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ARTICLE

Courtship tactics by male *Ilyoplax pusilla* (Brachyura, Dotillidae)

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Abstract Mating in the dotillid crab *Ilyoplax pusilla* occurs after the female enters the male's burrow in the tidal flat. Males use two tactics to cause females to enter their burrows for mating: the male either directs claw waving to the female (courting-wave display), to which the females responds by following the male to his burrow, or the male runs rapidly away from, then back toward, his burrow (dash-out-back display), which startles the female into his burrow. Males more often used the courting-wave than the dash-out-back display, but mating success did not differ between the two tactics. Male use of either tactic was influenced by date, female density and male size; the courting-wave display was used by larger males, later in the breeding period, and under higher female density.

Keywords Courtship tactics · Ocypodoid crab · Mating success · Sensory trap signal · Courtship display

Introduction

Courting males sometimes use signals that include stimuli to which females respond in other contexts (Christy 1995). Not surprisingly, food is often the model for such mimetic signals: females approach males that use food-like signals as they would approach food (e.g., Proctor 1992; Rodd et al. 2002) and this increases the chance that the male will mate with the female. However, male crabs of some ocypodoid species sometimes use displays that elicit responses from females that function for escape from predators not for finding food (Christy 2007; Christy and Rittschof 2011). These displays are used by males of at least three fiddler crab species, *Uca pugilator*, *U. terpsichores* and *U. beebei* (Christy and Rittschof 2011) and three species of the dotillid genus *Ilyoplax*, namely *I. pusilla* (Wada 1981), *I. pingi* and *I. dentimerosa* (Wada et al. 1996). If the burrow has a courtship structure, such as a sand hood as built by *U. terpsichores*, the male may move slowly behind the structure, then rapidly over the top, producing the back-and-over display. If the burrow lacks a structure at the entrance, which is always the case for *Ilyoplax* spp., the male may move quickly away from, then, with its claws raised high, back to, the burrow, producing the dash-out-back display. The female sees the rapidly moving and elevated claws or the body of the displaying male above her visual horizon; stimuli such as these from predators elicit an escape response (Layne 1998), and startle the female to enter the male's burrow. Although these startling displays have been seen frequently, they are less common than the courting-wave display that males usually use to attract females to their burrow. The contexts that favor the use of these displays are not known. In addition, relative success of these startling displays compared to the more common courting-wave display has not been measured.

Here, we report the results of a study of the contexts in which males of the dotillid crab *I. pusilla* uses the courting-wave and the dash-out-back displays and the relative success of each.

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Materials and methods

Study species

The dotillid crab *Ilyoplax pusilla* (De Haan, 1835) lives in burrows in intertidal mudflats. Males use both courting-wave and the dash-out-back displays to get females to enter their burrows (Wada 1981; Yoshimura and Wada 1992), where the crabs mate and the female stays and produces a clutch of eggs about 3 days later (Henmi and Murai 1999).

Courting-wave display (Fig. 1)

A male directs vigorous claw waving (the courting-wave display) to a female that is either using a burrow near the male or is moving on the surface and is not associated with a given burrow. The female approaches the waving male. The male then enters his burrow while waving to the female and she follows him into the burrow (male-first entry). Alternatively, the male may cease waving and step back from the female before she reaches his burrow. The female approaches and enters the burrow and the male quickly follows (female-first entry). Soon after the crabs enter the burrow, the male emerges, gathers sediment from the surface and plugs opening of the burrow as he reenters it, sealing both him and the female in the burrow.

Dash-out-back display (Fig. 2)

We recognize three forms of this display according to where the female is located, relative to the male and his burrow, and the path the male takes away from and back to the burrow: (1) the male circles the female with the female between the male and the burrow (circle, female-inside), (2) the male moves in a circle but the female is outside his path (circle, female-outside), and (3) the male moves linearly away from and back to his burrow (linear). The female responds to this display by moving toward and entering the male's burrow first and the male then follows. Soon after entering the burrow, the male emerges, gathers sediments and plugs the

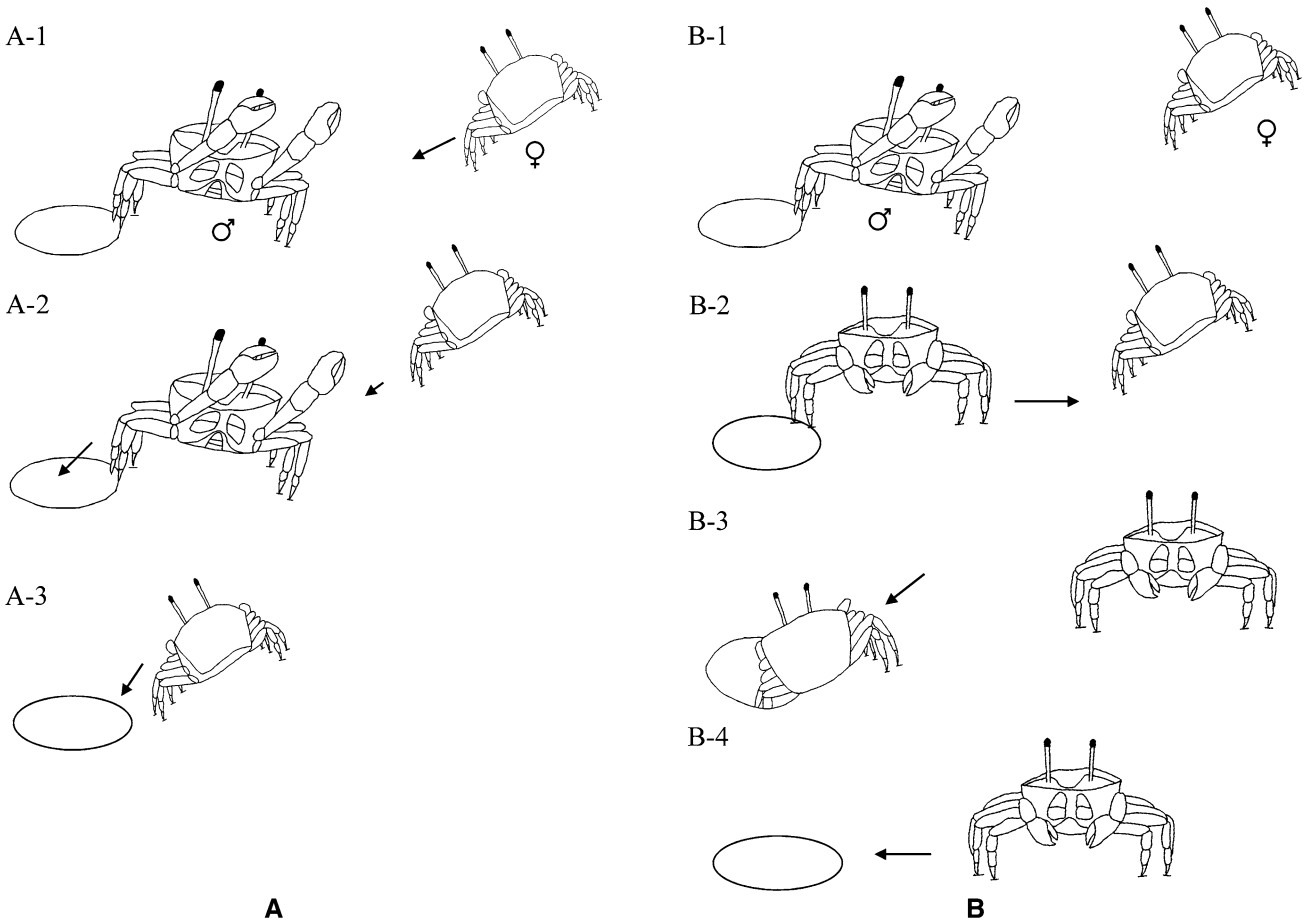

Fig. 1 Behavioral sequences during use of the courting-wave display when the male enters his burrow first (**A**) and when the female enters first (**B**). **A-1** A male directs his wave to a female; **A-2** the female approaches the male, then the male enters his burrow; **A-3** the female enters the male's burrow. **B-1** A male directs his wave to a female; **B-2** the female approaches then the male moves away from the female and his burrow; **B-3** the female enters the male's burrow, while the male is motionless; **B-4** the male quickly enters his burrow

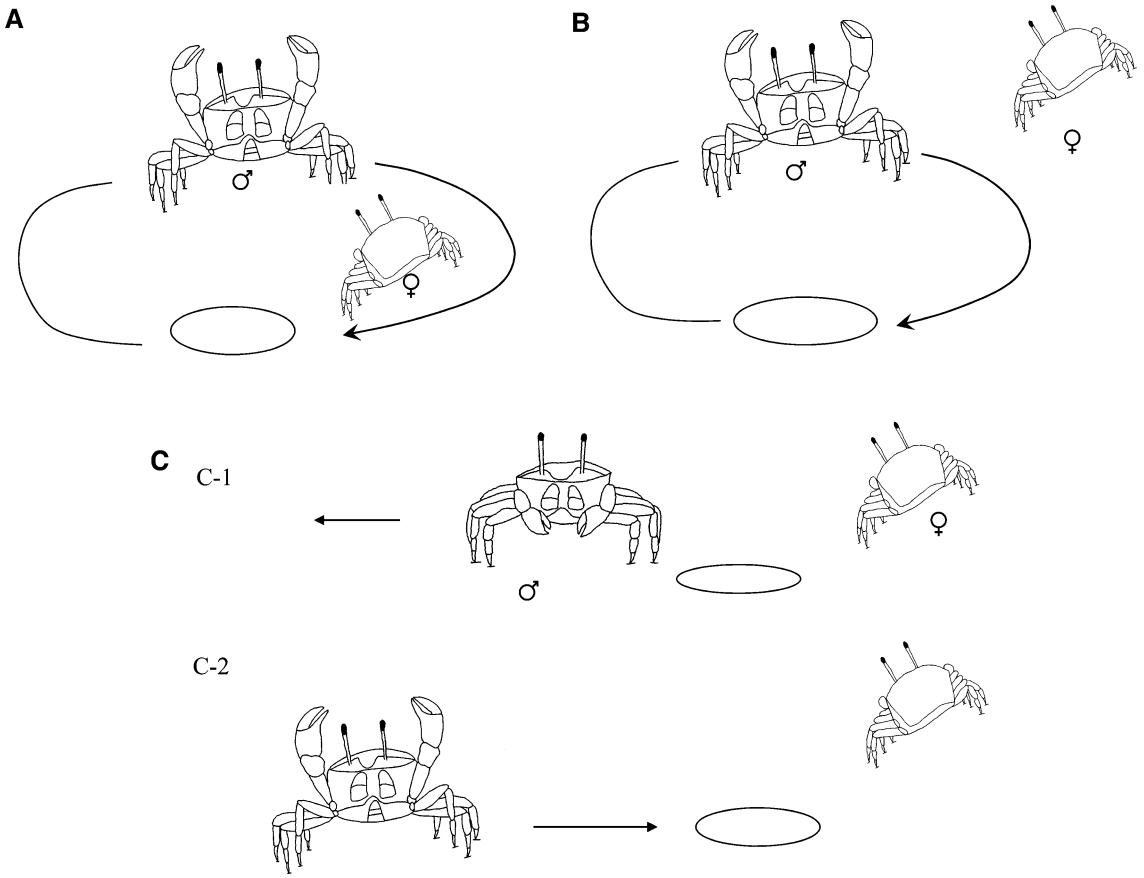

Fig. 2 Behavioral sequences during use of the dash-out-back display when **A** the male circles the female and she is inside the *circle*, **B** the female is outside the *circle*, and **C** the male moves linearly away from and back to his burrow. **A** A male quickly circles around a female, while raising his chelipeds. **B** A male quickly circles between his burrow and a female, while raising his chelipeds. **C-1** A male dashes away from his burrow, then **C-2** back to it with his chelipeds raised

burrow. Although the dash-out-back display looks like the courtship herding observed in *Uca vocans* (Salmon 1984) or *U. elegans* (How and Hemmi 2008), the dash-out-back display differs from the courtship herding in that the male startles the female to escape into his burrow.

Field observations

The courtship and mating behavior of *Ilyoplax pusilla* was observed on an intertidal mudflat at Uchinoura, Wakayama Prefecture, Japan (33°41′N, 135°23′E) from June to August 2009, covering the breeding period of this species (Yoshimura and Wada 1992). A permanent quadrat, measuring 2 × 2 m, was established on the tidal flat in area inhabited by *I. pusilla*. The crabs with burrows inside the quadrat were observed for 2–8 days around the spring tides, for a total of 19 days.

On each day, starting at low tide, a different half of the quadrat (2 × 1 m) was observed for 40 min during each of 4-h-long periods, ending with the period starting 3 h after low tide. When a courtship display by a male was witnessed, approximate carapace width (CW) of the male and the female was recorded, and it was noted whether the display was male-first type or female-first type in case of courting-wave display, or it was circle, female-inside, circle, male-inside or linear in case of dash-out-back display, whether the female entered the male's burrow or not, and whether the burrow that the couple entered was finally plugged by the male (mating) or not. At the end of each 40-min observation period, the numbers of active males, active females and waving males within the observation area were recorded. The size of each active crab was estimated as SS (under 4 mm CW), S (4–6 mm CW), M (6–8 mm CW), L (8–10 mm CW), and LL (larger than 10 mm CW). The sex of each crab larger than 4 mm CW was determined by the shape of its cheliped (thick in males and thin in females). Mature males were of size class M or larger because the minimum size of males that have been observed mating at Uchinoura ($n = 84$) is 7.0 mm CW (Ohata and Wada unpublished). Mature females were of size class S or larger because the minimum size of ovigerous females at Uchinoura is 4.2 mm CW (Yoshimura and Wada 1992).

At the end of the study, the density of crabs living inside the quadrat was estimated by digging all crabs out of 8 smaller quadrats, each measuring 25 × 25 cm, that were positioned randomly within the larger quadrat (2 × 2 m). The size and sex of each crab was recorded.

Data analysis

Activity and sex ratio

The density of active crabs (number of crabs per m^2) on each day was calculated as the average of the four counts each day. To study the difference by sex in the density of active adults, ANCOVA was used with sex and date as independent variables and the density as the dependent variable, after checking non-significance of the interaction term. The sex ratio, expressed as the proportion of males, was obtained by dividing the density of active males by the density of active adult males and females each day. The proportion of males that waved each day was calculated as the total number of waving males divided by the number of active males.

Frequency and success of the two courtship tactics

The frequencies of the courting-wave and the dash-out-back displays were the number of each divided by the total number of courtships observed during the study. The success of each display was measured at two steps in the interaction between courting males and females: (1) whether the female entered the male's burrow and (2) whether the female stayed in the burrow and the male plugged the burrow. *G* tests of independence were used to determine whether the success at each step depended on the courtship tactic males used.

Factors influencing use of the two courtship tactics

Logistic regression was used to identify the factors that affect which courtship display males use. All uses of either display by male crabs, irrespective of whether the display resulted in a mating, were used for this analysis. The display a mature male used was the dependent variable. Explanatory variables were date, days before or after spring tide, proportion of waving males, density of mature males, density of mature females, carapace width of the displaying male, and carapace width of the mature female to which the display was directed. We used stepwise backward elimination until the *P* values of all explanatory variables fell below 0.05. All the analyses were conducted using JMP version 8.0 (SAS Institute 2009).

Results

Activity and sex ratio

Most of the active crabs were mature adults (Table 1). Both sex and date had a significant effect on the density of active adults (ANCOVA, $F = 12.18$, $P < 0.01$ for sex; $F = 6.50$, $P < 0.05$ for date), with greater density for males and early in the season, respectively. The sex ratio of active crabs was therefore biased to males (Table 1). However, the sex ratio of mature crabs in the quadrat (estimated by digging) was not biased to either sex (20 males vs. 21 females; binomial test, $z = 0.0$, $P > 0.9$). The proportion of males that waved each day ranged from 5.7 to 75.3%.

Frequency and success of the two courtship displays

In total, 527 courtships were observed: males used the courting-wave display more often (396/527 = 75.1%) than the dash-out-back display (131/527 = 24.91%) (Binomial test, $z = 11.53$, $P < 0.01$).

The courting-wave display led more often to male-first entry ($n = 38$) than female-first entry ($n = 17$) (Binomial test, $z = 2.83$, $P < 0.01$). There was no significant difference in the proportion of male-first and female-first entries that resulted in mating (male-first entry 21/38, female-first entry 5/17) (*G* test, $G_{adj} = 3.12$, $P > 0.05$). The frequency of the three forms of the dash-out-back display were circle, female-inside, $n = 50$, circle, female-outside, $n = 60$, and linear, $n = 21$. Relative frequency of the burrow entry by the female was higher in circle, female-inside form (13/50 = 26.0%) than in circle, female-outside form (1/60 = 1.7%) or linear form (2/21 = 9.5%) (*G* test, $G_{adj} = 16.98$, $P < 0.001$). Only the circle, female-inside form resulted in mating ($n = 3$).

The mating success relative to the courtship display was low in the both tactics, and not different between the tactics (Table 2). The burrow-entry frequency relative to the courtship display was also not different between the two tactics (Table 2). However, females entering a male's burrow in response to the courting-wave display were

Table 1 Number of active crabs, the proportion of waving males and sex ratio (proportion of adult males among adult males and females) in the study area per day during study period ($n = 18$ days)

	Mean ± SD	Range
Number of mature males/m^2	18.3 ± 6.3	6.6–29.3
Number of mature females/m^2	9.9 ± 3.5	2.9–15.5
Number of subadults/m^2	3.3 ± 2.6	0.9–11.4
Proportion of waving males (%)	37.4 ± 20.9	5.7–75.3
Sex ratio	0.67 ± 0.12	0.53–0.84

significantly more likely to stay and mate, compared to females in response to the dash-out-back display (Table 2).

Factors influencing use of the two courtship tactics

Backwards elimination resulted in a logistic regression model that included three factors as predictors of the two male courtship displays: date (likelihood $\chi^2 = 14.84$, $P < 0.0001$), density of mature females (likelihood $\chi^2 = 24.74$, $P < 0.0001$) and carapace width of the courting male (likelihood $\chi^2 = 14.97$, $P < 0.001$). Males used the courting-wave display more frequently and the dash-out-back display less frequently later in the breeding period (Fig. 3). Large males used the courting-wave display more often than did small males (Fig. 3).

Discussion

This present study has demonstrated that courting male *Ilyoplax pusilla* more often use the courting-wave than the dash-out-back display. The dash-out-back display is thought to exploit a startle response of females by mimicking stimuli that are associated with a fast-approaching predator (Christy and Salmon 1991). If predation is infrequent, then the cost of failing to respond to the display should be small and females may be expected to habituate to the display if males used it frequently. This may explain why males used the dash-out-back display less often than courting-wave. Although the dash-out-back tactic was less common, there was no difference in the mating success (per courtship) of males that used the two kinds of courtship tactics. Hence, females do not prefer as mates males that use one tactic over the other and both are equally effective ways of obtaining a mate.

However, females that entered males' burrows in response to the courting-wave display were more likely to stay in those burrows and mate. Some of the females that were startled into males' burrows by the dash-out-back display may not have been sexually receptive while all of the females that entered males' burrows in response to the courting-wave probably were sexually receptive. Such a female condition may be responsible for the difference in burrow-staying of the females between the two tactics.

In courtship in which males used the courting-wave display, either the male or the female entered the male's burrow first. Males more often entered the burrow first, but the sex that entered first did not affect whether the crabs mated. In the fiddler crab *Uca tetragonon*, either sex may enter the male's burrow first. Unlike *I. pusilla*, both do so with equal frequency but, like *I. pusilla*, the frequency with which the crabs then mate does not depend on which sex entered first (Murai et al. 1995). The dash-out-back display had three forms differing in male movement and the location of the female relative to the male and his burrow. Among the three forms, the female was more likely to enter the male's burrow in circle, female-inside form, compared to other forms, and mating occurred only in circle, female-inside form. In this form of the display, the female is nearer the burrow than the male at the apex of the movement. If she startles, she will move away from the male and toward

Table 2 Success of the courting-wave and the dash-out-back displays measured as the number of matings per courtship, the number of burrow entries by the female per courtship and the number of matings per burrow entry

	Matings/ courtship	Entries/ courtship	Matings/ entry
Courting-wave	0.07 (26/396)	0.14 (55/396)	0.47 (26/55)
Dash-out-back	0.02 (3/131)	0.12 (16/131)	0.19 (3/16)
G test	$G_{adj} = 2.01$, $P > 0.05$	$G_{adj} = 0.24$, $P > 0.05$	$G_{adj} = 4.36$, $P < 0.05$

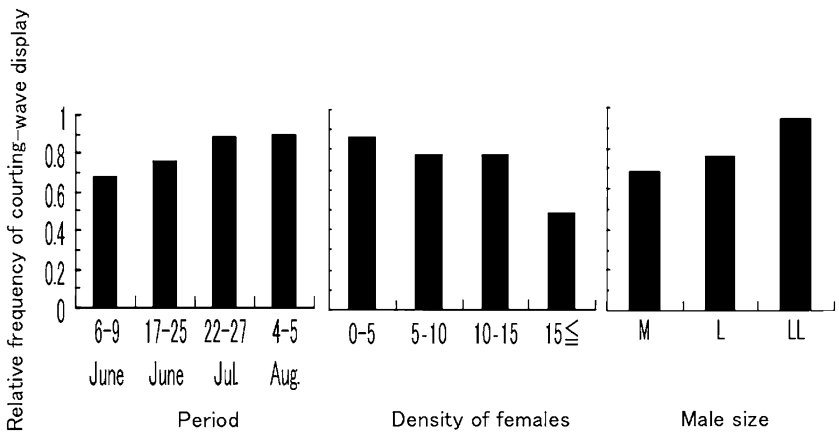

Fig. 3 Proportion of the courting-wave display in relation to date, female density and male size

his burrow. This would not typically be true for the other forms of the display.

The date, density of mature females, and the body size of the male all influenced which courtship display males used. The dash-out-back display was used more often early in the breeding period, by smaller males and when female density was high. The dash-out-back display is directed mostly to wandering females, whereas the courting-wave display is directed to both wandering and burrow-holding females (Yoshimura and Wada 1992). Wandering females of *I. pusilla* are less abundant later in the breeding period (Yoshimura and Wada 1992), which may explain why use of the dash-out-back display declined as the breeding period progressed. In the fiddler crab *Uca beebei*, female wandering increases with density (de Rivera et al. 2003). If this occurs in *I. pusilla*, then this may explain why males more often used the dash-out-back display when female density was high. Smaller males more often used this startling display than did large males perhaps because they are less able to attract females with the courting-wave display. It should be confirmed in future studies whether males use the dash-out-back display more often as the number of wandering females increases, and whether larger males are more attractive to females than are smaller males.

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References

Christy JH (1995) Mimicry, mate choice and the sensory trap hypothesis. Am Nat 146:171–181

Christy JH (2007) Predation and the reproductive behavior of fiddler crabs (genus *Uca*). In: Thiel M, Duffy JE (eds) Evolutionary ecology of social and sexual systems: crustaceans as model organisms. Oxford University Press, Oxford, pp 211–231

Christy JH, Rittschof D (2011) Deception in visual and chemical communication in crustaceans. In: Thiel M, Breithaupt T (eds) Chemical communication in crustaceans. Springer, Heidelberg, pp 313–333

Christy JH, Salmon M (1991) Comparative study of reproductive behavior in mantis shrimps and fiddler crabs. Am Zool 31:329–337

de Rivera CE, Backwell PRY, Christy JH, Vehrencamp SL (2003) Density affects female and male mate searching in the fiddler crab, *Uca beebei*. Behav Ecol Sociobiol 53:72–83

Henmi Y, Murai M (1999) Decalcification of vulvar operculum and mating in the ocypodid crab *Ilyoplax pusilla*. J Zool 247:133–137

How MJ, Hemmi JM (2008) Courtship herding in the fiddler crab *Uca elegans*. J Comp Physiol A 194:1053–1061

Layne JE (1998) Retinal location is the key to identifying predators in fiddler crabs (*Uca pugilator*). J Exp Biol 201:2253–2261

Murai M, Goshima S, Poovachiranon S (1995) Courtship and the evolution of underground mating in *Uca tetragonon* (Decapoda: Ocypodidae). J Crust Biol 15:655–658

Proctor H (1992) Sensory exploitation and the evolution of male mating behaviour: a cladistic test using water mites (Acari: Parasitengona). Anim Behav 44:745–752

Rodd FH, Hughes KA, Grether G, Baril CT (2002) A possible non-sexual origin of a mate preference: are male guppies mimicking fruit? Proc R Soc Lond B 269:475–481

Salmon M (1984) The courtship, aggression and mating system of a "primitive" fiddler crab (*Uca vocans*: Ocypodidae). Trans Zool Soc Lond 37:1–50

SAS Institute (2009) JMP version 8.0, Japanese edn. SAS Institute, Cary

Wada K (1981) Growth, breeding, and recruitment in *Scopimera globosa* and *Ilyoplax pusillus* (Crustacea: Ocypodidae) in the estuary of Waka River, middle Japan. Publ Seto Mar Biol Lab 26:243–259

Wada K, Choe LB, Park KJ, Yum SS (1996) Population and reproductive biology of *Ilyoplax pingi* and *I. dentimerosa* (Brachyura: Ocypodidae). Crust Res 25:44–53

Yoshimura S, Wada K (1992) Seasonality of reproductive activity in *Ilyoplax pusilla* (Brachyura: Ocypodidae). Res Crust 21:125–138 (in Japanese with English abstract)