WAVING DISPLAY BY MALE SCOPIMERA GLOBOSA
(BRACHYURA: OCYPODOIDEA) AS COURTSHIP BEHAVIOR

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Male sand-bubbler crabs Scopimera globosa perform a waving display during their reproductive season, but waving is not used when a male is paired with a female. A male grasps and brings a female into his burrow for mating. We conducted this study to clarify the function of the waving display of S. globosa. The frequency of waving was correlated with male size, and males that paired successfully underground waved significantly more often and were significantly larger than their neighbors. Females that were released in front of waving males either approached or fled from the waving male or they made no response. All the females that approached waving males completed underground pairing without resisting capture by the male, but most females that fled or did not respond resisted capture. Females that approached waving males had more developed ovaries compared to females that fled. These results suggest that waving in S. globosa functions as part of courtship behavior and that waving males detect females with ripe gonads according to how the female responds to the displaying male.

Male mating success generally increases with courtship intensity due to female preferences based on display intensity (Kodric-Brown and Nicotto, 1996; Kotiaho, 2002), and larger males often use more intensive displays and are more successful (Hagelin and Ligon, 2001; Shine et al., 2004). The waving display (the rhythmic motion of chelipeds) performed by ocypodoid crabs living on intertidal flats has been regarded as part of courtship behavior because females are attracted by waving males into the males' burrows where the pairs mate (Yamaguchi, 1972; Wada, 1981). There is, however, scant evidence that larger males have a higher waving rate and are preferred by females. In Uca annulipes, the waving rate by the male is correlated with male size, claw size, and body condition (Jennions and Backwell, 1998), and a male performing a more intensive display is preferred by a female (Backwell et al., 1999).

In the ocypodoid crab Scopimera globosa (de Haan, 1835), which lives on intertidal sand flats of Japanese coasts, the function of the waving display is unclear. Waving is not used to directly attract a female into the male’s burrow (Yamaguchi et al., 1979). Moreover, waving in S. globosa is infrequent compared with other species. For example, pillar-building male U. beebei spent 54.2% of social activity in waving (Christy, 1988), whereas burrow-holding males of S. globosa waved only 18.0% of their time on the surface (Koga, 1995). However, waving does appear to function in courtship of this species. Firstly, the display is observed mostly in burrow-holding males during their reproductive season (Morito and Wada, 1997). Secondly, waving often occurs immediately before precopulatory behavior (Morito and Wada, 1997). Thirdly, the male waving display occurs less frequently in the presence of male neighbors than female neighbors (Morito and Wada, 2000), suggesting that males direct waving to females. If the waving by S. globosa is part of courtship, we expect that (1) males that wave more frequently have higher pairing success, and (2) wandering receptive females are more likely to respond positively to male waving. The present study addressed these expectations in order to clarify the possible courtship function of the waving display of male S. globosa.

Mating Behavior of Scopimera globosa

Scopimera globosa reproduce during the spring and summer (Wada, 1981; Henmi, 1989; Morito and Wada, 1997). This crab has two types of mating behavior (Yamaguchi et al., 1979; Wada, 1981; Henmi et al., 1993). In surface mating, a male dashes to a female and captures her, and the couple copulates on the surface. In underground mating, a male dashes to a female, captures her, carries her to his burrow, enters the burrow, and plugs it. The couple copulate in the burrow (Koga et al., 1993).

MATERIALS AND METHODS

This study was conducted on an intertidal sand flat in the Waka River Estuary in the breeding periods of May to August 2001, May to August 2002, and April to August 2003.

Social Behaviors in Relation to Body Size

To determine whether the occurrence of social behaviors, including waving displays, depends on relative body size of neighboring crabs, the social behaviors of six neighboring burrow holders within an area of about 0.1 m² were observed at daytime low tide around spring tide from May to August in 2001 and 2002. Six crabs were the maximum number for which social behaviors by respective crabs could be recorded with naked eyes by one observer. Total observation days were 20 d in 2001 and 4 d in 2002. In 2001, frequencies of waving, dash, threat, and attack, and occurrence of pairing were recorded for 1 h, and in 2002, frequencies of waving and dash, and occurrence of pairing were recorded for 30 min. After the observation, the burrow diameter and the distance between burrows were measured, and observed crabs were captured by digging to determine carapace width (CW) and sex. Six neighboring crabs observed totalled 24 groups in 2001, and 4 groups in 2002. The number of males in each group varied from 1 to 5 in 2001 (1 male: n = 2, 2 males: n = 3, 3 males: n = 7, 4 males: n = 10, 5 males: n = 2), 2 to 6 in 2002 (2 males: n = 2, 4 males: n = 1, 6 males: n = 1).
Table 1. Comparison of waving frequency and carapace width (CW) between males that completed underground pairing (P male) and their neighboring males (NP male).

| Observation time (min.) | Number of waves | CW (mm) |
|-------------------------|-----------------|---------|
|                         | P male | NP male | P male | NP male |
| Group 1 24 May          | 20     | 6       | 0      | 12.5    | 6.0    |
| Group 2 22 July         | 10     | 0–1 (n = 5) | 10.8   | 4.6–9.9 (n = 5) |
| Group 3 23 July         | 23     | 88      | 0–7 (n = 3) | 10.3   | 4.9–8.3 (n = 3) |
| Group 4 24 July         | 17     | 71      | 2      | 11.0    | 8.8    |

Group 1 was observed on 24 May, Group 2 on 22 July, Group 3 on 23 July, and Group 4 on 24 July.

The correlations between body size and frequencies of waving and aggressive behaviors were analyzed by Kendall’s tau with a blocking variable (Kom, 1984), by calculating tau between crab size (CW) and frequency of each behavior in each group. In the analysis of waving and dash, the data were used from male crabs because these behaviors were performed only by males. Other aggressive behaviors were analyzed for the crabs of both sexes. Pairing success in relation to waving frequency was analyzed by comparing the waving frequencies of males that completed underground pairing with those of their neighbors that did not pair. For four groups in which underground pairing was observed, the number of waves was compared between the males during the period from the beginning of observation to the pairing event.

Female-Releasing Experiments

In order to clarify how a female responded to waving by a male, females were captured by digging and then released near males at daytime low tide on 46 days around spring tide in April to August, 2003. Each female was observed for 10 min to record her response to waving by a male. A total of 652 females were released. Males directed waving to 62 of these females. Response by these females was recorded as approach to the male, escape from the male, or no response. If a male attempted to capture the female, we recorded whether the waving male succeeded, whether the female resisted, and whether the male and the female completed pair formation (entered and remained in the male’s burrow). The positions of the waving male and the female were also described by measuring distances between the male, the female, and the male’s burrow. The male and the female were captured to measure their CW and fixed in 10% formalin. In the laboratory, the wet body weight of the female was measured and then, after dissecting, the wet gonad was weighed to the nearest 0.1 mg. The gonad index was calculated as wet gonad weight relative to wet body weight.

Some males attempted to capture the released females without directing waving. In such a case, we recorded whether the male succeeded in pair formation.

**RESULTS**

Social Behaviors in Relation to Body Size

Frequency of waving and frequency of threat were significantly correlated with body size (waving: Kendall’s rank correlation with a blocking variable, $Z = 2.51, P < 0.05$; threat: $Z = 3.55, P < 0.001$), but between body size and frequency of dash or between body size and frequency of attack there were no significant correlations (dash: $Z = 1.16, P > 0.20$; attack: $Z = 1.74, P > 0.05$).

In all the four groups in which underground pairing was observed, males that paired waved more frequently than did their neighbors ($P = 0.02$, randomization test after each of four groups was treated as a block, Table 1). The body size (CW) of males that paired was larger than their neighbors in all the four groups ($P = 0.02$, randomization test after each of four groups was treated as a block, Table 1).

Female-Releasing Experiments

Among 62 females to which males directed waving, 11 approached the males, 42 fled, and 9 exhibited no response. The CW of the female and CW of the male that waved at the female were not significantly different among the three categories of females (one-way ANOVA, female: $F = 0.72, P = 0.49$; male: $F = 0.68, P = 0.51$). There was no significant difference among the three categories of females in the distance between the male and the female (one-way ANOVA, $F = 0.15, P = 0.86$) or the distance between the female and the male’s burrow (one-way ANOVA, $F = 0.34, P = 0.71$). Females that approached the waving males were captured by the males and completed underground pairing significantly more frequently than females that fled (Table 2).

Among them, 42 males succeeded in pair formation.

**DISCUSSION**

Frequency of waving of *S. globosa* was significantly correlated with the male size, as reported in *Uca annulipes* (see Jennions and Backwell, 1998). Moreover, males that completed underground pairing were significantly larger in CW and waved significantly more often than their neighbors. These findings suggest that either large body size or more intensive waving is beneficial in capturing a female and enhances male’s mating success. Koga and Murai (1997) found that male *S. globosa* were often disturbed by other
males during attempts at pairing, and if the male attempting to pair was larger, he was able to repel the challenger and pair successfully. Thus, large males may be more successful because they are less likely to be disturbed by other males. Larger males may also detect the receptive females more efficiently, as suggested for the spider crab *Inachus phalangium* by Diesel (1986).

On the other hand, waving itself may facilitate capturing a female. This explanation can be supported from the female-release experiment. When a male waved at a female, she approached, fled, or did nothing. Females that approached did not resist capture or underground pairing, but females that fled did. There was no significant difference among the three categories of females in the body size or the distance between the male and the female. Females that approached showed significantly higher gonad index than other females. If a male waves at a female with ripe gonads, she approaches and accepts capture. Males attempted to capture females that approached but seldom those that fled. Males appear to detect receptive females with ripe gonads by their response to waving. Only about 18% of the females that responded approached the waving males. Males, however, captured these females without failure. If males attempt to capture females without waving, they often fail because the females resist or the males are disturbed by other males. In fact, waving is known to commonly occur immediately before precopulatory behavior (Moriito and Wada, 1997). Furthermore, we found in the female-release experiment that 63 of 105 males that attempted to capture females without waving lost females and failed in pair formation. Considering such occurrence of failure of the males in capturing females without waving, it is meaningful for the male to perform waving display because the receptive female responds positively to the waving, leading to perfect success in pair formation. Although many males seem to attempt to capture females without waving, those females would include not only receptive females but also nonreceptive ones with unripe gonads. Therefore, it is reliable means to attempt the capture following waving for acquiring receptive female. Consequently, it can be said that waving of male *S. globosa* functions as male courtship.

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