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ORIGINAL PAPER

Function of the major cheliped in male–male competition in the hermit crab *Pagurus nigrofascia*

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Abstract Functions of the major cheliped in pagurid hermit crabs have been studied in fights for shells. The major cheliped often shows sexual size dimorphism, suggesting that sexual selection favors the development of the male major cheliped. The function of the major cheliped in male–male competition was examined in *Pagurus nigrofascia* collected from April to June 2009 on the intertidal rocky shore in southern Hokkaido, Japan (41°N, 140°E). Sexual size dimorphism of the major cheliped was observed, and precopulatory guarding males had larger major chelipeds than solitary ones. Guarding males used the major cheliped to deter intruders during competitive interactions. Males without a major cheliped were disadvantaged even if they were larger than opponents and had ownership. Cheliped size affected the outcomes of contests between similar sized males. This suggests that the male major cheliped in *P. nigrofascia* protects mates from competitors and, consequently, enhances male mating success. Sexual selection may favor the development of the major cheliped in male pagurids.

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Introduction

Male-male competition can lead to the development of morphological traits that enable aggressive interactions (reviewed by Andersson 1994; Emlen 2008). For example, in fiddler crabs males have one greatly enlarged claw that they use to both attract mates and prevent other males from approaching their breeding burrows (Crane 1975; Jennions and Backwell 1996; Murai and Backwell 2006). Male amphipods have sexually dimorphic gnathopods (Wellborn 2000), and Takeshita and Henmi (2010) demonstrated that males of a skeleton shrimp use their gnathopods in fighting for females. Males of a polygamous shrimp compete for females and their major claws show sexual dimorphism (Baeza and Thiel 2007), whereas monogamous shrimp species have less marked sexual dimorphism in appendages because of infrequent intrasexual competitions (Baeza 2008).

Development of the morphology in crustacean appendages can also be explained in the context of natural selection, including foraging, predator avoidance, and intra/interspecific competitions. Shore crabs use their master (i.e., larger) chela to break open mussel shells (Elner and Hughes 1978), and crabs with larger master chelae can break prey items in a shorter time and are able to feed on larger mussels (Lee and Seed 1992). Some species of terrestrial crabs use their chelae for predator avoidance (Robinson et al. 1970) by displaying with chelae oriented toward the approaching predator and grasping at the predator. When crabs escape for refuge, they also display by holding the chelae above the carapace (Robinson et al. 1970). Male and female crayfish use the size of their enlarged chelae as signals of dominance during aggressive encounters (Wilson et al. 2007). Crayfishes with larger chelae are likely to win in territorial disputes and individuals engage in physical fights only when they are closely matched for chela size, suggesting that chela size is used as a signal of potential strength in crayfish (Wilson et al. 2007; Bywater et al. 2008).

Male and female pagurid hermit crabs have a large right (i.e., major) cheliped. The major cheliped functions as a weapon in contests for gastropod shells in *Pagurus bernhardus* (e.g., reviewed by Elwood and Neil 1992; Laidre and Elwood 2008; Laidre 2009). Hermit crabs of *P. bernhardus* defend their shell against opponents by "cheliped flicking" with the major cheliped, in which they physically prevent intruders from approaching (Elwood and Neil 1992). They also use their major cheliped to perform pre-fight displays, such as "cheliped presentation" and "cheliped extension", in fights for shell possession (Elwood and Neil 1992). Hermit crabs lacking a major cheliped are less likely to successfully defend their shells than intact crabs (Neil 1985).

Male pagurid hermit crabs compete for mates during precopulatory guarding (Hazlett 1968; Elwood and Neil 1992; Wada et al. 1999) by grasping the aperture of the gastropod shell occupied by sexually mature females with their minor (i.e., left) cheliped over several days (Hazlett 1968, 1972). When guarding pairs encounter other males, a contest for females often occurs. Previous research has found that a difference in body size and ownership asymmetry between competitors affects the outcomes of mate contests in some *Pagurus* spp. (Wada et al. 1999; Yoshino and Goshima 2002). Major chelipeds may function showing aggressive and/or defensive traits in the contests. Asakura (1987) suggested that males in the hermit crab *Diogenes nitidimanus* use their major cheliped in male–male contests. Sexual size dimorphism of the major cheliped has also been described in *P. bernhardus* (Briffa and Dallaway 2007; Doake et al. 2010) and other species of hermit crabs (Asakura 1987; Gherardi 1991), suggesting that sexual selection may also favor the development of the major cheliped in males. However, few studies have examined whether there is an advantage in using the major cheliped during male–male competition (Yoshino et al. 2011). We hypothesize that the major cheliped of males is used during male–male competition in the hermit crab *P. nigrofascia*.

In this study, we examine (1) whether major cheliped loss in male *P. nigrofascia* decreases the likelihood of winning contests for mates and (2) whether a larger major cheliped confers any advantage in a contest between similar sized males. We also describe (3) sexual size dimorphism in the major cheliped and (4) the differences in size of major cheliped between guarding and solitary males in *P. nigrofascia*. The mating season of *P. nigrofascia* occurs from late April to early June in our study site (Goshima et al. 1996). Males may lose their major cheliped during the reproductive season due to male–male contests. We then distinguish solitary males collected in late April (i.e., early reproductive season) from those collected in early June (i.e., late reproductive season) and (5) the frequency of major cheliped loss in guarding males was compared with the two groups of solitary males to examine whether the frequency of major cheliped loss increased through the reproductive season.

Materials and methods

Morphological characters

We collected solitary *Pagurus nigrofascia* in the intertidal rocky shore on 24 and 25 April ($N = 185$ males, $N = 159$ females) and on 8 and 9 June 2009 ($N = 109$ males, $N = 152$ females) at Kattoshi, southern Hokkaido, Japan (41°N, 140°E). We recorded whether the crabs had a major cheliped or not, identified the sex of each individual, based on the developmental level of the first pleopod, and measured the shield length (calcified anterior portion of cephalothorax, index of body size; hereafter, SL) to the nearest 0.1 mm under a stereomicroscope. For individuals with a major cheliped, collected in April, we also measured the major cheliped length (total length of propodus; hereafter, CL) to the nearest 0.1 mm under a stereomicroscope. There were strong correlations between CL and SL in both sexes (see Fig. 1). We then examined sexual dimorphism in major cheliped size by using a generalized linear model (hereafter, GLM) with a normal error distribution, in which

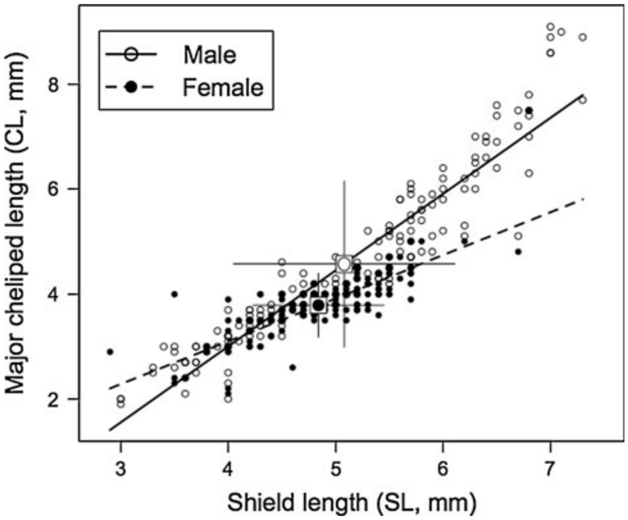

Fig. 1 Relationship in both sexes between major cheliped length (CL) and shield length (SL) of solitary hermit crabs of *Pagurus nigrofascia* collected in April ($N = 174$ males, $CL = -2.81 + 1.45\ SL$; $N = 158$ females, $CL = -0.17 + 0.82\ SL$). *Open squares* are mean CL and SL, and *error bars* show SD for each sex. Interaction between SL and sex was significant in the generalized linear model with a normal error distribution, indicating that slopes of regressions differed from each other

the response variable was CL, and the explanatory variables were SL, sex, and interaction between SL and sex.

To compare the frequencies of major cheliped loss in guarding males with the solitary males in early and late reproductive season, we collected 203 precopulatory guarding pairs from April 24 to May 1, 2009, at the study site. Each guarding pair was placed in a small vinyl pouch with seawater in the field. We measured SL of the guarding males and recorded whether they had a major cheliped or not. We did not use guarded females in the following morphological analyses since the objective of this study focused on male morphology. Frequency of cheliped loss was tested with the GLM with a binominal error distribution and logit link function. The response variable in the analysis was whether crabs had their major cheliped or not (Yes = 0, No = 1). The explanatory variables were SL and category of males, which was determined by sampling month and whether the male was solitary or guarding in the field (i.e., solitary males in April, solitary males in June, and guarding males). In the analysis of cheliped loss frequency in solitary females, the response variable was the same as that of males, and the explanatory variables were SL and sampling month (i.e., April and June). We also used the guarding pairs in the following experiment 1 (hereafter, Exp-1) before the above measurements. In each experimental trial, we used two pairs for each trial (both males and one female) of all the pairs collected on a day, and when the number of the collected pairs was an odd number, we had one pair as the remainder for that experimental day. Since there were 3 days when the number of pairs collected was an odd number, there were three pairs of remainders. We therefore used 200 of the total of 203 guarding pairs for the following Exp-1 [Appendix 1 (Electronic Supplementary Material)].

We also collected a further 244 precopulatory guarding pairs from April 29 to May 2, 2009, at the study site to compare CLs between solitary and guarding males. These pairs were different from those in the analysis of frequency of cheliped loss mentioned above. Each guarding pair was placed in a small vinyl pouch with seawater in the field. We measured SLs and CLs of guarding males. The difference in CLs between guarding and solitary males collected in April was tested by a GLM with a normal error distribution. Since the minimum SL of guarding males was 5.0 mm (see Results), we used a subset of data on solitary males in April, in which SLs of solitary males were 5.0 mm and larger in the analysis ($N = 94$ solitary males). The response variable in the GLM was CL, and the explanatory variables were SL, category of males (i.e., guarding or solitary) and interaction between SL and category. We used the guarding pairs in the following experiment 2 (hereafter, Exp-2) before the above measurements. From all pairs collected on a day, we chose two pairs in which males were of a similar size and, consequently, 86 of 244 pairs were used in Exp-2 [Appendix 1(Electronic Supplementary Material)].

Exp-1: effect of major cheliped loss on male–male competition

We used 200 precopulatory guarding pairs of *P. nigrofascia* collected from April 24 to May 1, 2009. We also filled several tanks (20 l) with seawater in the field, took the tanks to the laboratory, and the seawater was used for our experiments within 10 h. The male and the female of each pair were separately maintained in plastic cups (300 ml) after checking that the male continued to guard the female in the laboratory. All experimental trials were conducted within 10 h of collection. We placed the male (hereafter, owner) and his guarded partner in the field in a small plastic container (19.5 × 12.0 × 7.0 cm) filling it with seawater to a depth of about 3 cm. Another male (hereafter, intruder), which was randomly chosen from other guarding pairs on the sampling date, was then placed in the container after the owner male had initiated guarding of the female. After 15 min of observation, we recorded which of the males guarded the female. Since larger males were focal males in the analysis, when larger or smaller males guarded females at the end of observation, we recorded these outcomes as “win” or “lose”, respectively. If the contest did not finish by the end of the observation period, we recorded it as “draw”. We measured SLs of all males after the experiment and recorded whether they had a major cheliped, minor cheliped, and loss of walking legs. The number of trials was 100, and all crabs were used only once in the experiments.

A GLM with a binominal error distribution and logit link function was used to examine the effect of a lost limb (major cheliped, minor cheliped, or walking leg) and difference in the body size and ownership between males on outcomes of the contest. The response variable was outcome of competition (i.e., larger male win = 2, draw = 1, lose = 0). The explanatory variables were whether there was any limb loss in either of the two males in each contest, such as the major cheliped (i.e., loss in larger male = 1, no loss = 0, loss in smaller male = −1), minor cheliped (i.e., loss in larger male = 1, no loss = 0, loss in smaller male = −1), and walking legs (i.e., loss in larger male = 1, no loss = 0, loss in smaller male = −1).The SL difference between larger and smaller males and the position of larger males (i.e., owner = 1, intruder = 0) were also included as explanatory variables in the GLM.

Exp-2: effect of major cheliped size on male–male competition

To examine the effect of major cheliped size on the outcomes of male–male competition, we conducted experiments to account for the effect of body size difference between contestants (see Results). We chose 43 sets of two guarding males from 244 pairs collected from April 29 to May 2, 2009. The two males in each set were collected on the same date (mean SL ± SD = 6.52 ± 0.44 mm, $N = 86$ males) and were similar in size (mean difference in SL ± SD = 0.10 ± 0.48 mm, $N = 43$ sets). The male and the female of each pair were separately maintained in plastic cups (300 ml) after checking that the male guarded the female in the laboratory. All experimental trials were conducted on the day following collection. We used a set of guarding pairs for each trial and randomly selected one male as the owner. Then we randomly chose a receptive female and placed the owner and the female in the container (19.5 × 12.0 × 7.0 cm). After the owner male guarded the female, an intruder male was introduced to the container. We recorded the outcomes of male–male competition after 30 min. Since males with larger SL were focal males in the analysis, when the larger or smaller males guarded females at the end of observation, we recorded these outcomes as "win" or "lose", respectively. If the competition had not finished by the end of the observation period, we recorded it as "draw". We measured SLs and CLs of all males after the experiments. The number of trials was 43, and all crabs were used once in the experiment.

The data were analyzed using a GLM with a binominal error distribution and logit link function. The response variable was the outcome of contests (i.e., larger male win = 2, draw = 1, lose = 0). The explanatory variables were the difference in CL between males with larger SL and smaller SL, the position of the males with larger SL (i.e., owner = 1, intruder = 0) and difference in SL between the two males. There was no correlation between the CL difference and the SL difference ($r^2 = 0.003$, $N = 86$).

Results

Morphological characters

The CL increased with SL in both sexes ($N = 174$ solitary males; $N = 158$ solitary females; Fig. 1), and there was a significant interaction between SL and sex (GLM, $t = 9.31$, $P < 0.001$; Fig. 1), indicating sexual dimorphism in major cheliped size because males increased CL at a higher allometric rate than females.

The frequencies of major cheliped loss in solitary males were 5.95% in April ($N = 185$) and 11.00% in June ($N = 109$), and in solitary females 0.63% in April ($N = 159$) and 3.95% in June ($N = 152$); in guarding males, the frequency was 9.36% [$N = 203$; Appendix 1 (Electronic Supplementary Material)]. The frequency of major cheliped loss in all males increased with SL (GLM, $z = 4.39$, $P < 0.001$; Fig. 2), but not in solitary females (GLM, $z = -1.57$, $P = 0.12$). The occurrence of major cheliped loss in solitary males in June was significantly different from that of guarding males (GLM, $z = -1.16$, $P = 0.01$; Fig. 2), but not in April (GLM, $z = -0.70$, $P = 0.13$).

There was a significant interaction between SL and category of males (i.e., guarding or solitary; GLM, $t = 2.92$, $P = 0.004$; Fig. 3), and guarding males having a larger CL than solitary males collected in April ($N = 244$ guarding males, $N = 94$ solitary males (SL $\geq$ 5.0); Fig. 3).

Exp-1: effect of major cheliped loss on male–male competition

Males without a major cheliped ($N = 18$) had a significantly decreased probability of winning in the contest (GLM, $z = -2.83$, $N = 100$, $P = 0.005$; Table 1, Fig. 4), while the loss of a minor cheliped ($N = 5$) or walking leg ($N = 4$) had no effect on contest outcomes (minor cheliped, $z = -0.01$, $P = 0.99$; walking legs, $z = -1.87$, $P = 0.06$). Ownership and body size differences also significantly affected the probability of winning (GLM, ownership, $z = 2.55$, $P = 0.01$; SL difference, $z = 2.68$, $P = 0.007$). Males escalated the contest by fighting with direct physical contact observed in 99 of 100 trials, and the major cheliped was used in fighting, including cheliped extension against the opponents and/or preventing the

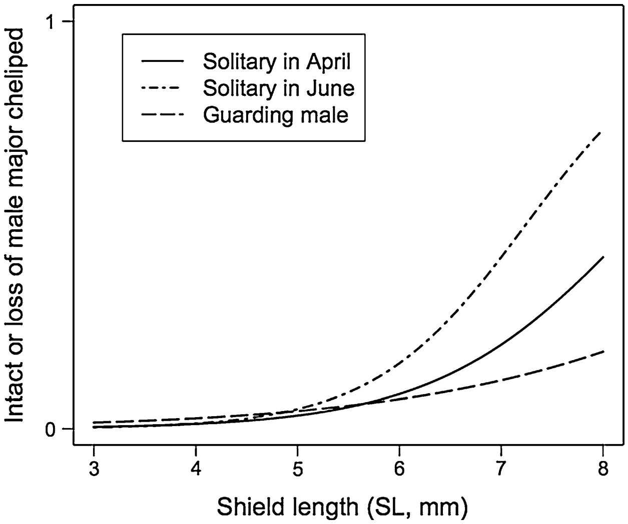

Fig. 2 Logistic regression lines, calculated from the generalized linear model with a binomial error distribution, between frequency of major cheliped loss (intact male = 0, male of cheliped loss = 1) and shield length of *Pagurus nigrofascia*. Three male categories, solitary males in April ($N = 185$), solitary in June ($N = 109$), and guarding males ($N = 203$), were compared for frequency of major cheliped loss, and there was a significant difference between solitary males in June and guarding males

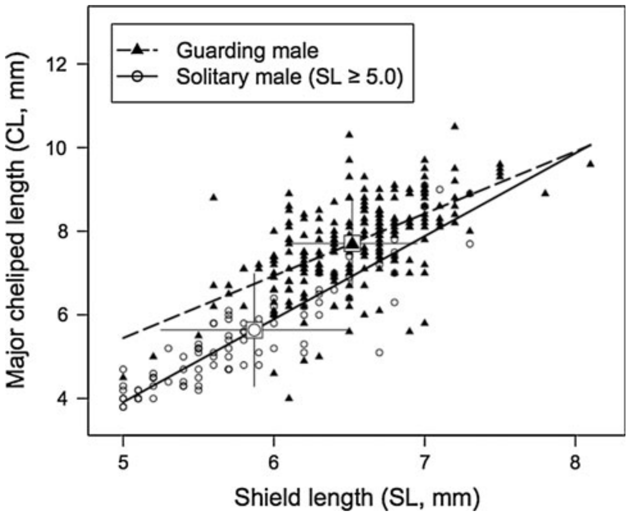

Fig. 3 Relationship between major cheliped length (CL) and shield length (SL) in guarding males ($N = 244$, $\mathrm{CL} = -1.99 + 1.49\ \mathrm{SL}$) and solitary ones collected in April ($\mathrm{SL} \geq 5.0$, $N = 94$, $\mathrm{CL} = -6.01 + 1.98\ \mathrm{SL}$) in *Pagurus nigrofascia*. *Open squares* are mean CL and SL, and *error bars* show SD for guarding or solitary males. Interaction between SL and category of males (guarding or solitary) was significant in the generalized linear model with a normal error distribution, indicating that slopes of regressions differed from each other

Table 1 Results of Exp-1 analyzed by generalized linear model with binomial error distribution

	Estimate	Std. Error	Z	P
Intercept	0.016	0.31	0.05	0.96
Major cheliped loss	−1.29	0.46	−2.83	0.005
Minor cheliped loss	−17.55	1220.39	−0.01	0.99
Walking legs loss	−1.68	0.90	−1.87	0.06
Ownership asymmetry	0.94	0.37	2.56	0.01
Difference in shield length	1.23	0.48	2.68	0.007

The probability of winning in larger males was significantly affected by major cheliped loss, the difference in body size, and ownership asymmetry between contestants ($N = 100$)

intruders from approaching. However, there were no trials in which a major cheliped of a male was injured or lost during contests.

Exp-2: effect of major cheliped size on male–male competition

Males with a larger CL showed a significantly higher probability of winning than males with smaller CL (GLM, $z = 2.13$, $N = 43$, $P = 0.03$; Table 2, Fig. 5) when the contestants were similar in SL. Ownership and SL difference had no effect on the probability of winning (GLM, ownership, $z = 1.49$, $P = 0.14$; SL difference, $z = 0.75$, $P = 0.45$). Although all males fought for mates and used the major cheliped in fighting, no injury or loss of the major chelipeds of males was observed.

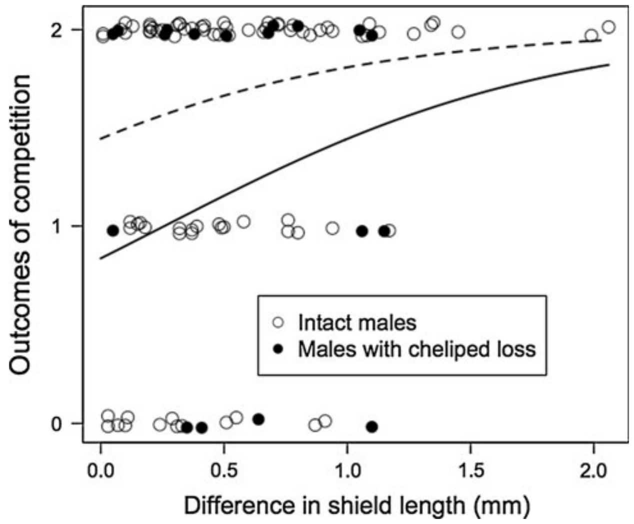

Fig. 4 Logistic regression representing outcomes of male–male contests in larger males with major cheliped ($N = 82$, dashed line) and major cheliped loss ($N = 18$, solid line) in *Pagurus nigrofascia*. Response variable was outcome of the contest (larger male win = 2, draw = 1, lose = 0), and difference in shield length and major cheliped loss significantly affected contest outcomes. Three variables, loss of minor cheliped or walking legs and ownership, were treated as constants in regression curve (loss of minor cheliped = 0, loss or walking legs = 0, ownership = 1)

Table 2 Results of Exp-2 analyzed by generalized linear model with binomial error distribution

	Estimate	Std. Error	Z	P
Intercept	−0.90	0.45	−2.00	0.05
Difference in major cheliped length	0.64	0.30	2.13	0.03
Ownership asymmetry	0.72	0.48	1.49	0.14
Difference in shield length	0.58	0.77	0.75	0.45

The probability of winning in males was significantly affected by the difference in major cheliped length between contestants, but not ownership and the difference in body size ($N = 43$)

Discussion

Our results demonstrate that the major cheliped is important in determining the outcome of male–male competitions in *Pagurus nigrofascia*. When a solitary male encountered a precopulatory guarding pair, the males used the major cheliped in contests with direct physical contact in most cases. Males with larger major chelipeds had a higher likelihood of winning in a contest against a competitor of similar body size. Males without a major

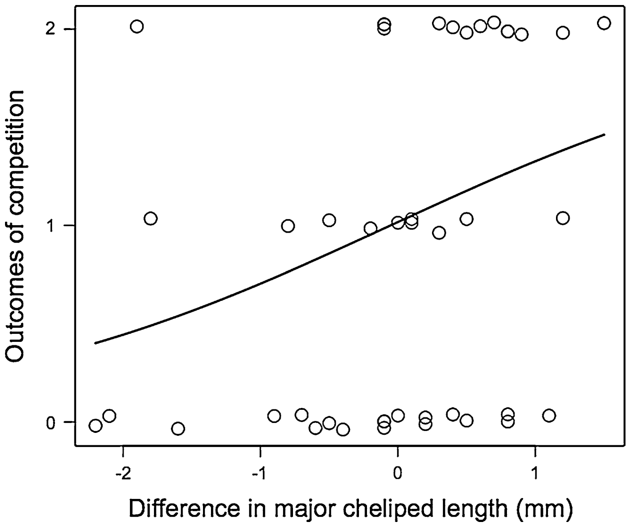

Fig. 5 Logistic regression representing outcome of male–male competitions in males with larger body size (shield length, SL) in *Pagurus nigrofascia* between similar sized males ($N = 43$). Response variable was outcomes of the contests (larger male win = 2, draw = 1, lose = 0), and difference in major cheliped length significantly affected contest outcomes. Two variables, ownership and difference in shield length, were treated as constants in regression curve (ownership = 1, mean of SL difference)

cheliped were less likely to win the contest for females even if they had initial ownership of the female and/or larger body size than their opponent. Guarding males had a larger major cheliped than solitary males in the field, and sexual dimorphism in major cheliped size increased with body size.

Sexual dimorphisms in cheliped size are found in other hermit crabs, such as *Diogenes nitidimanus* (Asakura 1987), *P. bernhardus* (Briffa and Dallaway 2007; Doake et al. 2010) and *P. middendorffii* (C. Yasuda, Y. Suzuki and S. Wada unpubl data), and the advantage of a large body size in male–male contests for mates is known in these species (Asakura 1987; Elwood and Neil 1992; Wada et al. 1999). Sexual selection may be a common evolutionary pressure for the development of major chelipeds in these species. While males and females of some species of hermit crab in the genera *Pagurus*, *Diogenes,* and *Calcinus* have left–right asymmetry in cheliped size, species in other genera, such as *Aniculus* and *Clibanarius*, have two similar sized chelipeds. Hazlett (1989) reported that male body size of *Clibanarius zebra* did not appear to be important in determining reproductive success and the largest males had lower success in obtaining copulations than medium-large ones, while shell condition had a strong effect on mating success of males. However, Gherardi (1991) described sexual size dimorphism of both chelipeds in *Clibanarius erythropus*. Sexual selection may affect the size of chelipeds in males of species with less morphological handedness. Since pagurid males grasp the rims of shells occupied by receptive females during precopulatory guarding, larger minor chelipeds may be favored in the context of interaction between males and females. We did not examine whether minor cheliped size was affected by sexual selection in this study partly due to the small sample size. Further studies will be needed to examine whether sexual selection commonly acts on the size of chelipeds in hermit crabs.

Major cheliped loss highly depressed the probability of winning even in larger and/or owner males in *P. nigrofascia*. The loss of chelae or chelipeds is well known to reduce success in defending resources such as shelters and/or mates in decapod crustaceans (Juanes and Smith 1995; Mariappan et al. 2000). Cheliped loss is also costly in general activities in the field (Juanes and Smith 1995). Asian shore crabs with the loss of one cheliped had a decreased feeding rate compared with crabs with intact chelipeds, particularly when feeding on large mussels, and crabs missing both chelae cannot crush large mussels (Davis et al. 2005). Red rock crabs regenerating both claws grow more slowly (Brock and Smith 1998). In *P. nigrofascia*, major cheliped loss might also reduce the efficiency of feeding, although *Pagurus* spp. uses the minor cheliped to feed (Yoshii et al. 2009). These ecological costs indicate that males without a major cheliped are less likely to win in male–male contests in *P. nigrofascia* since they probably allocate substantial energy and/or time to regenerating the major cheliped.

Cheliped size is a more reliable indicator of contest outcomes than body size (Barki et al. 1997; Sneddon et al. 1997) and critically important in determining male mating success in some decapods (Juanes and Smith 1995). For example, mating males in *Carcinus maenas* have larger chelae than males overall (Lee and Seed 1992), and chela size in this species strongly affects the outcomes of contests over food (Sneddon et al. 1997). Our results demonstrate the advantage of a larger major cheliped in male–male contests in *P. nigrofascia*. Guarding males of *P. nigrofascia* performed defensive behaviors such as cheliped extension using their major cheliped in mate competition and had larger major chelipeds than solitary males in the field. In *P. bernhardus*, the major cheliped has an important role during defense of their gastropod shells against opponents in shell fights (Neil 1985). This suggests that major cheliped size would be more important in defending resources, such as shells and mates, against competitors than in taking over the resources in *Pagurus* spp. Aggressive traits, such as morphological weapons and fighting behaviors, have an important function in the defense of essential resources in many species (Andersson 1994; Emlen 2008).

Major chelipeds may also be used as a morphological signal for resource holding potential during fights in crabs

(Mariappan et al. 2000). The percentages of major cheliped loss in *P. nigrofascia* were 9.36% in guarding males and 8.48% (mean of April and June samples) of all solitary males in the field. These are relatively low in comparison with previous studies of other crabs (Smith 1992; Abello et al. 1994; Daleo et al. 2009). Although males of *P. nigrofascia* used their major chelipeds as a physical weapon, the level of escalation would be low in most male–male contests because males did not injure their major chelipeds in our experiments. In shell fights in *P. bernhardus*, hermit crabs used their major cheliped in pre-fight displays, such as cheliped presentation and extension, to assess the size of opponents (Elwood et al. 2006; Arnott and Elwood 2007) and/or physiological condition (Laidre and Elwood 2008). Major chelipeds of hermit crabs now provide a further topic for study in the context of sexual selection.

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