, although the assumption that such signals function in the contexts of both male-male competition and female choice has rarely been tested. Examples of such presumed dual-function signals include the songs of male songbirds, anurans, and acoustic insects (Searcy and Andersson 1986; Ewing 1989; Bailey 1991; Gerhardt 1994), as well as visual signals such as the head-bobbing displays of lizards (Carpenter 1967).

The function of territorial signals is most often studied by measuring the responses of male and female receivers using such techniques as territorial playback or mate choice experiments (Falls 1992; Gerhardt 1994; Searcy and Yasukawa 1996), but a complementary method is to investigate signal function from the point of view of the signaling male by studying the context in which the signal is performed (reviewed for birdsong in Searcy and Yasukawa 1996). A key question in these studies of the context of male signaling is whether these presumed dual-function signals are directed to both males and females. Many studies have made inferences about the function of birdsong by correlating singing behavior with different phases of the breeding cycle (e.g., Cooney and Cockburn 1995; Whittingham et al. 1997) or time of day (e.g., Slagsvold et al. 1994). A more direct way to interpret the intended audience of a signal is to determine the social context in which the signal is most likely to be performed (e.g., Martins 1993; Wiley et al. 1994; Galeotti et al. 1997; Langmore 1997), although these interpretations depend upon the observers' ability to identify which conspecifics are interacting with the displaying male. Experimental manipulations of the social context can eliminate this problem by directly measuring which audiences evoke signaling behavior (e.g., Baptista 1978; Searcy and Yasukawa 1990; Capp and Searcy 1991; Eens et al. 1993; DeCourcy and Jenssen 1994). Here, I describe the effects of experimental ma-

D.S. Pope (✉)
Department of Zoology, Duke University, Box 90325,
Durham, NC 27708-0325, USA

Present address:
D.S. Pope, Smithsonian Tropical Research Institute, Unit 0948,
APO AA 34002-0948, USA
e-mail: poped@naos.si.edu

nipulations of the social context of male sand fiddler crabs (*Uca pugilator*) on their performance of the claw-waving display, to determine if the display is directed to both males and females.

Fiddler crabs (genus *Uca*, family Ocypodidae) are small, semi-terrestrial crabs that build burrows in the intertidal regions of protected shores and estuaries. These burrows are a critical resource for the crabs, providing shelter from tidal inundation, heat, desiccation, and predators (Crane 1975). In addition, in many species, including *U. pugilator*, the male's burrow is used as a site for mating and for the female to brood eggs until larval release (Crane 1975; Christy 1982). Males of these species attract females to their burrows with a claw-waving display (Backwell et al. 1998) in which the male's single enlarged claw is repeatedly raised and lowered in a species-typical pattern (Crane 1975). Males also defend these breeding burrows against intruders in ritualized fights (Crane 1975; Hyatt and Salmon 1978; Jennions and Backwell 1996).

The association of the claw-waving display with a defended territory in fiddler crabs has led many authors to conclude that the display serves as a territorial advertisement signal to both receptive females and rival males (Brown 1975; Crane 1975; Weygoldt 1977; von Hagen 1993). Some authors have noted that males of some species apparently increase their rate of waving when approached by either males or females (Doherty 1982; Crane 1975), although Salmon and Stout (1962) demonstrated that male *U. pugilator* increased their waving rate when presented with females, but not with males. In addition, male fiddler crabs have been reported to signal in the absence of any specific audience (Crane 1958), much like the spontaneous performance of song by songbirds or assertion displays by iguanid lizards (Carpenter 1967; Searcy and Andersson 1986; DeCourcy and Jenssen 1994). However, given the high density of many species of fiddler crabs (e.g., *U. pugilator* are found at densities of 34–65 crabs/m²; Colby and Fonseca 1984), individuals in these populations are unlikely ever to be isolated from all other crabs, making it difficult to determine if they truly display in the absence of any potential audience. High densities also make it hard to ascertain to which crab a male is displaying; even if an individual male or female is approaching a male's burrow, the presence of many neighbors of both sexes, as in Salmon and Stout's (1962) experiment, may still affect the signaling behavior of the resident male. Thus, in *U. pugilator*, the open habitat and high density of individuals renders impossible the determination of intended receivers of a signal in a natural situation.

Experimental manipulation of a male's social context allows direct measurement of which conspecifics evoke the display, hence, presumably, which are the intended recipients of the signal. This paper describes a field experiment in which I controlled the social context of *U. pugilator* males and measured the frequency of waving behavior in each context. If the display is truly a dual-function signal, no differences in males' signaling be-

havior in male-only, female-only, and mixed-sex groups would be expected; differential signaling to male or female audiences would indicate that the signal functions primarily for defense or courtship. The signaling of males when alone provides a baseline measurement of their display behavior to which the effect of different audiences can be compared.

Methods

I conducted this study from 28 May to 7 June, and 4–7 August 1998 on Pivers Island, Beaufort, N.C. The breeding season of *U. pugilator* in this location extends from mid April to early September (Salmon 1965), peaking in late July (Salmon and Hyatt 1983). Salmon and Hyatt (1983) demonstrated that in North Carolina, populations of this species living on sloped beaches showed a semi-monthly cycle of courtship activity, with broad peaks centering on neap tides. Test cages were located and animals were collected on sloping sand beaches. Neap tide in early June was on 1 June, so the first test period included the time of peak courtship activity. In the second test period, neap tides occurred on 31 July and 14 August, with spring tide occurring on 7 August, so this test period included the tail-end of one courtship cycle.

The study site was a small sand beach uninhabited by *U. pugilator* except at one extreme end. Enclosures of black Vexar plastic 6-mm mesh were installed in the upper intertidal zone. I fitted the rectangular cages, measuring 50×40×40 cm, with a mesh bottom and buried them into the sand to a depth of 15–20 cm. Cages were staked into the sand with PVC pipe at each corner, and I covered the top 12 cm of mesh with clear plastic sheeting to prevent crabs from climbing out. Eight cages, spaced 3.5 m apart, were installed more than 10 m from the small natural crab population.

I created four social-context treatments: (1) focal male alone ("male alone"), (2) focal male plus nine other males ("all male"), (3) focal male with nine females ("all female"), and (4) focal male, four other males and five females ("male and female"). I assigned two replicates of each treatment per day to cages using a Latin square design. I collected groups of crabs the day before testing from a large population 500 m from the study site. I chose focal males haphazardly from among the crabs collected, and marked them by affixing a square of white marking tape to their carapace with cyanoacrylate glue. The cages were stocked with the appropriate crabs for each treatment within 2.5 h after low tide. The following day, I videotaped each cage for 30 min within 2 h of diurnal low tide. Trials were videotaped on ten days: 29, 30 May, 2–5, 7 June, and 5–7 August.

After videotaping, I removed the crabs, and replaced them with a new group for videotaping the next day. Each crab, both focal males and non-focal individuals, was thus used only once. To ensure independence of samples, after removal from the cages, all crabs were held in an indoor seawater table until the end of the experiment. The sand was disturbed by digging to remove all crabs from the previous day, so there were no burrows available and crabs newly placed in cages had to dig their own burrows. *U. pugilator* can build new burrows in less than 30 min (Dembowski 1926; Hyatt and Salmon 1978), and are under pressure to build burrows quickly since individuals without burrows are washed away by tidal inundation. The crabs had the remainder of the low-tide period on the day I placed them in the cage, an entire nocturnal low-tide period, as well as part of the subsequent diurnal low-tide period until videotaping to complete their burrows. All crabs, including all focal males, had built burrows in all cages that I videotaped.

I scored from videotape the number of waves performed by the focal male during the 30-min sampling period. I also recorded whether the focal male was active on the surface in 5-min blocks and standardized each crab's waving behavior by his time active, for a resulting measure of waves/min. To examine the association between fighting and waving, fighting was scored in each of the

two treatments containing multiple males (i.e., the all-male and male-and-female treatments). I scored these trials for any fights involving the focal male (I defined fights conservatively as requiring claw-claw contact between two males and involving a burrow), and standardized these measurements by the amount of time the male was active as well as by the number of other males available to fight with (nine in the all-male treatment and four in the male-and-female treatment), for a resulting measure of fights/min per male.

I included in the analysis trials that fulfilled the following criteria: (1) focal males had to be present on the surface for at least 5 min of the 30-min period and (2) no other animals could be present that violated the treatment (e.g., a female in the all-male treatment, or any other crab in the male-alone treatment), which occurred occasionally because crabs escaped from other cages or remained from the previous day. There were also occasions where a cage washed out from tidal inundation, or rain prevented videotaping of a trial. On average, 5.9 trials from each of the 10 days of videotaping were included in the analysis. Sample sizes for each treatment were: male alone, $n=15$; all male, $n=14$; all female, $n=15$; male and female, $n=15$.

Because I conducted this experiment at two different times during the breeding season (May–June and August), I first performed a two-way ANOVA on ranked data (following Zar 1984, pp. 219–222), with time and treatment as factors, to determine if time had any effect on the level of fighting or waving. It did not: ANOVA on waves/min: time, $H=0.05$, $P>0.75$; treatment \times time, $H=3.78$, $P>0.25$; ANOVA on fights/min per male: time, $H=0.05$, $P>0.75$; treatment \times time: $H=0.34$, $P>0.5$). I then removed time as a factor to facilitate comparisons between groups, and used SYSTAT (Wilkinson et al. 1992) to test for differences in waving among treatments (Kruskal-Wallis non-parametric analysis of variance), and differences in fighting between two treatments (Mann-Whitney U -test). I tested for differences in waving between groups of treatments using multiple contrasts for Kruskal-Wallis tests (Zar 1984, pp. 201–202).

Results

Social-context treatments differed significantly in the level of waving by focal males (Fig. 1; $H=14.78$, $P<0.01$). Multiple contrasts revealed that the two groups with females (all female and male and female) differed significantly from the two groups without females (male alone and all male; $S=3.72$, $P<0.01$), demonstrating a significant effect of the presence of females on the level of waving. In contrast, there was no effect of the presence of males, as groups with males (all male and male and female) did not differ from groups without males (male alone and all female; $S=0.90$, $P>0.75$). Therefore, focal males waved significantly more in the presence of females, regardless of whether or not males were also present (Fig. 1).

Despite the low level of waving in the all-male treatment, focal males in this treatment still engaged in fights with other males (mean fights \pm SE=1.64 \pm 0.40; mean fights/min=0.07 \pm 0.02). Although focal males in the male-and-female treatment waved more than males in the all-male treatment (Fig. 1), their absolute level of fighting was slightly lower (mean fights \pm SE=1.13 \pm 0.27; mean fights/min=0.04 \pm 0.01), and there was no difference between these two treatments in the level of fighting corrected for time active and density of males (Fig. 2; $U=90$, $P>0.5$). Only 2 of the 40 fights involving focal males were preceded or followed within 1 min by

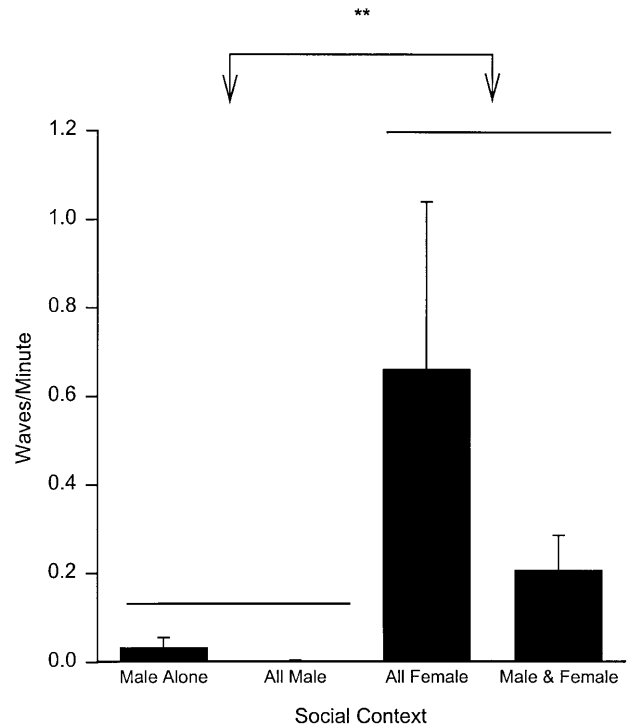


Fig. 1 Average waves/min of focal males in each social-context treatment (means \pm SE). There are significant differences ($P<0.01$) between groups without females (male alone and all male) and treatments with females (all female and male and female). Sample size in each treatment is 15, except the all male ($n=14$)

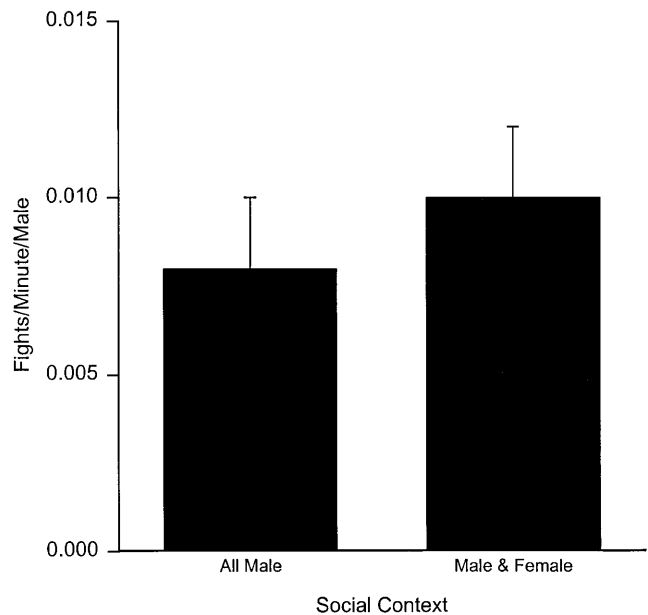


Fig. 2 Average (means \pm SE) fights/min per male of focal males in the two social-context treatments that included multiple males (all male and male and female). There is no significant difference between treatments ($P>0.5$)

waving by either participant. Thus there is no evidence from this experiment that waving behavior is associated with fighting between males.

Discussion

I designed this study to ask whether the fiddler crab claw-waving display is a dual-function signal, or whether it functions more in courtship or defense, by manipulating the social context of resident males. The data clearly indicate that males are unlikely to signal in the absence of any conspecifics (Fig. 1), that females evoke the display significantly more often than males, and that waving is not a necessary prerequisite to fighting between males since fighting was equally prevalent when males were not waving (Fig. 2).

Males displayed at a significantly higher level in the presence of females, whether or not males were also present. By controlling the social context of males and allowing some males access to only females, I can directly infer that it is the presence of females alone that primarily elicits waving behavior even when males are surrounded by individuals of both sexes, as in the natural situation. This result complements Salmon and Stout's (1962) work on the same species in which they demonstrated that territorial males (presumably surrounded by neighbors of both sexes) increased their rate of waving when presented with dead or model females, but switched to aggressive behavior when presented with males.

The males in Salmon and Stout's (1962) experiments were already waving at a low level when they were presented with conspecific stimuli, suggesting that there is some effect of the presence of neighbors in a natural colony that induces a background level of waving. Indeed, the isolated male *U. pugilator* in my experiment did not regularly wave in the absence of conspecifics (Fig. 1). These results confirm observations that males of the same species never wave when socially isolated in the laboratory (Pope 1998), and stop waving when a visual barrier is placed around their burrow (Salmon 1965), as well as the findings of Oliveira et al. (1998) that *U. tangeri* males spent significantly less time waving when completely visually isolated from conspecifics. Claw waving in this species may differ in this way from many other territorial advertisement signals such as birdsong and lizard headbobbing displays which are performed spontaneously in the absence of conspecifics (Carpenter 1967; Searcy and Andersson 1986; DeCourcy and Jensen 1994). This difference may be accounted for by several factors: the signal modality (birds may sing when visually isolated because the range of their acoustic signal may extend further than their visual range), habitat characteristics (the complex forest habitat of many iguanid lizards may select for spontaneous signaling because audiences may be present to detect the signal while remaining undetected themselves), and the high density of *U. pugilator* colonies (crabs that are always surrounded by

other individuals of the same species have no need to display in the absence of conspecifics). Males may wave at a baseline rate when surrounded by potential receivers although not directing the wave at any individual receiver, and then increase the rate when they perceive a female approaching. In contrast to my results, Aizawa (1998) demonstrated that the ocypodid crab *Ilyoplax pusilla* waves at a spontaneous rate even when visually isolated in the laboratory. Further comparative work on these and other ocypodid species may elucidate whether factors such as conspecific density or habitat characteristics explain this difference in spontaneous waving behavior.

The lack of background waving by crabs in my experiment is probably also an effect of the experimental manipulation. There are several estimates of average waving rate of displaying males in the same population: 12.8 waves/min (D.S. Pope, unpublished data; $n=8$), 16.2 waves/min (Salmon 1965; $n=30$), 18–28 waves/min (Hyatt 1977; sample size unclear), each of which is much higher than the average wave rate observed in this experiment (0.71 waves/min for the 19 males that waved). The lower wave rate I observed may be accounted for by several factors: the method I used to estimate a male's time on the surface had a resolution of 5 min and would tend to overestimate the time available for waving and hence underestimate the wave rate; the cage both visually screened most of the area beyond the cage perimeter and limited the number of conspecifics in visual range, and males may have not have completed in the time they were in the cage the specialized breeding burrows which males are known to construct in Florida populations of this species (Christy 1982). Nonetheless, it is unlikely that the experimental manipulation differentially affected crabs in different treatments, and the greater level of waving in the treatments with females present (Fig. 1) is most likely a response evoked by the females themselves rather than an unintended effect of caging.

In this experiment, males engaged in fights without waving first; thus waving is not a necessary preliminary to fighting. While in nature, the males that are waving in a population may also be primarily the males that are fighting, these results demonstrate that waving and fighting can be decoupled, as was suggested by Wolfrath (1993) for *U. tangeri*, and Moriito and Wada (1997) for another ocypodid crab, *Scopimera globosa*.

These results suggest that from the point of view of the displaying male, the claw-waving display of *U. pugilator* functions primarily as a signal to females and thus is not a dual-function signal. However, given the diversity of mating systems, habitats, and displays exhibited by fiddler crabs (Crane 1975), the display may well function differently in other species, and may in fact in many species serve a dual function or primarily function as a signal to males. There are many *Uca* species in which mating takes place primarily on the surface and not in males' burrows, and in these species the display is clearly not used to advertise a breeding burrow to fe-

males and so may function more in male-male interactions. Two experiments on other species of ocypodid crabs, which experimentally manipulated the social context of caged males, found very similar results to mine: both *U. annulipes* (P.R.Y. Backwell, unpublished data) and *S. globosa* (Moriito and Wada, in press) waved significantly more in the presence of females than only males. The fiddler crab, *U. annulipes*, mates primarily in males' burrows (Backwell and Passmore 1996), while *S. globosa* males chase and catch females prior to mating, which takes place either on the surface or in the male's burrow (Moriito and Wada 1997). These results suggest that the function of the claw-waving display and its association with mating systems is complex and deserving of future study.

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