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

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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

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Table 1. Study sites and periods for five species of *Ilyoplax* and the sex ratios of the populations studied.

	Site	Period	Sex ratio (male proportion)
I. pusilla	Shirahama, Japan (33°41′N, 135°23′E)	May–Aug. 2014 (14 days)	0.55
I. formosensis	Tungshi, Taiwan (23°28′N, 120°10′E)	Mar. 1996 (11 days)	0.64
I. ningpoensis	Haiphong, Vietnam (20°50′N, 106°46′E)	Dec. 1995 (8 days)	0.49
I. deschampsi	Ohkawa, Fukuoka, Japan (33°12′N, 130°22′E)	Jul. 1994 (4 days)	0.56
I. tansuiensis	Tungshi, Taiwan (23°28′N, 120°10′E)	Mar. 1996 (11 days)	0.64

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 cm^2 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).

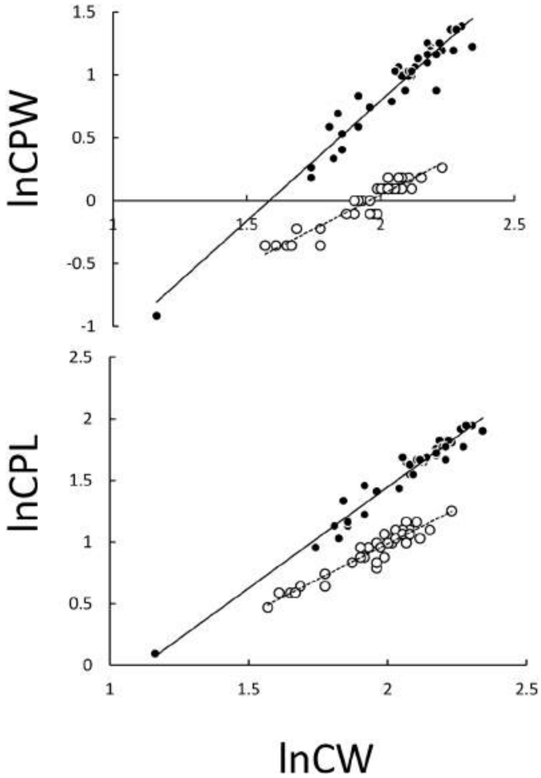

Fig. 1. Regression lines of chela propodus length (CPL) and chela propodus width (CPW) relative to carapace width (CW) for males (solid circles and solid lines) and females (open circles and dotted lines) of *Ilyoplax pusilla*. Regression equations: males, lnCPL = 1.64 lnCW–1.84, $P < 0.001$; lnCPW = 1.91 lnCW–3.03, $P < 0.001$; females, lnCPL = 1.15 lnCW–1.31, $P < 0.001$; lnCPW = 1.09 lnCW–2.14, $P < 0.001$.

***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

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*.

	Factor	F	P
CPL	lnCW	1125.1	<0.001
	sex	931.2	<0.001
	lnCW × sex	9.6	<0.001
CPW	lnCW	706.1	<0.001
	sex	1328.2	<0.001
	lnCW × sex	52.8	<0.001

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.

	Mean density	Male	Female	Ratio (male/female)
I. pusilla	15.7 (5–22)	10.4	9.3	1.12
	($N = 14$)	($N = 50$)	($N = 59$)	
I. formosensis	26.3 (9–51)	9.7	8.3	1.17
	($N = 8$)	($N = 112$)	($N = 96$)	
I. ningpoensis	8.9 (3–16)	9.5	9.4	1.01
	($N = 14$)	($N = 75$)	($N = 76$)	
I. deschampsi	14.3 (2–23)	10.8	10.0	1.08
	($N = 5$)	($N = 40$)	($N = 31$)	
I. tansuiensis	4.2 (2–6)	7.0	6.1	1.15
	($N = 6$)	($N = 28$)	($N = 8$)	

Table 4. Aggressive behaviors and sex differences in their frequencies for five species of *Ilyoplax*.

	Aggressive dash	Aggressive wave	Lateral leg push	Cheliped trembling	Wrestling	Mutual lateral push
I. pusilla	♂≒♀	♂＞♀	♂≒♀	—	♂	—
I. formosensis	♂＞♀	♂＞♀	♂≒♀	—	♂	—
I. ningpoensis	♂＞♀	♂	—	—	♂	♂≒♀
I. deschampsi	♂＞♀	♂＞♀	♂≒♀	—	♂	—
I. tansuiensis	♂	♂	—	♂	♂	—

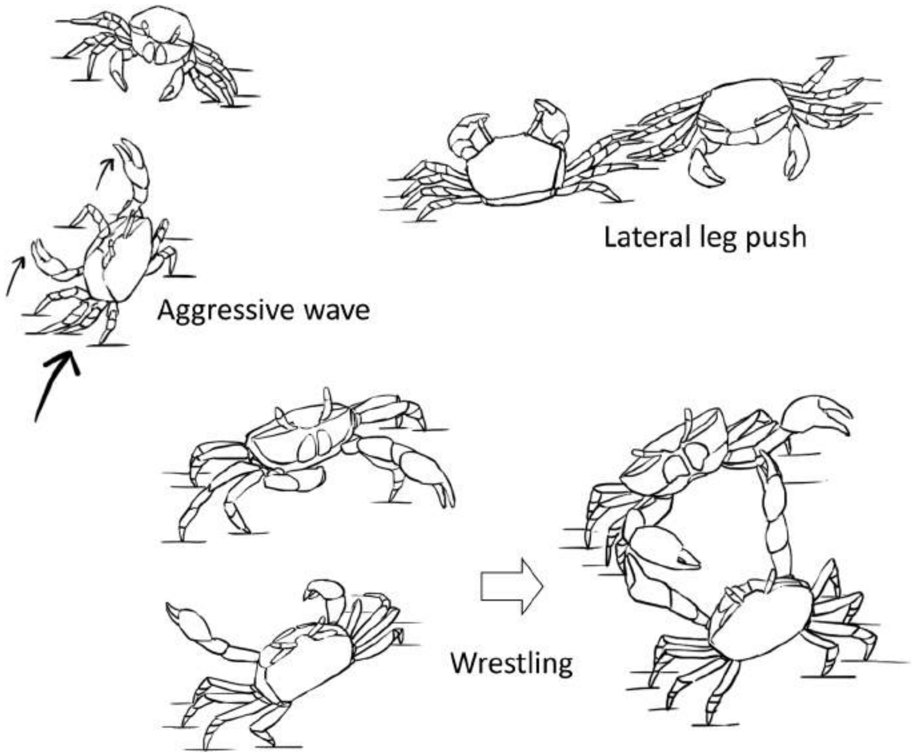

Fig. 2. Diagrams of the three of the aggressive behaviors (aggressive wave, lateral leg push, and wrestling) performed by *Ilyoplax pusilla*.

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 ($N = 21$ and 19, respectively; 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 lateral leg push, and one mutual aggression of wrestling. The aggressive dash and wave were performed significantly more frequently by males than by females (aggressive dash: $N = 45$ and 16, respectively, binomial test, $P = 0.003$; aggressive wave: $N = 33$ and 3, respectively, binomial test, $P < 0.0001$). The lateral leg push was observed on fewer occasions (male aggressors: $N = 1$, female aggressors: $N = 3$), and its frequency did not differ significantly between the sexes (binomial test, $P = 0.23$). Wrestling behavior was performed only between male crabs ($N = 50$), with no females displaying this behavior. This difference was significant (binomial test, $P < 0.0001$), as in *I. pusilla*, *I. formosensis*, and *I. ningpoensis*.

Aggressive behaviors in **I. tansuiensis**

The 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 ($\mathrm{N} = 8$) 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 congeneric 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 ocypodoid 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 respect 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

Beer, C. G., 1959. Notes on the behaviour of two estuarine crab species. Transactions of the Royal Society of New Zealand, 86: 197–203.

Crane, J., 1975. Fiddler Crabs of the World. 736 pp. Princeton University Press, Princeton, New Jersey.

Griffin, D. J. G., 1968. Social and maintenance behaviour in two Australian ocypodid crabs (Crustacea: Brachyura). Journal of Zoology (London), 156: 291–305.

Huber, M. E., 1987. Aggressive behavior of *Trapezia intermedia* Miers and *T. digitalis* Latreille (Brachyura: Xanthidae). Journal of Crustacean Biology, 7: 238–248.

Ida, H., & Wada, K., in press. Aggressive behavior and morphology in *Scopimera globosa*

(De Haan, 1835) (Brachyura: Dotillidae). Journal of Crustacean Biology.

Jachowski, R. L., 1974. Agonistic behavior of the blue crab, *Callinectus sapidus* Rathbun. Behaviour, 50: 232–253.

Jennions, M., & Backwell, P. R. Y., 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. Biological Journal of the Linnean Society, 57: 293–306.

Karplus, I., Fiedler, G. C., & Ramcharan, P., 1998. The intraspecific fighting behavior of the Hawaiian boxer crab, *Lybia edmondsoni*–fighting with dangerous weapons? Symbiosis, 24: 287–302.

Kitaura, J., & Wada, K., 2004. Allocleaning, fighting, waving and mating behavior in sentinel crabs (Brachyura: Ocypodidae: *Macrophthalmus*). Crustacean Research, 33: 72–91.

Kitaura, J., & Wada, K., 2006. Evolution of waving display in brachyuran crabs of the genus *Ilyoplax*. Journal of Crustacean Biology, 26: 455–462.

Lee, S. Y., & Seed, R., 1992. Ecological implications of cheliped size in crabs: some data on *Carcinus maenas* and *Liocarcinus holsatus*. Marine Ecology Progress Series, 84: 151–160.

Miyajima, A., Fukui, Y., & Wada, K., 2012. Agonistic and mating behavior in relation to chela features in *Hemigrapsus takanoi* and *H. sinensis* (Brachyura, Varunidae). Crustacean Research, 41: 47–58.

Salmon, M., 1984. The courtship, aggression and mating system of a "primitive" fiddler crab (*Uca vocans*: Ocypodidae). Transactions of the Zoological Society of London, 37: 1–50.

SAS Institute, 2010. JMP, Version 9, Japanese Edition. SAS, Cary, North Carolina, USA.

Seiple, W., & Salmon, M., 1982. Comparative social behavior of two grapsid crabs, *Sesarma reticulatum* (Say) and *S. cinereum* (Bosc). Journal of Experimental Marine Biology and Ecology, 62: 1–24.

Sneddon, L. U., Huntingford, F. A., & Faylor, A. C., 1997. Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carninus maenas* (L.). Behavioral Ecology and Sociobiology, 41: 237–242.

Sneddon, L. U., Huntingford, F. A., & Faylor, A. C., & Orr, J. F., 2000. Weapon strength and competitive success in the fights of shore crabs (*Carcinus maenas*). Journal of Zoology, 250: 397–403.

Swartz, R. C., 1978. Agonistic and sexual behavior of the xanthid crab, *Neopanope sayi*. Chesapeake Science, 17: 24–34.

Takayama, J., & Wada, K., 1992. Are barricading and neighbor burrow-plugging by male crabs of *Ilyoplax pusilla* (Crustacea: Brachyura: Ocypodidae) related to feeding or mating? Journal of Ethology, 10: 103–108.

Vannini, M., & Sardini, A., 1971. Aggressivity and dominance in river crab *Potamon fluviatile* (Herbst). Monitore Zoologico Italiano (N.S.), 5: 173–213.

Wada, K., 1984. Barricade building in *Ilyoplax pusillus* (De Haan) (Crustacea: Brachyura). Journal of Experimental Marine Biology and Ecology, 83: 73–88.

Wada, K., 1987. Neighbor burrow-plugging in *Ilyoplax pusillus* (Crustacea: Brachyura: Ocypodidae). Marine Biology, 95: 299–303.

Wada, K., 1993. Territorial behavior, and sizes of home range and territory, in relation to sex and body size in *Ilyoplax pusilla* (Crustacea: Brachyura: Ocypodidae). Marine Biology, 115: 47–52.

Wada, K., 1994. Earthen structure built by *Ilyoplax dentimerosa* (Crustacea, Brachyura, Ocypodidae). Ethology, 96: 270–282.

Wada, K., Kosuge, T., & Trong, P. D., 1998. Barricade building and neighbor burrow-plugging in *Ilyoplax ningpoensis* (Brachyura, Ocypodidae). Crustaceana, 71: 663–671.

Wada, K., & Park, J. K., 1995. Neighbor burrow-plugging in *Ilyoplax pingi* Shen, 1932 and *I. dentimerosa* Shen, 1932 (Decapoda, Brachyura, Ocypodidae). Crustaceana, 68: 524–526.

Wada, K., & Wang, C.-H., 1998. Territorial and sexual behaviors in *Ilyoplax formosensis* and *I. tansuiensis* (Crustacea, Brachyura, Ocypodidae). Journal of Taiwan Museum, 51: 119–125.
Wada, K., Yum, S. S., & Park, J. K., 1994. Mound building in *Ilyoplax pingi* (Crustacea: Brachyura: Ocypodidae). Marine Biology, 121: 61–65.
Warner, G. F., 1970. Behaviour of two species of grapsid crab during intraspecific encounters. Behaviour, 36: 9–19.
Warner, G. F., 1977. The Biology of Crabs. 202 pp. Paul Elek, London.
Wolfrath, B., 1993. Observations on the behaviour of the European fiddler crab *Uca tangeri*. Marine Ecology Progress Series, 100: 111–118.

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