When is waving performed in the ocypodid crab *Scopimera globosa*?

Maki Moriito and Keiji Wada

**Abstract.** — Waving displays of the intertidal ocypodid crab *Scopimera globosa* were observed in the field in relation to other behaviors. Most of the crabs observed to wave were males holding burrows. The proportion of waving crabs was higher in the summer months when ovigerous females and precopulatory behavior (males chasing females) occurred. A negative correlation between waving and precopulatory behavior was found i.e., males performing waving intensively exhibited less frequent precopulatory behavior. However in more than half of the precopulatory behaviors, waving occurred both immediately before and after precopulatory behavior. No correlation was found between the waving frequency and either the frequency of aggressive encounters or the density of neighboring crabs. Immediately before and after an aggressive encounter, the case when waving occurred was observed at a similar frequency to the case when no-waving occurred. These observations suggest that waving in *S. globosa* functions as a courtship behavior advertising burrow-holding males.

**Introduction**

*Scopimera globosa* (De Haan) is a small ocypodid crab inhabiting intertidal sand flats. Each crab holds its own vertical burrow around which it shows surface activity such as feeding during daytime low tides. Population and reproductive biology of this species have been described by several authors (Yamaguchi & Tanaka, 1974; Yamaguchi & Noguchi, 1979; Wada, 1981, 1982, 1983; Suzuki, 1983; Henmi et al., 1989; Henmi, 1991; Koga et al., 1993; Koga, 1995), but none of them have addressed the waving display which is a characteristic behavior of ocypodid crabs where the body moves rhythmically whilst the cheliped is raised and lowered (Crane, 1975).

Waving in fiddler crabs (genus *Uca*) is considered to have both courtship and agonistic functions (Crane, 1975). Salmon (1965) reported that waving rates of male *U. pugilator* intensified when the male was presented with a female. On the other hand, waving of male *U. thayeri* intensified when other large males approached (Salmon, 1987). In other ocypodid species, *Ilyoplax pusilla* (Wada, 1981), *Macrophthalmus japonicus* (Wada, 1984) and tropical *Ilyoplax* species (Kosuge et al., 1994), the males wave intensively to entice the females to their burrows, and in *I. pusilla* (Wada, 1993) and *M. japonicus* (Wada, unpublished), the males also wave to repel other males. All these observations support Crane's (1975) hypothesis that waving has both courtship and agonistic functions in these ocypodids. In *S. globosa*, however, waving (Fig. 1) is not performed when a male pairs with a female (Yamaguchi et al., 1979) and also there have been no observations that the male waves during agonistic interactions. Hence, the function of waving in *S. globosa* is unclear. In this study, the temporal pattern of waving by *S. globosa* is described and the behavioral
Quantitative sampling

In order to describe monthly changes in the population structure of *S. globosa*, samples were collected monthly at daytime during spring low tides, between May and September, 1995, and April and May, 1996. For each sample date, one to five 50 cm × 50 cm quadrats, were selected, where active crabs were abundant. The number of quadrats sampled in each month was varied so that at least 100 crabs were collected. Within each quadrat, crabs were captured by carefully digging the substrate with a shovel to a depth of 20 cm. For all the collected crabs, their sex, carapace width (CW) (the widest part of the carapace), and for females their ovigerous condition were noted. After examination, the crabs were released back into the same collecting sites. The proportion of ovigerous females in each month was calculated for females not smaller than the smallest ovigerous female (4.9 mm CW).

Daily and seasonal changes of waving frequency

The proportion of waving crabs was surveyed every other day during the periods of 16–18, 25–27 May, 19–30 June, 12–30 July, 3–13 August, 20–30 September, 1995, and 14–18 April, 14–19 May, 1996. A permanent quadrat (0.5 m × 5 m) was established in an area (22 cm below the mean tidal level) where *S. globosa* were abundant. Each individual of all the active crabs within the quadrat was observed for 10 sec. to note whether the crabs performed waving or not. On each day, 5 series of quadrat censuses were made at 1 hour intervals between 2 hours before and 2 hours after the estimated time of low tide.

Sex, size and behaviors of waving crabs

During the periods of 16–18, 25–27 May, 19–30 June, 8–30 July, 1–13 August, 1995, small to large crabs (*N* = 457, CW: 3.5–12.6 mm) were selected for 5 min.
observations of their activities. Each crab was classified into one of the following three categories.

Burrow holder – The crab centers its activity about the same burrow, often returning directly back to the burrow.

Wanderer – The crab walks around in a zigzag pattern, without returning to the same burrow.

Wanderer with an occasional burrow holding – During 5 min. observation period the crab is initially a wanderer and then becomes a burrow holder.

For each individual, the frequencies of the following behaviors observed during the 5 min. period were noted.

Waving – Crab extends its chelipeds laterally and raises them upward, with the 1st and the 4th legs lifted off the ground, and then promptly lowers them vertically (Fig. 1).

Aggressive encounter – Aggressive interaction with other individuals including duel (making abdomen-abdomen contact and pushing each other), repelling and entering another crab’s burrow (sometimes with excavation) to usurp it.

Precopulatory behavior – Male chases and catches a smaller crab, which sometimes leads to coupling (surface copulation or entry of the pair into the male’s burrow), when the latter is female.

After the observation, all the crabs were captured by catching for wanderers and by digging burrows for burrow holders, to determine their sex and CW.

A video camera was used to record specimens that waved intensively ($N = 101$) and the behaviors of the surrounding crabs during 19–30 June, 8–30 July, 6–13 August, 1995. Recording time for each crab ranged from 5 to 58 min. After recording, all the crabs were captured, by digging their burrows, to determine their sex and CW. For each of the crabs videotaped for more than 10 min. ($N = 30$), the number of waving strokes, aggressive encounters and precopulatory behaviors during the 10 min. from the start of recording was counted, and the number of neighboring crabs having burrows within 9 to 23 cm from the recorded individual’s burrow were counted to determine the density per 500 cm$^2$. In addition, for crabs videotaped for more than 20 min. ($N = 6$), the occurrence of waving during 10 sec before and after precopulatory behaviors and before and after aggressive encounters were noted.

Results

Density and proportion of ovigerous females

Figure 2 shows monthly changes of population density and the proportion of ovigerous females from May to September, 1995, and April to May, 1996. The density decreased from May to September, and increased slightly afterwards. CW of collected crabs ranged from 2.3 to 12.0 mm in males ($N = 369$) and from 2.2 to 9.2 mm in females ($N = 302$). Ovigerous females occurred from June to September, and peaked in July (51.1%).

Waving crabs

The number of crabs that waved at least once during the 5 min. observations, is summarized, separately for burrow
Table 1. The number of crabs that waved at least once during 5 min. observation periods. Values are given separately for burrow holders, wanderers and wanderers with occasional burrow holding (see Materials and Methods).

<table>
<thead>
<tr>
<th></th>
<th>No. observed crabs (N₁)</th>
<th>No. waving crabs (N₂)</th>
<th>N₂×100 / N₁</th>
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</thead>
<tbody>
<tr>
<td>Burrow holder</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>181</td>
<td>82</td>
<td>45.3</td>
</tr>
<tr>
<td>Female</td>
<td>73</td>
<td>1</td>
<td>1.4</td>
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<tr>
<td>Wanderer</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>72</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Female</td>
<td>36</td>
<td>1</td>
<td>2.8</td>
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<tr>
<td>Wanderer with occasional burrow holding</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>72</td>
<td>16</td>
<td>22.2</td>
</tr>
<tr>
<td>Female</td>
<td>23</td>
<td>1</td>
<td>4.3</td>
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holders, wanderers and wanderers with intermittent burrow holding (see Table 1). Of the burrow holding males (CW: 4.9–12.6 mm), 45.3% (82/181) showed waving behavior. The mean (± SD) number of waving strokes per 5 min. was 7.92±7.63. None of the wandering males waved, but 22.2% (16/72) of the male wanderers (CW: 6.1–10.9 mm) with an occasional burrow holding performed waving when they occupied burrows. Few females (3/132), including a burrow holder and a wanderer, showed waving behavior. The number of strokes per 5 min. by waving females was 1 or 2.

Daily and seasonal changes of waving frequency

Figure 3 shows the number of active crabs and proportion of them showing waving behavior as a function of time before and after low tide on days of spring tides and neap tides from May to September. On each day, the number of active crabs was usually highest 2 hours before low tide, and then decreased gradually. In contrast, the proportion of waving crabs became higher later in the exposed period, and this was more pronounced during spring than neap tides.

The maximum number of active crabs and the maximum proportion of waving crabs on each survey day are shown for the periods from May to September, 1995, and April to May, 1996, in Fig. 4. The proportion of waving crabs increased from May to August, but in September no waving crabs were observed. The proportion of waving crabs was lower around neap tides, and higher around spring tides for each month. Similarly the number of active crabs was higher around spring tides, though the tendency was less pronounced compared to the proportion of waving crabs.

Temporal changes in the frequency of precopulatory behaviors and aggressive encounters

Figure 5 shows the monthly change in the frequencies of precopulatory behaviors and aggressive encounters by burrow-holding males between May and August. Precopulatory behaviors occurred in June to August, with June showing a slightly higher frequency. Aggressive encounters occurred in slightly higher frequency in June, as compared to other 3 months.

Occurrence of waving in relation to precopulatory behaviors and aggressive encounters

The frequency of waving by individual crabs exhibited a significantly negative correlation with the frequency of precopulatory behavior by the individual during the same period excluding the duration spent waving (Fig. 6) (Kendall's test, N = 30, P = 0.0217). In contrast, the frequency of waving exhibited no significant correlation with the frequency of aggressive encounters by the individual during the same period excluding duration spent waving (Fig. 6) (Kendall's test, N = 30, P = 0.4436). Density of neighboring crabs was also not significantly correlated with the frequency of waving (Fig. 6) (Kendall's test, N = 30, P = 0.8853).

Tables 2 and 3 summarize the occur-
Fig. 3. Diurnal changes in the number of active crabs (solid circles) and in the proportion of waving crabs to active crabs (open circles), on 5 days of spring tides (S) and on 3 days of neap tides (N).
Fig. 4. Daily change in the maximum number of active crabs (solid circles) and the maximum proportion of waving crabs from May to September 1995 and from April to May 1996. Arrows indicate rainy days. S: spring tide. N: neap tide.

<table>
<thead>
<tr>
<th>Table 2. Occurrence of waving immediately (within 10 sec.) before and after precopulatory behaviors.</th>
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<tbody>
<tr>
<td>Before</td>
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<tr>
<td>With waving</td>
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<td>After</td>
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<td>With waving</td>
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<th>Table 3. Occurrence of waving immediately (within 10 sec.) before and after aggressive encounters.</th>
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<td>Before</td>
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<td>With waving</td>
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<td>After</td>
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<tr>
<td>Without waving</td>
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<tr>
<td>Total</td>
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Discussion

The proportion of waving crabs increased from May to August, but in September no waving crabs were observed (Fig. 4). Ovigerous females occurred from June to September, with a peak in July (Fig. 2). Precopulatory behavior occurred...
from June to August, with a peak in June (Fig. 5). Consequently, the period of occurrence of waving displays almost corresponds to the reproductive period. Wada (1981) reported that the minimum size of pairing *S. globosa* males was almost the same as that of the waving males. In addition, the present study demonstrates that most of waving crabs were burrow holding males. From these findings, it is hypothesized that waving is performed by burrow holding males for courtship. We suggest burrow holding gives an advantage to a courting male as follows. *S. globosa* is known to have two types of copulatory behavior, i.e., copulation on the sediment surface and underground copulation (Yamaguchi *et al.*, 1979; Wada, 1981). Regardless of the type, in fertilization, the sperm of the last male to mate has precedence (Koga *et al.*, 1993). Because males pairing in their own burrows can guard females until oviposition, underground copulation is an advantageous strategy for males. Hence, a male holding a burrow, a prerequisite for underground copulation, can potentially profit more from copulation than a male without a burrow, because his
paternity is assured.

A possible function of waving by a burrow holding male in the breeding season, is to repel other males out of his burrow's environs. In another ocypodid, *Ilyoplax pusilla*, males repel neighboring crabs by aggressive waving, and such territorial behavior is highly developed in larger males performing sexual behavior (Wada, 1993). We have not observed in *S. globosa* that the male's waving results in any repelling of neighboring males. Immediately before and after aggressive encounters of males, occurrence and non-occurrence of waving showed similar frequencies (Table 3). Waving intensity of an individual exhibited no significant correlation with the frequency of its aggressive encounters or with the density of neighboring crabs. The proportion of waving crabs in the population was higher when the density of active crabs decreased (Fig. 3). Thus it is unlikely that waving is performed to repel other males.

Another possible function of waving by a burrow holding male in the breeding season, is to entice females to approach his burrow. In *Uca tangeri* and *U. pugilator* the male has been shown to change his courtship behavior according to the distance to the female; the male performs waving when the female is far from his burrow, but when she approaches his burrow, he produces sound (Hagen, 1962; Salmon, 1965). The present study shows that immediately before and after precopulatory behavior waving occurred in 15 of 26 precopulatory behaviors (Table 2). When a male captures a female farther from his burrow, the probability that the captured female will be usurped by another male (Wada, 1982) is higher. Hence, the presence of females near the burrow of a courting male would be favorable for the male. Waving by the male possibly serves to attract the female nearer to his burrow in order to reduce the energetic cost of mating, but no data are available to show that females are enticed to approach waving males. This needs to be verified in a future study.

A negative correlation between waving and precopulatory behavior was found in the present study; that is, the proportion of waving crabs was higher in August (Fig. 4) when precopulatory behavior was less frequent (Fig. 5), and males performing waving intensively exhibited less frequent precopulatory behavior. These phenomena can be explained by that the male performs waving when females are less available, whereas males undertake precopulatory behavior when females occur within reach of the male. It should be confirmed in a future study that the male's waving becomes less intensive with increased proximity to mature females.

Female waving was recognized on 3 occasions in the present study. Female waving, though less common compared to male waving, has been shown in the following ocypodid species: *Uca vocans* (Salmon, 1984), *U. polita*, *U. dampieri*, *U. bursutimanus*, *U. vomeris* and *U. seismella* (Hagen, 1993), and *Ilyoplax pusilla* (Wada, 1993). Female waving in fiddler crabs seems to have an agonistic function rather than a courtship function of attracting a mate (Hagen, 1993). Female *S. globosa* waved not only while burrow holding but also during wandering, in contrast to male *S. globosa* that could not be observed to perform waving during wandering in the present study (Table 1). In *Uca polita*, females engage in waving displays when they hold burrows, as do males (Hagen, 1993). The discrepancy between the sexes in waving behavior of *S. globosa* possessing a burrow, implies a different function of waving for males and females. This should be clarified in a future study by gathering more data on the context in which female *S. globosa* show waving.

Acknowledgments

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Literature Cited

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