Characteristics of aggressive behaviors of five species of the genus *Ilyoplax* (Brachyura, Dotillidae) in East Asia

Keiji Wada, Haruka Ida

**Abstract.**— Aggressive behaviors are described for five species of the genus *Ilyoplax* (Dotillidae), *I. pusilla* (De Haan, 1835), *I. formosensis* (Rathbun, 1921), *I. ningpoensis* Shen, 1940, *I. deschampsi* (Rathbun, 1913), and *I. tansuiensis* Sakai, 1939, and the male/female ratios are compared relative to the sex ratio of the population. Aggressive behaviors were similar in all species. The main types of aggressive behaviors, including aggressive dash, aggressive wave, and wrestling, were common to the five species. The mutual aggression of wrestling was confined to male crabs in all five species. The frequencies of aggressive behaviors were higher in male crabs than in female crabs, suggesting male-biased aggressiveness. This may be reflected in the male-biased carapace and chela size dimorphisms observed in *I. pusilla*.

**Key words:** aggressive behavior, *Ilyoplax*, sex differences in aggressiveness, sexual size dimorphism

**Introduction**

Many brachyuran crab species display marked sexual dimorphism. Males have larger bodies and chelae than females have (Warner, 1977), perhaps because males face more intense intrasexual aggression than females do. However, few studies have examined the frequencies of aggressive behaviors in relation to sex ratios to support the assumption that males perform these behaviors more frequently than do females (Ida & Wada, in press).

The crab species of the genus *Ilyoplax* (Brachyura, Dotillidae) live on intertidal mud flats in the temperate to tropical Indo-West Pacific region. Wada (1993) described aggressive anti-neighbor behaviors in one species of the genus, *I. pusilla*, and noted that male aggressors were more common than female aggressors. However, sexual size dimorphism remains undescribed. In addition, there have been few reports of aggressive behaviors in other congeneric species (Wada & Wang, 1998), though mud-using anti-neighbor behaviors have been described in detail for some species (Wada, 1984, 1987, 1994; Takayama & Wada, 1992; Wada et al., 1994, 1998; Wada & Park, 1995).

This paper describes sexual dimorphism in the carapace and chela sizes of *I. pusilla* (De Haan, 1835). Additionally, the sex ratios of aggressive behaviors in five congeneric species, i.e. *I. pusilla, I. formosensis* Rathbun, 1921, *I. ningpoensis* Shen, 1940, *I. deschampsi* (Rathbun, 1913) and *I. tansuiensis* Sakai, 1939, which are distributed in East Asia, were compared in terms of behavior type and aggression frequency relative to the population sex ratio.

**Materials and Methods**

*Morphometric characters of Ilyoplax pusilla*

To clarify sexual size dimorphism in *Ilyoplax pusilla*, we measured carapace width (CW; measured across the widest part of the carapace), chela propodus length (CPL), and chela propodus width (CPW) of 50 male and 59 female specimens collected in Shirahama, Wakayama, Japan. The chelae were measured.
from the right side of the body. Measurements were taken to the nearest 0.1 mm using a caliper.

The data on CW, CPL, and CPW were transformed into natural logarithms. We then plotted the regressions of CPL and CPW relative to CW, doing so separately for males and females. We used a general linear model (GLM) to compare the sexes for all size measurements. Statistics were calculated in JMP9 (SAS Institute, 2010).

Sex ratio of the population and the maximum body size of each sex
For all the five species (I. pusilla, I. formosensis, I. ningpoensis, I. deschampsi, and I. tansuiensis), crabs were collected from 4 to 14 quadrats (25 × 25 cm) in the field (mid- to high intertidal mud flat) (Table 1) to determine the sex ratios of the populations and the maximum body sizes of each sex. The maximum CW of each sex in the collected specimens was used to represent the sexual difference in the body size. We did not use the average size of the collected specimens as the body size of each sex, because the proportion of the mature crabs was not consistent among the five species.

Aggressive behaviors
Aggressive behaviors of the five species (I. pusilla, I. formosensis, I. ningpoensis, I. deschampsi, and I. tansuiensis) were observed in the field (mid- to high intertidal mud flat) during the daytime low tide around the spring tide (Table 1). Observed aggressive behaviors were described, and the sexes of crabs displaying the aggressive behavior were determined by collecting the crabs.

We identified four types of aggressive behaviors in each species (see Results section). To assess the frequencies of the different types of aggressive behaviors by sex, we compared the sex ratio of the aggressors (crabs that performed each of the aggressive behaviors) with the sex ratio of the population (Table 1), which was obtained from the quadrat sampling. For each of the four types of aggressive behaviors, the number of aggressors observed was totaled separately for males and females, and the male/female frequency ratio was compared with the sex ratio of the population using a binomial test.

Results
Proportional feature of chelae in I. pusilla
In both males and females of I. pusilla, the CPL and CPW were positively correlated with CW (Fig. 1). Furthermore, these size measurements were larger in males than in females relative to CW; males had longer and wider chelae than females. The slopes of the regression lines for chela length and chela width against body size were steeper in males than in females (Fig. 1, Table 2).

Density and maximum body sizes of five species
Mean density per 625 cm² was highest in I. formosensis (26.3) and lowest in I. tansuiensis (4.2) (Table 3). The maximum CW was larger...
in males than in females in *I. pusilla*, *I. formosensis*, *I. deschampsi*, and *I. tansuiensis* (male/female CW ratio: 1.1–1.2), but in *I. ninpoensis*, the maximum CW was similar in males and females (male/female CW ratio: 1.0) (Table 3).

### Aggressive behaviors in *I. pusilla*

Four types of aggressive behaviors were identified: three one-sided aggressions of aggressive dash, aggressive wave and lateral leg push, and one mutual aggression of wrestling. In the aggressive dash, one rival directed an aggressive dash toward the neighboring crab without raising its chelipeds (Fig. 2). The aggressive dash was observed equally in male (*N* = 14) and female aggressors (*N* = 14) (binomial test, *P* = 0.77).

In the aggressive wave, one rival waved the chelipeds toward the neighboring crab (Fig. 2). The aggressive wave was observed significantly more frequently in male aggressors (*N* = 75) than in female aggressors (*N* = 6) (binomial test, *P* < 0.001).

In the lateral leg push, one rival pushed the

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**Table 2.** Results of a general linear model that included two factors, carapace width (CW) and sex, as predictors of chela propodus length (CPL) and chela propodus width (CPW) in *Ilyoplax pusilla*.

<table>
<thead>
<tr>
<th>Factor</th>
<th><em>F</em></th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>CPL</td>
<td>1125.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>sex</td>
<td>931.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>lnCW × sex</td>
<td>9.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>CPW</td>
<td>706.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>lnCW × sex</td>
<td>52.8</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

**Table 3.** Mean densities (per 625 cm$^2$) with ranges for five species of *Ilyoplax* and the maximum carapace widths (mms) of males and females and their ratios (male/female) in the populations studied.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean density</th>
<th>Male</th>
<th>Female</th>
<th>Ratio (male/female)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>I. pusilla</em></td>
<td>15.7 (5–22)</td>
<td>10.4</td>
<td>9.3</td>
<td>1.12</td>
</tr>
<tr>
<td></td>
<td>(<em>N</em> = 14)</td>
<td>(<em>N</em> = 50)</td>
<td>(<em>N</em> = 59)</td>
<td></td>
</tr>
<tr>
<td><em>I. formosensis</em></td>
<td>26.3 (9–51)</td>
<td>9.7</td>
<td>8.3</td>
<td>1.17</td>
</tr>
<tr>
<td></td>
<td>(<em>N</em> = 8)</td>
<td>(<em>N</em> = 112)</td>
<td>(<em>N</em> = 96)</td>
<td></td>
</tr>
<tr>
<td><em>I. ninpoensis</em></td>
<td>8.9 (3–16)</td>
<td>9.5</td>
<td>9.4</td>
<td>1.01</td>
</tr>
<tr>
<td></td>
<td>(<em>N</em> = 14)</td>
<td>(<em>N</em> = 75)</td>
<td>(<em>N</em> = 76)</td>
<td></td>
</tr>
<tr>
<td><em>I. deschampsi</em></td>
<td>14.3 (2–23)</td>
<td>10.8</td>
<td>10.0</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>(<em>N</em> = 5)</td>
<td>(<em>N</em> = 40)</td>
<td>(<em>N</em> = 31)</td>
<td></td>
</tr>
<tr>
<td><em>I. tansuiensis</em></td>
<td>4.2 (2–6)</td>
<td>7.0</td>
<td>6.1</td>
<td>1.15</td>
</tr>
<tr>
<td></td>
<td>(<em>N</em> = 6)</td>
<td>(<em>N</em> = 28)</td>
<td>(<em>N</em> = 8)</td>
<td></td>
</tr>
</tbody>
</table>
neighboring crab laterally with the ambulatory legs (Fig. 2). The lateral leg push was observed more frequently in male ($N = 25$) than in female aggressors ($N = 17$), but the difference between the sexes was not significant (binomial test, $P = 0.34$).

In the wrestling behavior, two neighboring crabs were aggressive toward each other; both crabs intertwined their chelipeds, occasionally with one crab grasping the other crab (Fig. 2). The wrestling was performed only between male crabs ($N = 48$); none of the female crabs showed this behavior. This difference was significant (binomial test, $P < 0.0001$).

**Aggressive behaviors in I. formosensis**

As in *I. pusilla*, four types of aggressive behaviors were identified: three one-sided aggressions of aggressive dash, aggressive wave and lateral leg push, and one mutual aggression of wrestling. The aggressive dash was observed significantly more frequently in male ($N = 24$)
than in female aggressors \((N=2)\) (binomial test, \(P<0.001\)). The aggressive wave was also observed significantly more frequently in male \((N=14)\) than in female aggressors \((N=2)\) (binomial test, \(P=0.04\)). The lateral leg push was performed with similar frequency in males and females \((N=21 \text{ and } 19, \text{ respectively}; \text{ binomial test, } P=0.95\)). The wrestling behavior was performed only between male crabs \((N=35)\), with no female crabs engaging in this behavior. This difference was significant (binomial test, \(P=0.0001\)).

Aggressive behaviors in \(I. \) ningpoensis

Aggressive dash, aggressive wave, and wrestling were recognized, as in \(I. \) pusilla and \(I. \) formosensis, but mutual aggression other than wrestling was observed in a mutual lateral push. In this last behavior, the two neighboring crabs pushed each other laterally. The aggressive dash was observed significantly more frequently in male \((N=25)\) than in female aggressors \((N=9)\) (binomial test, \(P=0.005\)). The aggressive wave was performed by male crabs \((N=14)\), but not by any of the females (binomial test, \(P<0.0001\)). Wrestling was performed only between male crabs \((N=6)\); this difference was significant (binomial test, \(P=0.0002\)). The mutual lateral push was observed between male crabs \((N=21)\), between male and female crabs \((N=25)\), and between female crabs \((N=8)\). This behavior was not biased toward either sex (binomial test, \(P=0.063\)).

Aggressive behaviors in \(I. \) deschampsi

As in \(I. \) pusilla, four types of aggressive behaviors were identified: three one-sided aggressions of aggressive dash, aggressive wave and cheliped trembling, and one mutual aggression of wrestling. In cheliped trembling, one rival faced the neighboring crab and trembled both flexed chelipeds. The aggressive dash \((N=13)\), aggressive wave \((N=8)\), cheliped trembling \((N=21)\), and wrestling behaviors \((N=8)\) were all performed exclusively by male aggressors (binomial test, \(P<0.001\) for all four types of aggressive behavior).

Discussion

This study revealed similarities in aggressive behaviors among five congenic species of the genus \(Ilyoplax\); the aggressive dash, aggressive wave, and wrestling behaviors were performed commonly by all the species, and more frequently by males than by females in most of the species (Table 3). In all of these species, the mutual aggression of cheliped-using wrestling was confined to male crabs. In no type of aggressive behaviors females were more aggressive than males (Table 3). In the ocypodid species, \(Uca\) (Salmon, 1984) and \(Macrophthalmus\) (Kitaura & Wada, 2004), wrestling types specific to females are known, such as fighting in a dorsal-to-dorsal position, but none of the five species studied here showed any female-specific aggressive behaviors. The results demonstrated that males are more aggressive than females in these five \(Ilyoplax\) species with re-
spect to the frequency and types of aggressive behaviors. The present finding that aggressive behaviors were more frequent in males than in females, however, may be responsible for the sexual difference in the surface activity. During the reproductive season the females more often hide in the burrows than the males, which can cause more male-biased sex ratio of the active crabs than the population sex ratio. Male-biased aggressiveness has been reported in many brachyuran species in terms of both aggression frequency (Beer, 1959; Griffin, 1968; Seiple & Salmon, 1982; Salmon, 1984) and the relative frequency of the behavioral elements of mutual aggressive acts (Warner, 1970; Vannini & Sardini, 1971; Crane, 1975; Jachowski, 1974; Swartz, 1976; Salmon, 1984; Worfrath, 1993; Miyajima et al., 2012). By contrast, in some brachyuran species, both sexes are similarly aggressive in terms of frequency and types of behaviors (Huber, 1987; Karplus et al., 1998).

Because the sizes of the chela and the carapace influence the outcome of fighting, with larger individuals more likely to win (Lee & Seed, 1992; Jennions & Backwell, 1996; Sneddon et al., 1997, 2000), the male-biased aggressiveness observed in these Ilyoplax species likely drives the observed male-biased carapace and cheliped size dimorphism (Fig. 1, Table 2). Although males have a larger carapace than do females in I. pusilla, I. formosensis, I. deschampsi, and I. tansuiensis, the maximum carapace size of I. ningpoensis was similar between the sexes. Among these five species, mutual aggression by female crabs (lateral push behavior) was observed in I. ningpoensis, while females of the other four species did not exhibit any mutual aggressions. Such female aggressiveness in I. ningpoensis may be reflected in the lack of sexual dimorphism in carapace size.

Among our study species, only I. tansuiensis showed cheliped trembling in their aggressive behaviors. Chela quivering, a similar behavior in which a crab trembles one or both cheliped between cheliped waving acts, is known in some species of Ilyoplax, including I. tansuiensis, but is absent in I. pusilla, I. formosensis, I. ningpoensis, and I. deschampsi (Kitaura & Wada, 2006). Cheliped trembling in I. tansuiensis may have the same origin as chela quivering during the waving display. It is probable that species that show chela quivering during a waving display, such as I. orientalis (De Man, 1888) or I. strigicarpa Davie, 1988 (Kitaura & Wada, 2006), also exhibit cheliped trembling during aggressive encounters. This should be investigated in a future study.

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Literature Cited


AGGRESSIVE BEHAVIORS OF *ILYOPLAX*


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