Male-male competition in hermit crabs:
Assessment of fighting ability with focusing on the role of major cheliped

(ヤドカリのオス間闘争：大鋏脚の機能に着目した闘争能力の評価戦略)

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Chapter 1: GENERAL INTRODUCTION

Sexual selection and male-male contest competition

Sexual selection is one of the fundamental concepts in evolutionary biology, which is originally argued by Charles Darwin (1871). This type of selection leads to evolution of various sexual differences in life history, behavior and morphology (Andersson 1994; Lailvaux & Irschick 2006; Emlen 2008; Davies et al. 2012). For example, sexual differences in longevity have been demonstrated in many taxa, and males often live shorter than females (e.g. Clutton-Brock et al. 1985; Zajitschek et al. 2009). In agonistic interactions, males of vole show higher aggressive and less avoidance behaviors than females (Rosell et al. 2008). Also, males have heavier body weight than females in several marine mammals such as seals and sea lions (Andersson 1994). Male fiddler crabs possess extremely larger chela than females and use the chela as a weapon in contesting over burrows and demonstrating waving display (Crane 1975). Males of guppy show bright body coloration to function as ornaments for females (Berglund et al. 1996). Common behavioral mechanisms of sexual selection are mate choice and male-male competition.

Males compete for females and/or any resources used by females. Male-male competition is common in various taxa, such as mammals (Le Boeuf 1974), birds (Sorenson & Derrickson 1994; Järvistö et al. 2013), reptiles (Garcia et al. 2012), fishes (Jirotkul 1999; Candolin 2000), insects (Hack 1997; Kemp & Wiklund 2001) and crustaceans (Abello et al.

1994; Backwell et al. 2000). There are several types of male-male competition such as scramble

and contest (reviewed in Andersson 1994). For scramble competition, males search and locate

their mates with sensory and locomotory organs. On the other hand, for contest competition,

males directly display to or physically fight each other during agonistic interactions. Since the

winners in male-male contests acquire more females than the losers, sexual selection should

favor some morphological traits and/or behavioral strategies that increase the probability of

winning in male-male contests (Arnnot & Elwood 2009).

Parker (1974) introduced the concept of "resource holding potential (RHP)" to

represent the fighting ability of contestants, and males with larger RHP typically win (Briffa &

Sneddon 2010; Hardy & Briffa 2013). Since males with larger size in body and weapon than

their opponents achieve a higher fighting success, these variables are thought as the most

important RHP proxies (Arnnot & Elwood 2009). Various morphological traits are known as

weapons (Emlen 2008), such as horns in mammals (ungulates) (Clutton-Brock 1982), mandible

in insects (Emlen & Nijhout 2000; Bean & Cook 2001; Judge & Bonanno 2008) and enlarged

cheliped in crustaceans (Backwell et al. 2000; Mariappan et al. 2000). Males use these weapons

as visual display and physical weapon during the contests. The owner-intruder asymmetry also

affects the behaviors and the outcomes of male-male contests. Owners possess resources, such

as potential mates and territory (e.g. Le Boeuf 1974; Davies 1978; Kemp & Wiklund 2001), and

defend them while intruders aggressively attack to the owners and try to takeover the resources.

Owners are more likely to win than intruders in many animals (Davies 1978; Hack et al. 1997;

Olsson & Shine 2000). This is partly because owners are expected to have more information

about resources than intruders. Such information asymmetry would improve RHP of owners to

increase the motivation for defending the resources (Arnott & Elwood 2008; Kokko 2013).

Male-male contests are costly, in terms of time (Kemp & Wiklund 2001), energy

(Hack 1997) and risk of injury (Silverman & Dunber 1980) or possible death (Le Boeuf 1974).

Appropriate tactical decisions are, therefore, important as well as an exerting higher RHP

(Arnott & Elwood 2009). Males assess own and/or opponent's RHP and determine whether they

initiate, continue and/or give up the contest (Arnott & Elwood 2009; Briffa & Sneddon 2010;

Hardy & Briffa 2013). When males assess their opponent's RHP relative to their own, males

with lower RHP quickly give up the contest (i.e. mutual-assessment model; Enquist & Leimar

1983; Enquist et al. 1990). On the other hand, if males behave only based on their own RHP,

contest is settled when weaker individual reaches his limit (i.e. self-assessment model; Payne &

Pagel 1996). Although many theoretical models assume that contestants use a single assessment

strategy (i.e. self or mutual) through the contest, empirical studies have recently demonstrated

that they often modify the RHP assessment during a contest. For example, when males escalate

the contest behavior, they sometimes switch the assessment tactics (Morrell et al. 2005; Hsu et

al. 2008). Males use mutual-assessment during low intensity display and switch to

self-assessment when contests are escalated to physical struggle. Also, males assess again their

own RHP depending on the prior contest experiences, especially to avoid the costs of

overestimate its RHP (Hsu et al. 2006; Rutte et al. 2006).

Recent review of animal contest (Hardy & Briffa 2013) highlights that the studies of

contest behavior and/or the decision-making mechanisms have mainly been conducted by using

various terrestrial animals and how limited taxa are used in aquatic organisms: nine chapters

deal with a range of terrestrial animals (i.e. several insects, spiders, amphibians, reptiles, birds

and mammals) but only two ones focus on aquatic organisms (i.e. crustaceans and fish).

Moreover, in aquatic organisms, studied species and/or taxonomy are also limited in a few

animals. For example, most studies of male-male contests in crustaceans have been conducted

by using fiddler crabs of the genus *Uca* (Crane 1975; Jennions & Backwell 1996; Koga et al.

1999; Morrell et al. 2005; Pratt & McLain 2006; Bywater & Wilson 2012) and crayfishes

(Rubenstein & Hazlett 1974; Rutherford et al. 1995; Villanelli & Gherardi 1998; Gherardi &

Daniels 2003; Wilson et al. 2007). In fish, there are two main families as model systems (Earley

& Hsu 2013), which is cichlids (Enquist et al. 1990; Evans & Norris 1996; Dijkstra et al. 2012)

and poeciliids (Jirotkul 1999; Beaugrand & Goulet 2000; Prenter et al. 2008). The limited

species diversity might impair our ability to understand the contest behavior and the process of

decision-making associated with contests (Earley & Hsu 2013), suggesting the importance of

the study by using other organisms in aquatic environments.

Pagurus hermit crabs show active male-male contests during mating season, and we

can easily observe it. Although they seem to be good materials for behavioral study of sexual

selection, there are few studies dealing with above topics of male-male contest. I here

investigate (1) how morphological weapons are used by males and affect the contest outcomes

during male-male contests, (2) what and how assessment tactics are performed by contestants

depending on the contests conditions, and (3) how males utilize their weapon in effective

assessment. I also examine (4) whether male-male contests relate to other aspects of

characteristic such as sexual size dimorphisms and generating process of weaponry traits.

Males of *Pagurus* hermit crabs show the precopulatory guarding behavior in which the male grasps the aperture of the gastropod shell occupied by sexually mature female in the reproductive season (Hazlett 1968; Imafuku 1986; Goshima et al. 1998; Wada et al. 1999; Suzuki et al. 2012). When guarding males encounter solitary males (intruders), male-male contests often occur between these two males. Previous studies have demonstrated that larger males are more likely to win in *Pagurus middendorffii* Brandt, 1851 (Wada et al. 1999) and *Pagurus filholi* (de Man, 1887) (Okamura & Goshima 2010), and that males are larger in body size than females (Goshima et al. 1996; Yoshino et al. 2002; Briffa & Dallaway 2007). Contreras-Garduño & Córdoba-Aguilar (2006) suggests that male-male contest is a direct reason to lead the sexual size dimorphism in *Pagurus* hermit crabs. Additionally, males with guarding position (owners) show a greater probability of winning than intruders (Wada et al. 1999). Therefore, body size and ownership would function as the proxies of RHP during male-male contests in these species.

However, other factors may also be indicators of RHP and predict the contest winner in male-male contests of *Pagurus* hermit crabs. Larger right (major) cheliped possessed by crabs, for example, is possible as an important trait to reflect RHP since both intruders and owners aggressively use their major cheliped during male-male contests. Indeed, the importance of major cheliped is demonstrated in the contest over gastropod shell in both physical function (Elwood & Neil 1992) and RHP assessment (Elwood et al. 2006) in *Pagurus bernhardus* (Linnaeus, 1758). Moreover, although there has been growing interest (Arnott & Elwood 2009;

Hardy & Briffa 2013), few studies focus on the process of the decision-making and/or the manner of RHP assessment during male-male contests in *Pagurus* hermit crabs. Therefore, I examine the assessment tactics during male-male contest with the function of major cheliped in *Pagurus* hermit crabs.

This paper is composed of the following four topics (Chapters 2-5) and general discussion (Chapter 6). Two species of *Pagurus* hermit crabs, *Pagurus nigrofascia* Komai, 1996 and *P. middendorffii*, were used as the materials of this study. Contents of chapters are as follows.

Chapter 2: To examine the function and the contribution of major cheliped in male-male contests, I described sexual size dimorphism of major cheliped and conducted the experiments of male-male contests by using *P. nigrofascia*.

Chapter 3: Male major cheliped is a crucial trait during male-male contests, and males without major cheliped decreased the probability of winning (Chapter 2). I then conducted a rearing experiment to examine the pattern of major cheliped regeneration in males of *P. middendorffii* that were experimentally induced major cheliped loss.

Chapter 4: Since both major cheliped size and body size affected the contest outcomes (Chapter 2), I examined whether males switch assessment tactics during two phases of male-male contests in *P. middendorffii* with focusing on the relative importance of major cheliped size and body size as index of RHP.

Chapter 5: Intruders of *P. middendorffii* use both self- and mutual-assessment to determine the contest behavior (Chapter 4), suggesting that information of their own and opponents

would affect male-male contests. I then examined whether intruders alter their

contest behavior depending on the prior losing experience (own state) and the

familiarity with the opponent (opponent state).

Chapter 6: I discuss the assessment strategy during male-male contest competitions and sexual

selection on male major cheliped in *Pagurus* hermit crabs. I also refer the possibility

of male-male scramble competition in the field.

Chapters 2 to 5 are based on the following papers:

Chapter 2: Yasuda C, Suzuki Y, Wada S (2011) Function of the major cheliped in male-male

competition in the hermit crab *Pagurus nigrofascia*. Mar Biol 158:2327-2334

Chapter 3: Yasuda CI, Matsuo K, Wada S (2014) Rapid regeneration of the major cheliped in

relation to its function in male-male contests in the hermit crab *Pagurus

middendorffii*. Plankton Benthos Res 9:122-131

Chapter 4: Yasuda C, Takeshita F, Wada S (2012) Assessment strategy in male-male contests of

the hermit crab *Pagurus middendorffii*. Anim Behav 84:385-390

Chapter 5: Yasuda CI, Matsuo K, Hasaba Y, Wada S (2014) Hermit crab, *Pagurus middendorffii*,

males avoid the escalation of contests with familiar winners. Anim Behav 96:49-57

Chapter 2: Function of the major cheliped in male-male contests in the hermit crab *Pagurus nigrofascia*

Introduction

Male-male contest can lead to the development of morphological traits that enable aggressive interactions (Chapter 1; Andersson 1994; Emlen 2008) in several crustaceans such as amphipods (Wellborn 2000; Takeshita & Henmi 2010) and decapods (Jennions & Backwell 1996; Murai & Backwell 2006; Baeza & Thiel 2007).

Development of the morphology in crustacean appendages can also be explained in the context of natural selection, including foraging, predator avoidance and intra/interspecific contests. Shore crabs use their master (i.e. larger) chela to break open mussel shells (Elner & 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 & Seed 1992). Some species of terrestrial crabs use their chelae for predator avoidance by displaying with chelae oriented toward the approaching predator and grasping at the predator (Robinson et al. 1970). When crabs escape for refuge, they also display by holding the chelae above the carapace (Robinson et al. 1970). In female crayfish, chelae size and its strength are positively correlated and females possess larger and stronger chelae are likely to win in territorial disputes (Bywater et al. 2008).

The major cheliped of *Pagurus* hermit crabs functions as a weapon in shell fights

(Elwood & Neil 1992; Laidre & 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 & Neil 1992). They also use their major cheliped to perform pre-fight displays, such as "cheliped presentation" and "cheliped extension", during shell fights (Elwood & Neil 1992). Hermit crabs lacking a major cheliped are less likely to successfully defend their shells than intact crabs (Neil 1985).

On the other hand, male pagurid hermit crabs directly compete for mates during precopulatory guarding (Chapter 1; Hazlett 1968; Elwood & Neil 1992; Wada et al. 1999) by using major cheliped (Asakura 1987). I therefore used *Pagurus nigrofascia* to examine (1) whether major cheliped loss in male decreases the likelihood of winning in contests for mates, and (2) whether a larger major cheliped confers any advantage in a contest between similar sized males. I also described (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 this study site (Goshima et al. 1996). Males may lose their major cheliped during the reproductive season due to male-male contests. I 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 & Methods

Morphological characters

I collected solitary *Pagurus nigrofascia* in the intertidal rocky shore on 24 and 25 April (male, $N = 185$; female, $N = 159$) and on 8 and 9 June 2009 (male, $N = 109$; female, $N = 152$) at Kattoshi, southern Hokkaido, Japan (41°44'N, 140°36'E). I 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; SL) to the nearest 0.1 mm under a stereomicroscope. For individuals with a major cheliped, collected in April, I also measured the propodus length of major cheliped (from the tip of the fixed finger to the base of the palm; PL) to the nearest 0.1 mm under a stereomicroscope. There were strong correlations between PL and SL in both sexes (see Fig. 2-1). I then examined sexual dimorphism in major cheliped size by using a generalized linear model (GLM) with a normal error distribution, in which the response variable was PL 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, I collected 203 precopulatory guarding pairs from 24 April to 1 May 2009 at the study site. Each guarding pair was placed in a small vinyl pouch with seawater in the field. I measured SL of the guarding males and recorded whether they had a

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major cheliped or not. I 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. 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 (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 (April and June). I also used the 200 of the total 203 guarding pairs in the following experiment 1 (Exp-1) before the above measurements. In each experimental trial, I used two pairs for each trial (both males and one female) of all the pairs collected on a day (Table 2-1).

I also collected a further 244 precopulatory guarding pairs from 29 April to 2 May 2009 at the study site to compare PLs between solitary and guarding males. Each guarding pair was placed in a small vinyl pouch with seawater in the field. I measured SLs and PLs of guarding males. The difference in PLs 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), I 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 PL, and the explanatory variables were SL, category of males (guarding or solitary) and interaction between SL and category. I used the guarding pairs in the following experiment 2 (Exp-2) before the above measurements. From all pairs collected on a

day, I chose two pairs in which males were of a similar size and, consequently, 86 of 244 pairs

were used in Exp-2 (Table 2-1)

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Exp-1: Effect of major cheliped loss on male-male contest

I used 200 precopulatory guarding pairs of *P. nigrofascia* collected from 24 April to 1 May

2009. 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. I placed the male (owner) and his guarded

partner in the field in a small plastic container (19.5 x 12.0 x 7.0 cm) filling it with seawater to a

depth of about 3 cm. Another male (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, I 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, I recorded these outcomes as "win" or "lose",

respectively. If the contest did not finish by the end of the observation period, I recorded it as

"draw". I 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 was used to examine the effect of a lost

limb (i.e. 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 contest (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 (loss in larger male = 1, no loss = 0, loss in smaller male = -1), minor cheliped (loss in larger male = 1, no loss = 0, loss in smaller male = -1) and walking legs (loss in larger male = 1, no loss = 0, loss in smaller male = -1). The SL difference between larger and smaller males (DSL_{L-S}) and the position of larger males (owner = 1, intruder = 0) were also included as explanatory variables in the GLM.

Exp-2: Effect of major cheliped size on male-male contest

To examine the effect of major cheliped size on the outcomes of male-male contest, I conducted experiments to account for the effect of body size difference between contestants (see Results). I chose 43 sets of two guarding males from 244 pairs collected from 29 April to 2 May 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. I used a set of guarding pairs for each trial and randomly selected one male as the owner. Then I randomly chose a receptive female and placed the owner and the female in the container (19.5 x 12.0 x 7.0 cm). After the owner male guarded

the female, an intruder male was introduced to the container. I recorded the outcomes of

male-male contest 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, I recorded these

outcomes as "win" or "lose", respectively. If the contest had not finished by the end of the

observation period, I recorded it as "draw". I measured SLs and PLs 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. The

response variable was the outcome of contests (larger male win = 2, draw = 1, lose = 0). The

explanatory variables were the difference in PL between males with larger SL and smaller SL

(DPL_{L-S}), DSL_{L-S} and the position of the males with larger SL (owner = 1, intruder = 0). There

was no correlation between DPL_{L-S} and DSL_{L-S} ($r^2 = 0.003$, $N = 86$).

Results

Morphological characters

The PL increased with SL in both sexes (solitary male, $N = 174$; solitary female, $N = 158$; Fig.

2-1), and there was a significant interaction between SL and sex (GLM, $t = 9.31$, $P < 0.001$; Fig.

2-1), indicating sexual dimorphism in the size of propodus of major cheliped because males

increased PL 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% ($N = 203$; Table 2-1). The frequency of major cheliped loss in all males increased with SL (GLM, $z = 4.39$, $P < 0.001$; Fig. 2-2), 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. 2-2), but not in April (GLM, $z = -0.70$, $P = 0.13$).

There was a significant interaction between SL and category of males (guarding or solitary; GLM, $t = 2.92$, $P = 0.004$; Fig. 2-3), and guarding males having a larger PL than solitary males collected in April (guarding male, $N = 244$; solitary male (SL ≥ 5.0), $N = 94$; Fig. 2-3).

Exp-1: Effect of major cheliped loss on male-male contest

Males without a major cheliped ($N = 18$) had a significantly decreased a probability of winning in the contest ($N = 100$; Table 2-2, Fig. 2-4), while the loss of a minor cheliped ($N = 5$) or walking leg ($N = 4$) had no effect on contest outcomes (Table 2-2). Ownership and larger body size than the opponent (DSL_{L-S}) also significantly increased the probability of winning (Table 2-2). Owner males showed cheliped extension against intruders even before the combat. Almost all intruders (99/100 trial), however, escalated the contest by fighting with direct physical combat, and most of them aggressively used major cheliped to takeover the females from the

owner males. In spite of such active using by both contestants, 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 contest

PL difference (DPL_{L-S}) significantly affected the contest outcomes, and males with a larger PL

showed a higher probability of winning than males with smaller PL ($N = 43$; Table 2-3, Fig.

2-5) when the contestants were similar in SL. Ownership and SL difference (DSL_{L-S}) had no

effect on the probability of winning (Table 2-3). 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.

Discussion

Results in this study demonstrate that the major cheliped is important in determining the

outcome of male-male contests 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 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* Terao, 1913 (Asakura 1987), *P. bernhardus* (Briffa & Dallaway 2007; Doake et al. 2010) and *P. filholi* (Yoshino & Goshima 2002). Also, the advantage of a large body size in male-male contests for mates is known in these species (Asakura 1987; Elwood & Neil 1992; Tanikawa et al. 2012). Sexual selection may be a common evolutionary pressure for 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* (Dana, 1852) 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* (Latreille, 1818). 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. I 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 & Smith

1995; Mariappan et al. 2000). Cheliped loss is also costly in general activities in the field

(Juanes & Smith 1995). Asian shore crabs with the loss of one cheliped had a decreased feeding

rate compared to 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 & Smith 1998). In *P. nigrofascia*, major

cheliped loss might also reduce the efficiency of feeding, although *Pagurus* spp. use 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 & Smith 1995). For example, mating males in shore crab have larger

chelae than overall males (Lee & Seed 1992), and chela size in this species strongly affects the

outcomes of contests over food (Sneddon et al. 1997). Results in this study 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 male-male contest 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

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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 (RHP; Chapter 1) 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). It is partially explained by no injury of major cheliped during male-male contests of *P. nigrofascia* although males used their major chelipeds as a physical weapon. 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 & Elwood 2007) and/or physiological condition (Laidre & Elwood 2008). Major chelipeds of hermit crabs now provide a further topic for study in the context of sexual selection.

Figure 2-1 Relationship in both sexes between propodus length of major cheliped (PL) and shield length (SL) in solitary males ($N = 174$, PL = -2.81 + 1.45 SL) and females ($N = 158$, PL = -0.17 + 0.82 SL) collected in April. Open squares are mean PL and SL, and error bars show SD for each sex. The slopes of regressions significantly differed from each other
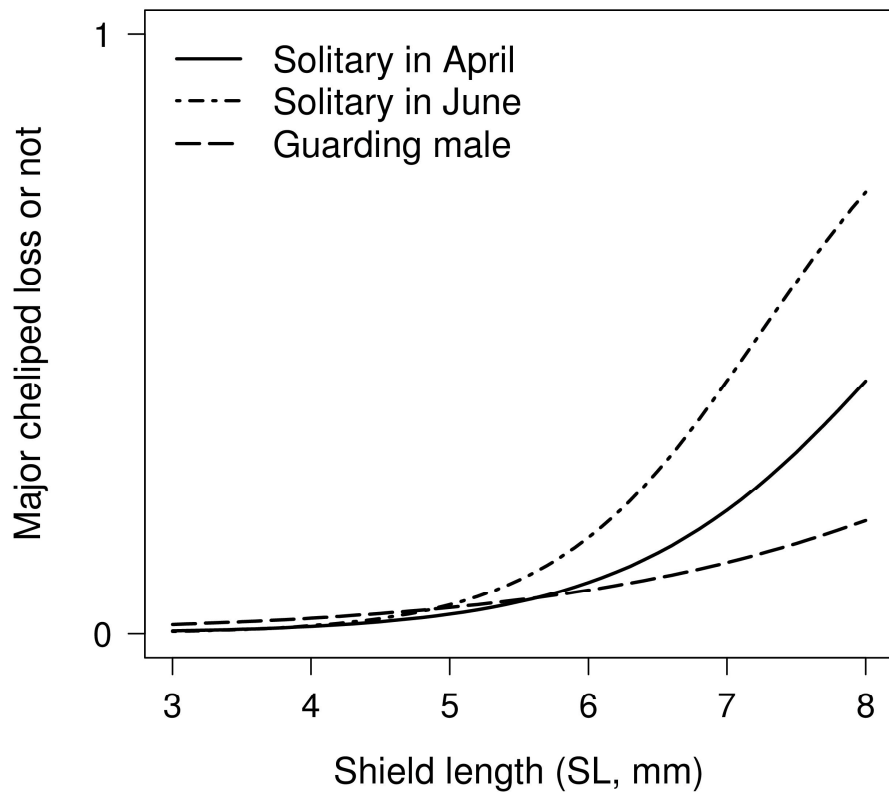
Figure 2-2　Logistic relationships between frequency of major cheliped loss and shield length (SL) in three male categories: solitary males in April ($N = 185$), solitary in June ($N = 109$) and guarding males ($N = 203$). Points at 0 and 1 are intact male or male of major cheliped loss, respectively. The slopes of regression significantly differed between solitary males in June and guarding males
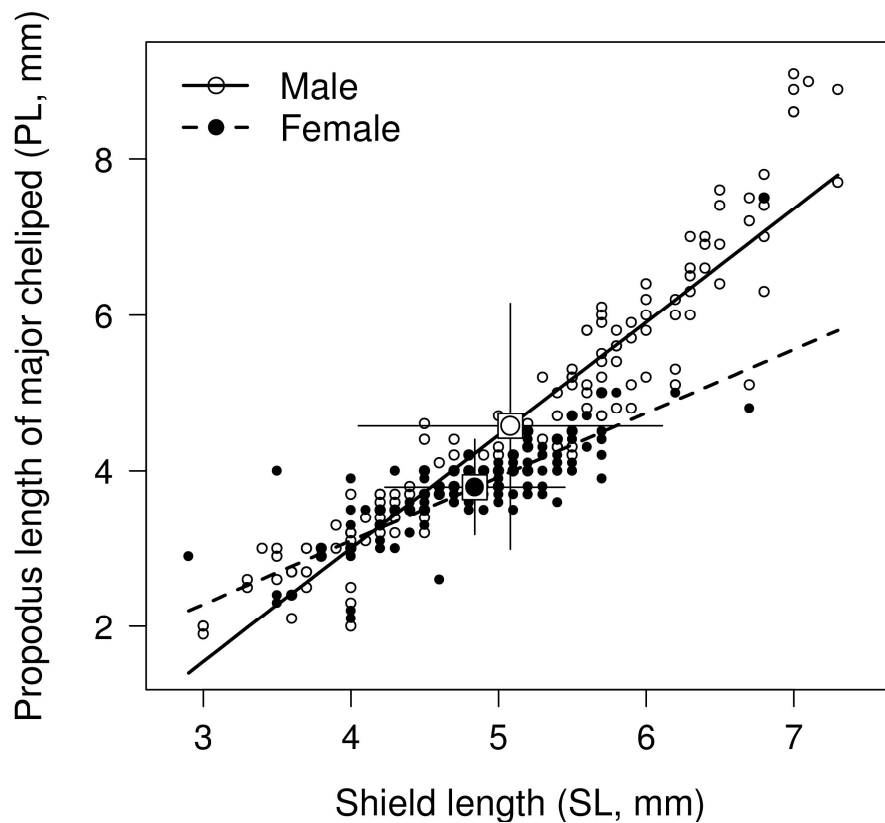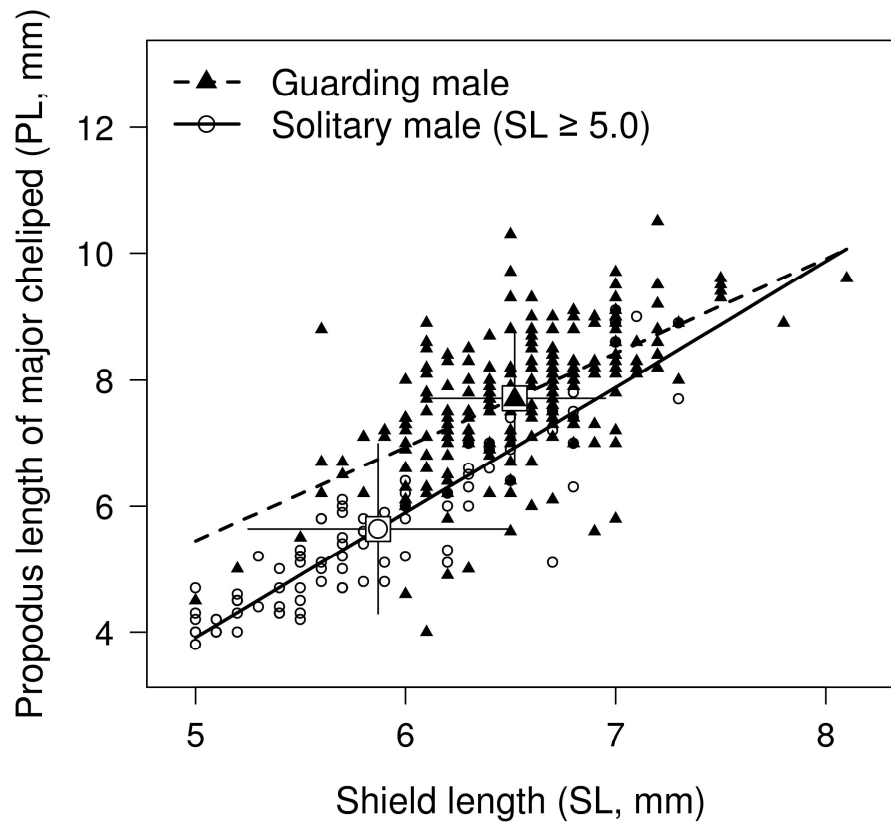
Figure 2-3 Relationship between propodus length of major cheliped (PL) and shield length (SL) in guarding males ($N = 244$, PL = -1.99 + 1.49 SL) and solitary ones collected in April (SL ≥ 5.0, $N = 94$, PL = -6.01 + 1.98 SL). Open squares are mean PL and SL, and error bars show SD for guarding or solitary males. The slopes of regressions significantly differed from each other
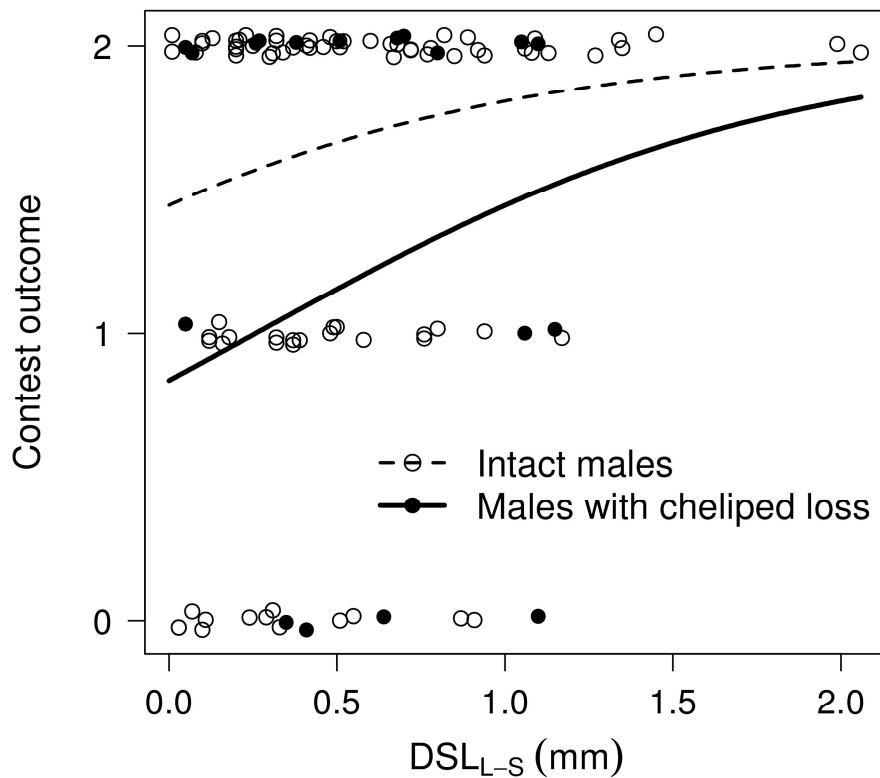
Figure 2-4 Logistic relationship in outcomes of male-male contests in larger males with major cheliped (*N* = 82) and major cheliped loss (*N* = 18). DSL_{L-S} indicates the difference in shield length (index of body size) between the larger and the smaller male in each contest, respectively. Points at 0 to 2 are larger and smaller males win or lose, respectively. 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)
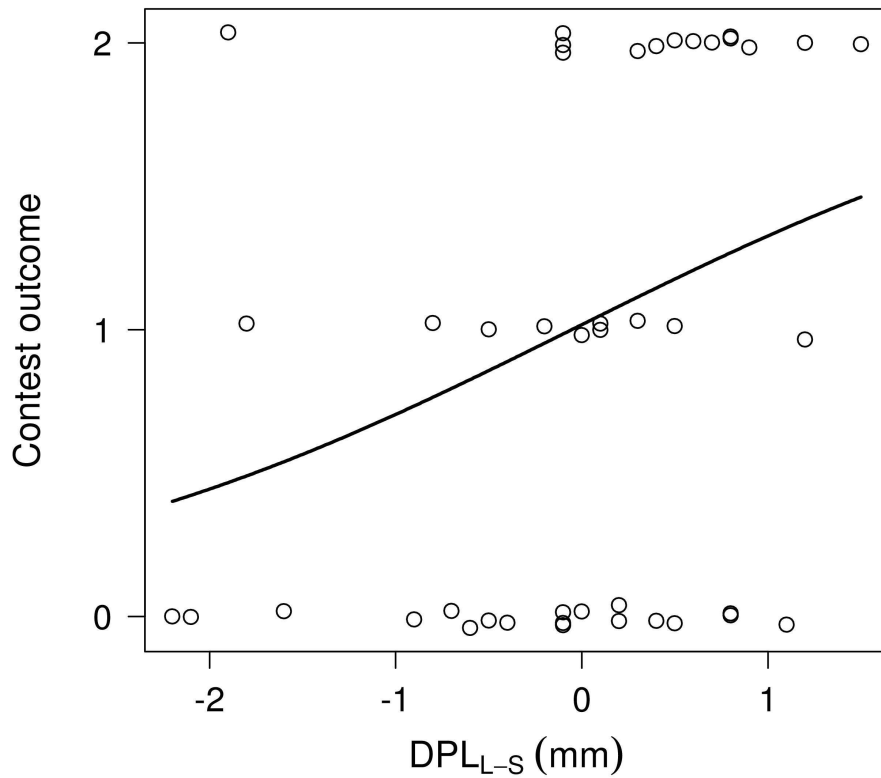
Figure 2-5　Logistic relationship in outcome of male-male contests in males with larger body size (shield length, SL) between similar sized males ($N = 43$). DPL_{L-S} indicates the difference in propodus length of major cheliped between the larger and the smaller male in each contest, respectively. Points at 0 to 2 are larger and smaller males win or lose, respectively. Two variables, ownership and difference in shield length were treated as constants in regression curve (ownership = 1, mean of DSL_{L-S})

Table 2-1   Sample size for each generalized linear model of this study

Date	Type	N	Morphological character				Experiment	
			Sexual dimorphism in PL	Frequency of major cheliped loss (%)		PL difference between solitary and guarding males	Exp-1	Exp-2
24 Apr - 25 Apr	Solitary males	185 inds	174 inds	11/185 inds	(5.95)	94 inds[2]		
24 Apr - 25 Apr	Solitary females	159 inds	158 inds	1/159 inds	(0.63)			
8 Jun - 9 Jun	Solitary males	109 inds		12/109 inds	(11.00)			
8 Jun - 9 Jun	Solitary females	152 inds		6/152 inds	(3.95)			
24 Apr - 1 May	Guarding pairs[1]	203 pairs		19/203 inds	(9.36)		100 trials	
29 Apr - 2 May	Guarding pairs[1]	244 pairs				244 inds		43 trials[3]

PL indicates the propodus length of major cheliped in each crab. Blank cells indicate that there was no data in each sampling date.
[1] These two samples were different from each other and males of the guarding pairs were used for measuring morphological characters
[2] The number of solitary males that shield lengths (i.e., index of body size) were 5.0 mm and larger
[3] Two similar sized males in experimental trials were chosen by collected pairs

Table 2-2 Results of Exp-1 analyzed by a generalized linear model with the binomial error distribution

	Estimate	SE	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
DSL_{L-S}	1.23	0.48	2.68	0.007

DSL_{L-S} indicates the difference in shield length (index of body size) between larger and smaller males in each contest

Table 2-3 Results of Exp-2 analyzed by a generalized linear model with the binomial error distribution

	Estimate	SE	*Z*	*P*
Intercept	-0.90	0.45	-2.00	0.05
DPL_{L-S}	0.64	0.30	2.13	0.03
DSL_{L-S}	0.58	0.77	0.75	0.45
Ownership asymmetry	0.72	0.48	1.49	0.14

DPL_{L-S} and DSL_{L-S} indicate the differences in propodus length of major cheliped or shield length (index of body size) between larger and smaller males in each contest

Chapter 3: Rapid regeneration of the major cheliped in the hermit crab *Pagurus middendorffii*

Introduction

Decapod crustaceans form one of the most studied taxa for the functioning of morphological weapons (i.e. major cheliped) in male-male contests and the sexual size dimorphisms of these traits (Chapters 1, 2; Andersson 1994; Hughes 1996; Searcy & Nowicki 2005; Moore 2007; Wilson et al. 2007; Emlen 2008; Yoshino et al. 2011). The loss of the major cheliped therefore would be a severe problem in crustaceans. Crabs of many species can shed their appendages (autotomy; Juanes & Smith 1995; Maginnis 2006; Fleming et al. 2007) when they escape from predatory interactions (Robinson et al. 1970; Wasson et al. 2002). Although autotomy of the cheliped is highly effective in immediate benefits for survival (Wasson et al. 2002), the loss of the cheliped is known to have negative impacts on subsequent contests (Chapter 2; Juanes & Smith 1995). Weaponless crabs have a decreased probability of winning in dyadic contests compared with intact crabs (Berzins & Caldwell 1983; Neil 1985; Smith 1992; Abello et al. 1994) even if they are larger in body size than the opponents (Daleo et al. 2009) or they have ownership of the resource (Chapter 2).

Rapid regeneration of a major cheliped may be an appropriate strategy for crabs which autotomized the major cheliped. In fiddler crabs, individuals with regenerated chelipeds

have an improved mating success in comparison with individuals without the cheliped during reproductive season (Backwell et al. 2000; Reaney et al. 2008) because the regenerated cheliped allows to bluff in male-male contests and to attract potential mates (Backwell et al. 2000). In *Pagurus* hermit crabs, Neil (1985) also has reported the effectiveness of regenerated major cheliped during shell fights in *P. bernhardus*. Although the regenerated major cheliped was relatively small than original ones, crabs with regenerated major cheliped showed a higher probability of defending their own shell than crabs with major cheliped loss.

Pagurus hermit crabs also use major cheliped as weapon during male-male contests (Chapter 2) and several studies have reported its sexual size dimorphism (Chapter 2; Briffa & Dallaway 2007). The presence and the size of major cheliped strongly affected the outcomes of male-male contests (Chapter 2). Males therefore would regenerate their major cheliped after autotomy especially if they autotomized their major cheliped before the mating season.

In the present study, I examined the pattern of major cheliped regeneration in the hermit crab *Pagurus middendorffii*. The mating season of this species occurs from late October to early December in the study site (Wada et al. 1995, 1999) and individuals show lower molt frequencies from September to February in the study site (Wada 2000). Experiment was thus initiated in late July and completed in late September. Additionally, after cheliped autotomy, regeneration pattern of the appendage often differs according to the body size of each animal in several crabs (Smith 1990; Brock & Smith 1998). I therefore also examined the effects of male body size on the degree of major cheliped regeneration in *P. middendorffii*.

Materials & Methods

Experimental design

Intact male *Pagurus middendorffii* (i.e. males had all appendages) were collected on 14, 15 and 19 July 2011. In the laboratory, I placed crabs in a large container (45.4 x 31.0 x 11.5 cm), and allowed them to acclimate to aquarium conditions (15 °C, 12L: 12D) for at least a week before the experiment. Each male was randomly assigned to two experimental groups: regeneration (R-male, $N = 94$) or control (C-male, $N = 91$). R-males were induced to autotomize their major cheliped by grasping it with forceps, which usually happened within three minutes. No crabs lost other appendages during this experimental procedure.

I measured propodus length (PL; see Chapter 2 for the measurement) and propodus width of the major cheliped (maximum width of the palm; PW) of the autotomized major cheliped in R-males and used the data as the original size of the major cheliped for each crab. Autotomy treatment was conducted on 27 and 28 July 2011 which formed the start of rearing experiments. All crabs were kept individually in small containers (14.3 x 10.8 x 7.2 cm) filled with natural seawater at 15°C and a depth of about 3 cm. They were fed artificial food (TETRA, Tetra Plankton) and *ad libitum* red alga (*Neorhodomela aculeata,* collected from the

study site). The seawater was changed each day.

I observed all crabs once a day and recorded whether or not each crab had molted. I measured shield length (SL; see Chapter 2 for the measurement), PL and PW of the molted exoskeleton in R-males and SL in C-males to the nearest 0.01 mm under a stereomicroscope. This experiment ended on 25 September 2011, and final measurements were made of SL, PL and PW (i.e. size of regenerated major cheliped) of males in R-males and SL in C-males.

Analyses

The original and regenerated PL or PW at the first molt (molt-1) were compared using a generalized linear model (GLM) with a normal error distribution. The response variables were PL or PW, and the explanatory variables were SL and category (size of original or regenerated) and interaction between SL and category. The effect of PL on PW was also compared between original and regenerated PW by using GLM with a normal error distribution. The response variable was PW, and the explanatory variables were PL and category and interaction between two variables.

The duration until molt-1 (days) was compared between R-males and C-males by using *t*-test and *F*-test. Since there were several R-males without regeneration of the major cheliped at molt-1 (see Results), the factors affecting regeneration were examined by using GLM with a binomial error distribution. The response variable was whether or not the male

regenerated the major cheliped (Yes = 1, No = 0, $N = 94$), and the explanatory variables were initial SL (at the start of the experiment) and the duration until molt-1 (days).

Growth in body size was compared between R-males and C-males using a GLM with a normal error distribution. Since all R-males regenerated the major cheliped after 15 days (see Results), to analyze the data on growth in SL, a subset of data was used in which molt-1 occurred after 15 days (R-males, $N = 87$; C-males, $N = 78$). The response variable was difference between SL after molt-1 and initial SL, and the explanatory variables were the experimental group (R- or C-male), initial SL and the duration until molt-1 (days). Also, the effect of major cheliped regeneration on SL growth in molt-1 was tested by a GLM with a normal error distribution. The response variable was the same as above, and the explanatory variable was PL or PW.

Finally, since most males molted twice (see Results), the interval between molt-1 and the second molt (molt-2) was analyzed using a Cox's proportional hazard model (Cox 1972). In this type of regression model the data are expressed in terms of the tendency of occurrence of an event (so called hazard rate), which is the probability per unit of time that the molt-2 occurs in each crab. Regression coefficients of the model were estimated from the data by partial likelihood maximization, and the significance of each explanatory variable was tested using standard likelihood ratio tests through an iterative procedure. The response variable was the interval between two molts (days), and the explanatory variables were SL at molt-1 and the experimental manipulation. The effect of SL on PL or on PW was compared between the

original and molt-2 with using GLM with a normal error distribution. The response variable

was PL or PW and the explanatory variable were SL and category (original size or size in

molt-2) and the interaction between SL and category. The effect of PL on PW was also

compared between original and PW in molt-2 by using GLM with a normal error distribution.

The response variable was PW, and the explanatory variables were PL and category and

interaction between two variables.

Results

Most R-males largely regenerated their major cheliped in molt-1 after the experimental

autotomy (Fig. 3-1). Of these, the mean PL regeneration rate at molt-1 (regenerated PL as a

percentage of original PL) was 86.63 ($\pm$ 17.12 SD) % ($N = 87$), and the mean duration from the

day of autotomy to occurrence of molt-1was 29.1 days $\pm$ 4.56 SD. There was a significant

interaction between SL and categories of PL (Table 3-1). The gradient of the linear regression

between SL and PL shows is lower for regenerated PL than for the original (Fig. 3-2),

indicating an obvious decrease in PL regeneration rate at molt-1 in relation to body size.

Similarly, the mean regeneration rate in PW as a percentage of the original PW at the molt-1

was 71.71 ($\pm$ 13.03 SD) %, with significant interaction between SL and categories of PW

(Table 3-1), and a shallower gradient for the regenerated compared with original PW (Fig. 3-3).

There was a significant interaction between PL and categories of PW (Table 3-2), indicating

that the regenerated major cheliped is a more slender than the original.

R-males showed a significantly more synchronized timing of molt-1 than C-males

(F-test, $F = 3.239$, $P < 0.001$; Fig. 3-4), although there was no difference in the mean number

of days to molt-1 (Welch's t-test, $t = -0.433$, $P = 0.666$): 28.2 days (± 6.76 SD, $N = 94$) days

from experiment initiation for R-males; 27.5 days (± 12.24 SD, $N = 91$) for C-males. Seven

R-males did not regenerate the major cheliped at molt-1, and frequency of regeneration

significantly increased with the number of days (GLM, $z = 3.220$, $P = 0.001$). All males with

major cheliped regeneration molted after 15 days from the start of the experiment, and four of

seven males molted within six days (Fig. 3-4). Initial SL had no effect on whether or not the

major cheliped was regenerated at molt-1 (GLM, $z = -0.789$, $P = 0.430$).

The growth in SL after molt-1 was significantly lower for R-males (0.35 ± 0.14 SD

mm) than for C-males (0.42 ± 0.16 SD mm) (GLM, $t = -3.163$, $P = 0.002$), and some R-males

showed no SL growth increment in molt-1. Initial SL and duration until molt-1 had no effect

on the growth in SL (initial SL, $t = 1.552$, $P = 0.123$; duration until molt-1, $t = -0.713$, $P =$

0.477). Neither PL nor PW of the regenerated major cheliped had an effect on SL growth ($N =$

87; PL, $t = 1.615$, $P = 0.110$; PW, $t = 1.841$, $P = 0.069$).

Most individuals molted twice during the rearing period, with intervals between

molt-1and molt-2 24.8 days (± 3.72 SD, $N = 62$) for the R-males and 28.4 days (± 9.00 SD, N

$= 33$) for the C-males. The molt interval significantly increased with SL for molt-1 (Cox's

proportional hazard model, $N = 185$, $z = -8.012$, $P < 0.001$) with R-males having a significantly

shorter molt interval than the C-males ($z = 4.817$, $P < 0.001$).

R-males showed large growth of the regenerated major cheliped in molt-2.

Interaction between SL and size category (original size or size in molt-2) was significant for

PW (GLM, $t = -4.772$, $P < 0.001$) but not for PL ($t = -1.435$, $P = 0.154$). Also, a significant

interaction between PL and size category was found in the analysis to examine the effect of PL

on PW ($t = -5.842$, $P < 0.001$). These results indicate that males could regenerate the major

cheliped with a similar PL but smaller PW relative to the original cheliped by molt-2. R-males

showed significantly lower SL growth than the C-males in molt-2 ($t = 3.043$, $P = 0.003$).

Discussion

A large regeneration of the major cheliped was observed at the first molt following autotomy in

the hermit crab *Pagurus middendorffii*. Males recovered approximately 80% of the major

cheliped size relative to their original major cheliped by the first molt. At the second molt,

males could regenerate major cheliped with a similar length as that of original one. On the

other hand, males in the regenerated group showed a smaller growth in body size than intact

males at both the first and the second molt after autotomy. These results differ from other

studies dealing with cheliped regeneration of other crabs. Although many studies have

demonstrated that major cheliped regeneration decreases body size increment at first molt (Bennett 1973; Hopkins 1982; Smith 1990; Cheng & Chang 1993; McLain & Pratt 2011), this smaller growth increment is not observed for the second molt in the blue crab (Smith 1990) and the fiddler crab (McLain & Pratt 2011). Additionally, the interval between the first and second molt was shorter in males in the regeneration group than individuals in the control group, suggesting an acceleration of the molt cycle. Major cheliped regeneration in *P. middendorffii* males thus continues to be highly costly even at the second molt. This suggests that the major cheliped regeneration is important in this species and males regenerating the major cheliped to possess a larger major cheliped until the reproductive season would be favored.

Small males regenerated a relatively larger major cheliped than large males at the first molt following autotomy. Such large regeneration in small individuals has been reported in other crustaceans (Smith 1990; Brock & Smith 1998). Brock & Smith (1998) suggest that selection for rapid regeneration may be more important in small crabs than large crabs because cheliped loss in small crabs would have a greater negative impact on foraging and predation risk. The hermit crab *P. middendorffii* shows relatively wider rage of body size in guarding males than *P. nigrofascia*, especially the presence of smaller males (*P. middendorffii*, 2.10 to 7.10 mm in SL; Chapter 4; *P. nigrofascia*, 5.00 to 8.10 mm in SL; Chapter 2). To achieve mating success in small males of *P. middendorffii*, a larger regenerated cheliped would be important. It is therefore an advantage for males of this species to regenerate a major cheliped

even if their body size is small. The pattern of major cheliped regeneration therefore appears to be strongly related to its functional importance in both natural and sexual selection.

First molts were more synchronous in the regeneration group than the control group, although there was no significant difference in the mean date between the two groups. Decapod crustaceans have been shown to be able to either shorten or prolong intermolt period before the molt following cheliped autotomy (Hopkins 1982; Juanes & Smith 1995), indicating alteration in physiological conditions in order to regenerate the lost cheliped. Alteration in molt timing would also be expected to occur in male *P. middendorffii* with major cheliped loss as a result of physiological requirements for regeneration. Although molting date was not adjusted before the present set of experiments, most *P. middendorffii* males in the regeneration group molted around 28 days after the day of experimental autotomy and body size had no effect on whether or not the major cheliped was regenerated. These results suggest that it would need approximately one month to regenerate the cheliped regardless of the body size and phase of the molting cycle in each crab.

The pattern of major cheliped regeneration in *P. middendorffii* may be related to the unique life style of gastropod shell use by hermit crabs, in which growth in body size is affected by the size of the gastropod shell occupied by the crab (Fotheringham 1976; Blackstone 1985; Wada 2000). The results of the present study suggest that regeneration of the major cheliped in *P. middendorffii* might not be facilitated or obstructed by the stress of occupying an inadequate shell, although shell adequacy was not investigated or manipulated.

There was no relationship between the amount of major cheliped regeneration and growth in body size by the first molt in *P. middendorffii*, so this species apparently does not allocate more energy into regeneration even body growth is suppressed due to use of a small shell. However, for *Pagurus longicarpus* Say, 1817, Blackstone (1985) has reported that when males use small, high-spired shells they produce longer major chelipeds than males in large, low-spired shells. Therefore the effect of shell stress on energy allocation among regenerating body parts, including the major cheliped, requires further investigation in *P. middendorffii*.

Finally, I consider the effectiveness of regenerated major chelipeds although it was not examined in the present study. In male fiddler crabs, they regenerate a slender cheliped than their original cheliped after losing the original one (Lailvaux et al. 2009). While their original chelipeds are used both as display to their rivals and mates and as physical weapons in male-male contests, the regenerated slender chelipeds are considered to function as dishonest signals during the pre-fight phase and courtship behavior for females (Backwell et al. 2000). Both males and females do not discriminate whether the claw is original or not in fiddler crabs (Reaney et al. 2008). On the other hand, in hermit crabs, no studies have demonstrated that females choose their mates based on the major cheliped size. Since precopulatory guarding behavior is initiated by males approaching and assessing females in *Pagurus* spp. (Suzuki et al. 2012), the regenerated major cheliped may not be effective as a signal to females.

The regenerated cheliped in males of *P. middendorffii* would be effective as a weapon in male-male contests. In this study, males of *P. middendorffii* regenerated 86% of the major

cheliped length but 71 % of the width relative to their original major cheliped by the first molt.

They also completely recovered major cheliped length by the second molt. This length-biased

major cheliped regeneration would be consistent with the importance of major cheliped length

during male-male contests in *Pagurus* hermit crabs. For example, both owner and intruders of

P. nigrofascia aggressively use their major cheliped during male-male contests, and the length

of major cheliped strongly affects the contest outcomes (Chapter 2). Males of *P. middendorffii*

also use major cheliped as weapon, and major cheliped length is more important to determine

the contest winner (see Chapter 4) as well as other decapods (Barki et al. 1997; Sneddon et al.

1997; Yoshino et al. 2011; Matsuo et al. in press). Further studies would be needed to

investigate how the regenerated major cheliped functions in male-male contests of *Pagurus*

hermit crabs.
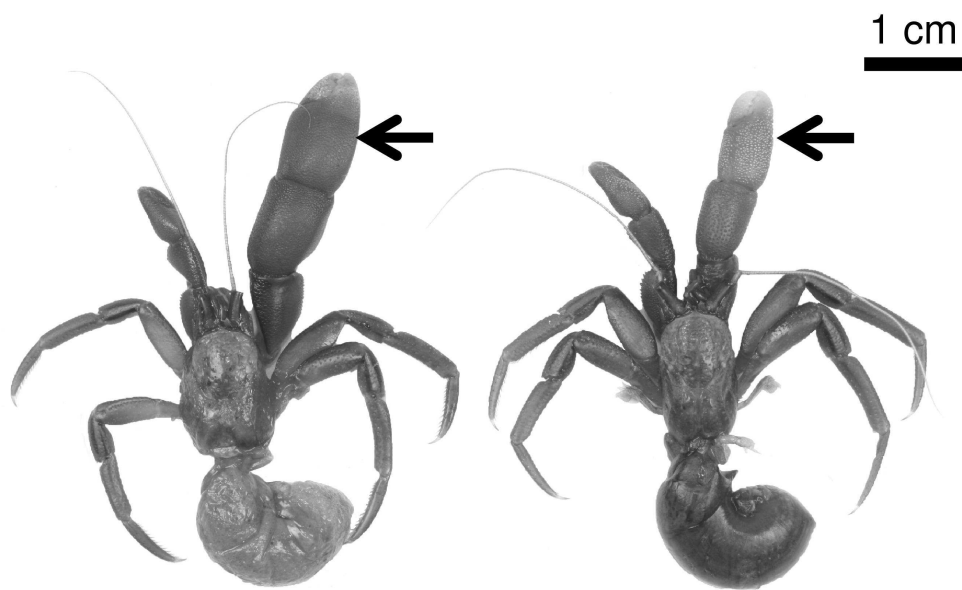
Figure 3-1 Males of *Pagurus middendorffii* with a regenerated major cheliped at the first molt (right) and an original major cheliped (left). The number of days until the first molting in males that regenerated major cheliped was 29.1 ± 4.56 SD. Males could largely regenerate the major cheliped in the first molt after autotomy
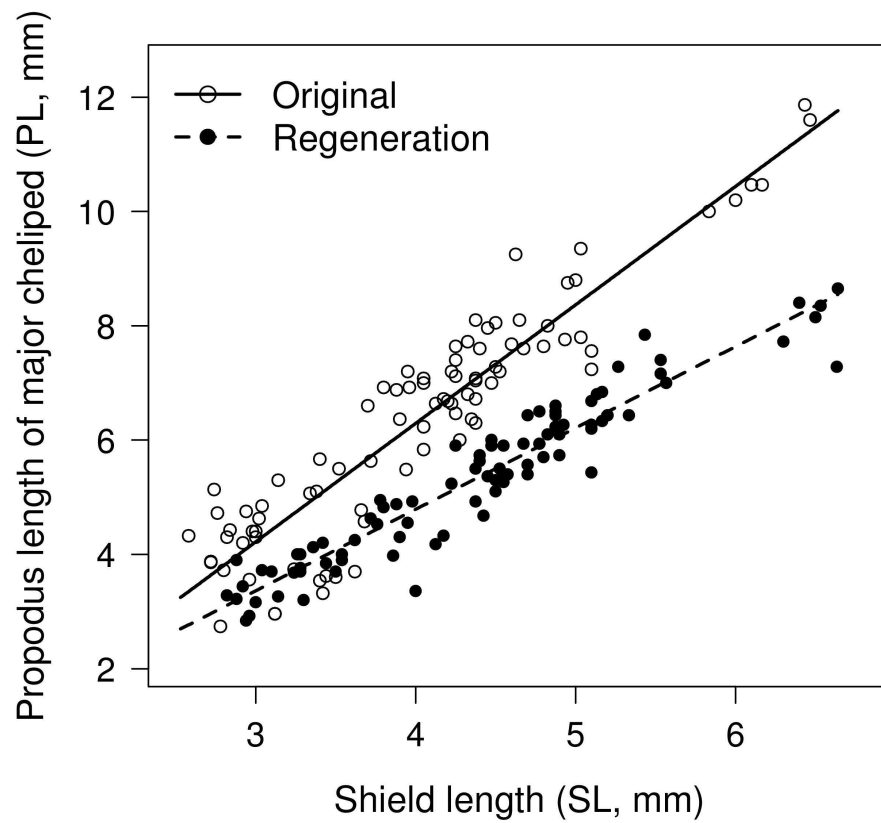
Figure 3-2　Relationships between propodus length of major cheliped (PL) and shield length (SL) in original size ($N = 87$, PL = -2.00 + 2.07 SL) and regeneration size at the first molt ($N = 87$, PL = -0.91 + 1.42 SL). The slopes of regressions significantly differed from each other
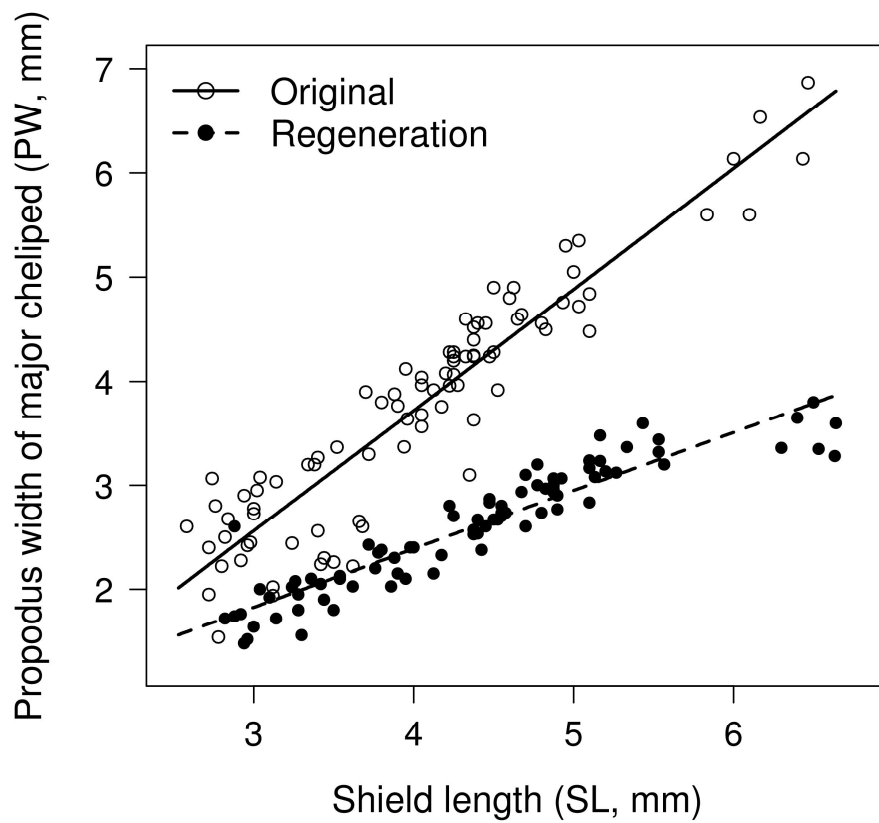
Figure 3-3 Relationships between propodus width of major cheliped (PW) and shield length (SL) in original size ($N = 87$, PW = -0.92 + 1.16 SL) and regeneration size at the first molt ($N = 87$, PW = 0.14 + 0.56 SL). The slopes of regressions significantly differed from each other
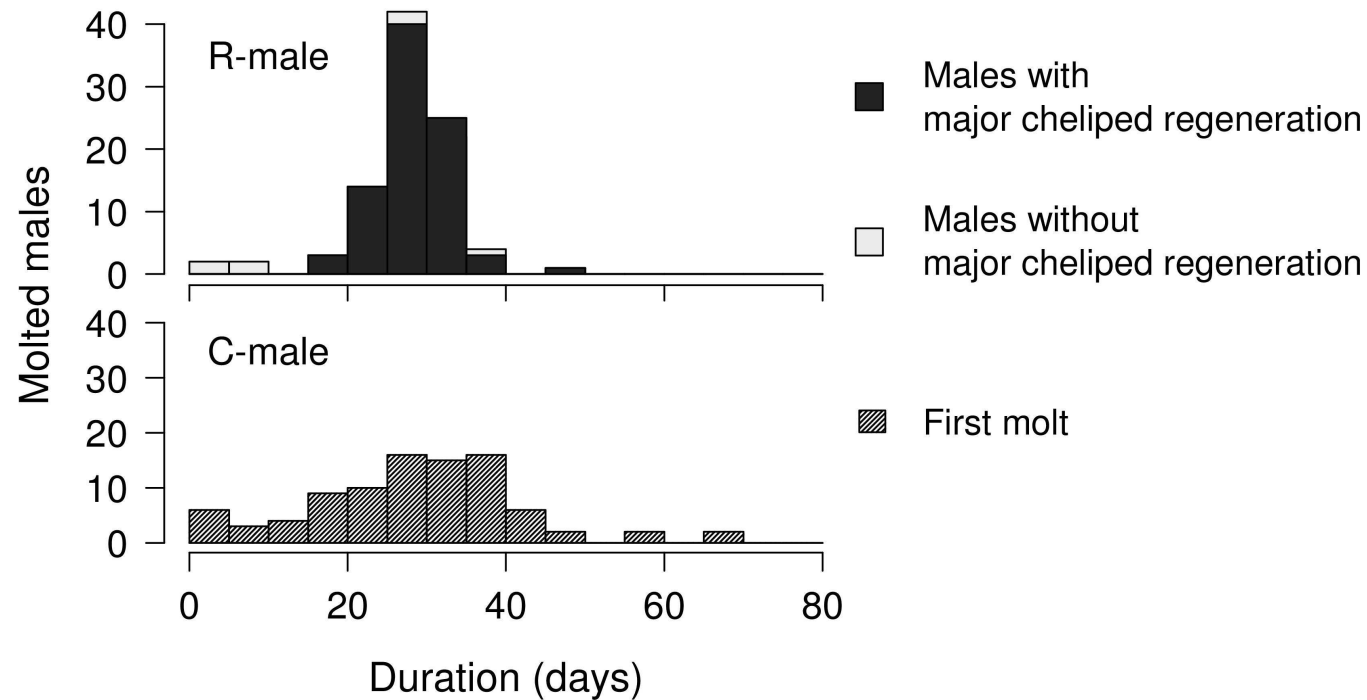
Figure 3-4 Number of molted males in the regeneration group (R-male; upper) and the control group (C-male; lower) at the first molt. X-axis indicates the duration (days) from experiment initiation. In the R-male, *solid* and *open* bars indicate the number of males with a major cheliped regeneration (solid) and males without a major cheliped regeneration (open), respectively. In the C-group, diagonal bars indicate the number of males at the first molt. Mean durations (days) until the first molt were 28.2 (± 6.76 SD) in R-males and 27.5 (± 12.24 SD) in C-males, respectively

Table 3-1 Comparisons between original and regenerated major cheliped analyzed by a generalized linear model with the normal error distribution

	Estimate	SE	*t*	*P*
Relationship between PL and SL				
Intercept	-19.990	3.057	-6.539	< 0.001
SL	2.073	0.074	28.026	< 0.001
Regeneration	10.916	4.392	2.486	0.014
SL x Regeneration	-0.649	0.102	-6.356	< 0.001
Relationship between PW and SL				
Intercept	-9.229	1.641	-5.740	< 0.001
SL	1.161	0.039	29.843	< 0.001
Regeneration	10.063	2.310	4.356	< 0.001
SL x Regeneration	-0.589	0.054	-10.970	< 0.001

PL, PW and SL indicate the propodus length and width of major cheliped and shield length (index of body size), respectively. Males were experimentally induced major cheliped autotomy and regenerated this appendage in the first molt after autotomy ($N = 87$)

Table 3-2 Comparison of the relationship between PW and PL between original and regenerated major cheliped analyzed by a generalized linear model with the normal error distribution

	Estimate	SE	t	P
intercept	2.972	0.692	4.292	< 0.001
PL	0.544	0.010	52.456	< 0.001
Regeneration	1.645	1.070	1.537	0.126
PL x Regeneration	-0.145	0.018	-8.037	< 0.001

PW and PL indicate the propodus width and length of major cheliped, respectively

Chapter 4: Assessment strategy in male-male contests of the hermit crab *Pagurus middendorffii*

Introduction

Dyadic contests for resources are typically determined by the asymmetries of resource holding potential (RHP) (Parker 1974) between contestants (Chapter 1). Contestants make a decision regarding the contest behavior based on RHP assessment (Chapter 1) reflected by body size and/or weapon size (Briffa & Sneddon 2007; Arnott & Elwood 2009), such as 'mutual assessment' (Enquist & Leimar 1983; Enquist et al. 1990) and 'self-assessment' (Payne & Pagel 1996, 1997; Taylor & Elwood 2003).

Phase transitions often occur in animal contests. Contestants often start with a display ('display phase'), in which they show an index of their RHP, such as body and weapon sizes, to each other. If the contestants cannot determine the outcome during the display phase, they then escalate to the 'physical fighting phase', which involves a direct attack and/or aggressive struggle (Briffa & Sneddon 2010). For example, male deer initiate contests by parallel walking to display and assess each other's shoulder height and subsequently escalate the interaction by antler locking and jumping clashes (Jennings et al. 2005). Crayfish display chela size as a visual signal to opponents and engage in aggressive behavior when they cannot resolve the fight in the

display phase (Wilson et al. 2007). In spite of the assumption that contestants use a single assessment strategy in throughout the contest in many theoretical models, switching assessment tactics among contest phases have been reported in several animals (Chapter 1). Contestants may thus use multiple assessment tactics to make decisions when phase transitions and/or escalation occur during a fight.

In male-male contests of *Pagurus* hermit crabs, although larger males are more likely to win the contest (Chapters 1, 2), I demonstrated the importance of the presence and larger size of major cheliped in *P. nigrofascia* (Chapter 2). Additionally, males of *Pagurus middendorffii*, which is the focal species in this study, showed a large regeneration of major cheliped following major cheliped loss before their reproductive season (Chapter 3). Thus, both body size and major cheliped size of males probably function as indexes of RHP during male-male contests and could be used as a basis for a decision as to whether to initiate and/or escalate the fighting in *Pagurus* hermit crabs.

I therefore examined whether males switch tactics and which index of RHP males use for assessment during male-male contests of the hermit crab *P. middendorffii*. In the first experiment (Exp-1), I conducted trials of male-male contests that guarding and solitary males were randomly assigned. I investigated the pathways of phase transitions in the contests and recorded the assessment tactics and the index of RHP in both initial and combat phases. Because I found a correlation between body size and major cheliped size in male *P. middendorffii* (see Analyses), crabs with a larger body size typically had a larger cheliped than their opponents in

Exp-1 (42/46 sets). To investigate the effects of body size and major cheliped size separately, I conducted the second experiment (Exp-2) in which guarding males and intruder males were visually similar in size, and some males with a larger body size had smaller major chelipeds than the opponents (20/46 sets). These two experiments differed only by the size difference between contestants.

Materials & Methods

I collected 184 precopulatory guarding pairs of *Pagurus middendorffii*, in which males were intact, from my study site (see Chapter 2) during 4-23 November 2010 (i.e. mating season; Chapter 3). After transportation, I checked that the males were still guarding females, and the male and female of each pair were separately maintained in plastic cups (300 ml). All experimental trials were conducted within 6 h of collection. The number of trials in each experiment was 46, and all crabs were used only once.

Experimental design

For each experimental contest, I used two males, which were either randomly assigned from guarding pairs collected on the same sampling date as each other (Exp-1, mean absolute

difference in shield length (SL; see Chapter 2 for measurement) ± SD = 1.39 ± 0.973 mm, N = 46 sets) or were chosen from all the males of the pairs that looked similar in size (Exp-2, mean absolute difference in SL ± SD = 0.40 ± 0.330 mm, N = 46 sets). I firstly introduced one male (owner) and his guarded partner and then another male (intruder) in the container previously described (Chapter 2). I used the video function built into digital cameras (Pentax, Optio-W80) to record the interactions between contestants from the time of introducing all individuals. I observed the recorded data for up to 15 min starting from when the intruder initiated movement.

To describe the pattern of male-male contests in *P. middendorffii*, I recorded three behaviors during the interaction: 'initial physical contact' involved any direct contact between contestants during the initial interactions; 'fencing' involved the intruder attacking his opponent with his major cheliped held horizontal to the substrate, and the owner used his major cheliped to block the intruder; and 'grappling' involved the intruder grasping his opponent with his appendage and wrestling using both chelipeds and walking legs (Elwood et al. 2006; personal observation). In contests that escalated to fencing and/or grappling behaviors (Exp-1, N = 33; Exp-2, N = 46), we recorded the duration(s) of combat behavior (sec; i.e. a series of fencing and/or grappling interactions) as escalation duration. If contestants did not perform fencing and/or grappling for more than 3 min, we defined the fight as settled and recorded which of the males guarded the female at that time. Since intruder males were the focal males, when the intruder or owner male guarded females, we recorded these outcomes as 'win' or 'lose',

respectively. If the contest did not finish by the end of the observation period, I recorded it as a 'draw'.

The male and female of each guarding pair in the field were then placed together in small plastic containers (19.5 x 12.0 x 7.0 cm) to allow precopulatory guarding behavior (Chapter 1) and females were checked for spawning every day until spawning. After females spawned, I measured SL of all crabs and propodus length of major cheliped (PL) in males (see Chapter 2 for measurement) to the nearest 0.01 mm under a stereomicroscope. Although I used both male and female traits for the following statistical analyses, since males of *P. middendorffii* can assess the female's body size and receptivity during mate choice (Wada et al. 2011), I did not focus on the effect of the female on male-male contests.

Analyses

To examine how intruders decide whether to give up the contest without escalation in Exp-1, I conducted model selection focusing on both assessment tactics (i.e. self or mutual) and index of RHP (i.e. body size or weapon size). Model selection was based on Akaike's information criterion (AIC), which provides a measure of parsimonious balance between model predictive power (i.e. goodness of fit) and complexity (i.e. number of parameters), and models with the lowest AIC values are considered the most parsimonious (Akaike 1983). I used a generalized linear model (GLM) with the binomial error distribution. The response variable was

whether intruders gave up the contest without escalation following initial physical contact, such as fencing and/or grappling (Yes = 1, No = 0, $N = 46$; Fig. 4-1). Since there was a strong correlation between SL and PL (intruder, $r^2 = 0.892$; owner, $r^2 = 0.923$; $N = 46$), I used each measurement as an explanatory variable separately in a GLM to avoid multicollinearity. The explanatory variables were therefore one of four measurements: PL and SL of intruder (PL_I, SL_I), and differences in PL and SL between intruders and owners (DPL_{I-O}, DSL_{I-O}). The SL of females guarded by owners (SL_F) and the number of days until the female spawned (DAY) were also included as explanatory variables in each GLM, and I thus conducted model selection with three explanatory variables.

I also used model selection based on AIC to understand the assessment tactics and RHP index that determine the duration of the contest after escalation (Exp-1, $N = 33$; Exp-2, $N = 46$). Since the data included the unresolved contests (see Results), I analysed the data using a Cox's proportional hazards model (see Chapter 3). The response variable was the duration of a series of escalations (sec). Since there was also a strong correlation between SL and PL of males in contests that escalated in Exp-1 (intruder, $r^2 = 0.760$; owner, $r^2 = 0.938$; $N = 33$), SL and PL were used separately to avoid multicollinearity. Since RHPs of both contestants were expected to affect the escalation duration, the explanatory variables were one of six measurements of males: PL_I, SL_I, PL_O, SL_O, $|DPL_{I-O}|$ and $|DSL_{I-O}|$. Two measurements of females (SL_F and DAY) were also included as explanatory variables in each model that was conducted for model selection.

Contest outcome after escalation (intruder win = 2, draw = 1, lose = 0; Exp-1, $N = 33$; Exp-2, $N = 46$) was also treated as a response variable to examine whether the best model was different from that for fighting escalation and the duration. In this analysis, the explanatory variables were one of six measurements: PL_I, SL_I, PL_O, SL_O and the differences in PL and SL between contestants (DPL_{I-O}, DSL_{I-O}). The measurements of females (SL_F and DAY) were also included as explanatory variables in each model.

Results

Phase transition in male-male contests

Four pathways of phase transitions were observed in Exp-1 ($N = 46$; Fig. 4-1). In the first pathway, intruders did not show aggressive interactions, such as fencing and/or grappling, after the initial physical contact and hence the intruder lost the competition without any escalation ($N = 13$). In the second pathway, after the initial physical contact, contestants started fencing and then the intruder lost the competition ($N = 7$). In the third pathway, contestants started grappling after fencing ($N = 7$), and in the fourth pathway the intruder started grappling, without fencing, after the initial physical contact ($N = 19$). All cases of taking over of the female were observed during grappling. In all pathways, owners use major cheliped against intruders regardless of the

contest escalation.

Exp-1: Random-sized contestants

Giving-up decisions

Whether intruders gave up the contest without escalation ($N = 46$) was best described by the

model of SL in intruders (SL$_I$ model; Table 4-1) and intruders with smaller SL were

significantly more likely to give up fighting at an early stage (Fig. 4-2a, Table 4-2).

Escalation duration and contest outcomes

After the contest escalation ($N = 33$), the duration of escalation was best described by the model

of absolute value in PL difference between contestants (|DPL$_{I-O}$| model; Table 4-1), and contest

outcome was best described by the model of PL difference between intruders and owners

(DPL$_{I-O}$ model; Table 4-1). The escalation duration increased significantly when contestants had

major chelipeds with a similar size (Table 4-2), and intruders significantly increased the

probability of winning when they had a larger major cheliped than owners (Fig. 4-2b, Table 4-2).

Although most of male-male contests (44/47 trial) were settled within 10 min, three of them that

contestants had evenly size-matched major cheliped were defined as draw (Fig. 4-2b).

Exp-2: Similar-sized contestants

Both duration of escalation and contest outcome were best described by the model of relative

value in PL between contestants ($N = 46$; duration, $|DPL_{I-O}|$ model; outcome, DPL_{I-O} model;

Table 4-3). The escalation duration increased significantly when contestants had major

chelipeds with a similar size (Table 4-4), and intruders significantly increased the probability of

winning when they had a larger major cheliped than owners (Table 4-4). Intruders were

significantly less likely to win the contest when owners guarded larger females (Table 4-4).

Discussion

Results in this study demonstrated that male *Pagurus middendorffii* switched both assessment

tactics and RHP index during the two phases of male-male contest competition. When contests

escalated to physical combat, outcomes were explained by the difference in major cheliped

length between contestants, suggesting the asymmetry of RHP based on the major cheliped

predicts fighting success in *P. middendorffii*. Intruders of this species, however, gave up the

competition without any subsequent aggressive behavior (i.e. escalation) if they were smaller.

They thus used self-assessment of RHP based on their own body size in that situation. On the

other hand, the duration of escalation could be explained by mutual assessment of contestants.

Contestants continued aggressive behavior for longer when there was a small difference in the relative size of the major cheliped between contestants. The best explanation for the escalation duration and outcomes were the relative size of the major cheliped between contestants in the similar-sized trials, as well as in the random-sized contests. These results suggest that competitors in this species switch from self-assessment to mutual assessment and also change the index of RHP (i.e. body size and major cheliped size) used in assessment during male-male contests.

Some studies have demonstrated that individuals switch assessment tactics during contests (Chapter 1; Arnott & Elwood 2009). For example, fiddler crabs in size-assortative contests initiate mutual assessment to decide whether to escalate interaction with potential competitors, and once the contest changes to physical fighting, they switch to self-assessment to determine the fighting duration (Morrell et al. 2005). Fights in killifish start with mutual display and the losers use self-assessment in physical contact to decide when to give up (Hsu et al. 2008). One species of fig wasp appears to use a prefight assessment for opponent's RHP and switches to self-assessment to determine the escalation duration (Moore et al. 2008). Hermit crabs also compete over gastropod shells (Chapter 2), and shell fights of *P. bernhardus* are initiated with ritualized displays (Elwood & Neil 1992; Elwood et al. 2006) for mutual size assessment before the physical attack (Elwood et al. 2006). After escalation, attackers have to decide when to give up based on their own rapidly changing physiological state in *P. bernhardus* (Briffa & Elwood 2001, 2002, 2005), suggesting they use self-assessment tactics

during the latter part of shell fights (Briffa & Elwood 2001). These animals therefore use mutual assessment during the early stage and switch to self-assessment during escalation of interactions. In contrast, in this study male *P. middendorffii* used self-assessment before the fight, and then switched to mutual assessment in the escalation phase.

The difference between *P. middendorffii* and the above-mentioned animals might be explained by differences in the type of resources. Contestants need to assess the resource and opponent carefully before fighting for long-term resources such as burrows for fiddler crabs and gastropod shells for hermit crabs. Mature females, however, are an ephemeral resource for male hermit crabs, since a female crab can copulate with only one male before spawning. Intruder males should therefore try to takeover the potential mates as soon as possible to ensure a reproductive opportunity. Food is another such type of resource, and food theft (kleptoparasitism) observed in birds (e.g. Shealer et al. 2005; Mordan-Ferron et al. 2007) is also initiated with a physical struggle without a ritualized display. Thus, for how long resources are available and the type of struggle may affect how contestants switch assessment tactics.

Body size and/or weapon size have an important function as an index of RHP to determine the phase transition during contests. Body size has been considered to be an important factor to decide whether to give up a contest (e.g. Stuart-Fox et al. 2006; Prenter et al. 2008) and/or start high-intensity behavior in some animals (e.g. Jennings et al. 2004). Weapon size is often a more reliable indicator of the contest activity than body size (Chapter 2; Barki et al. 1997; Sneddon et al. 1997). Morrell et al. (2005) and Moore et al. (2008) used sizes of body

and weapon in individuals as an index of RHP and found that both traits affected an individual's

decision whether to escalate, fighting duration and contest outcomes in fiddler crabs and fig

wasps, respectively (although Morrell et al. 2005 showed solely the results of chela size).

Yoshino et al. (2011) found relative size of the major cheliped contributed to both whether to

initiate physical combat and the outcome more than that of body size in male-male contests of

the hermit crab *Diogenes nitidimanus*. These studies suggest that the index of RHP was

consistent throughout the contest.

However, model selection results in this study indicate that male *P. middendorffii*

changed the index of RHP they used between the two contest phases (i.e. initial phase and

combat phase). Body size of intruders had a stronger effect on the decision to give up the

contest without escalation than major cheliped size. In contrast, the major cheliped of males was

used in the fencing and grappling phases, and was more effective than body size in determining

the escalation duration and the contest outcome in both random-sized and similar-sized contests.

These suggest that male major cheliped size had a strong contribution to the fighting behavior

during the escalation phase irrespective of the size difference between contestants. *P.*

bernhardus also uses multiple indexes of RHP during shell-fighting contests, but the relative

importance of traits is different from those in male-male contests of *P. middendorffii*. Male *P.*

bernhardus use the major cheliped in displays in the early stage of shell fights (Chapter 2), and

attackers carry out 'shell rapping' with their walking legs during physical fighting in the late

stage (Elwood & Neil 1992). The major cheliped thus has a strong effect in the display phase

but not for contest outcomes (Elwood et al. 2006; Arnott & Elwood 2010; but see Neil 1985), which depends on the power of rapping (Briffa & Elwood 2000). These differences arise from the type of aggressive behavior, and the major cheliped could be considered as a physical weapon in male-male contests in *P. middendorffii* and a visual signal for RHP in shell fights of *P. bernhardus*. Although various differences in aggressive behavior and assessment strategy between species may occur in different ecological contexts, few studies have compared the contest activities for different resources using the same species. Further study is thus needed to reveal whether such differences in contests are caused by differences in genetics or ecological contexts and how contestants are able to assess the information provided by their opponents.
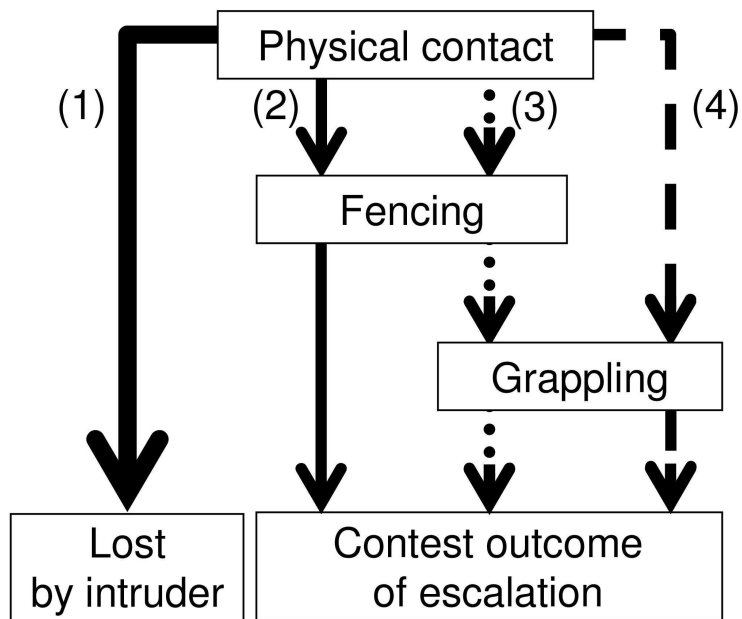
Figure 4-1　A graphical summary of the phase transitions in male-male contests ($N = 46$ trials). All contests were initiated from physical contact between contestants ($N = 46$). Four pathways of escalation until the contest outcome were determined. (1) No aggressive interaction by the intruder after contact and hence the intruder lost ($N = 13$, bold arrow). (2) Intruders fenced after initiation of physical contact and then lost the contest ($N = 7$, solid arrow). (3) Phase transition to grappling from fencing ($N = 7$, dotted arrow). (4) Intruders conducted grappling straight after physical contact ($N = 19$, dashed arrow)
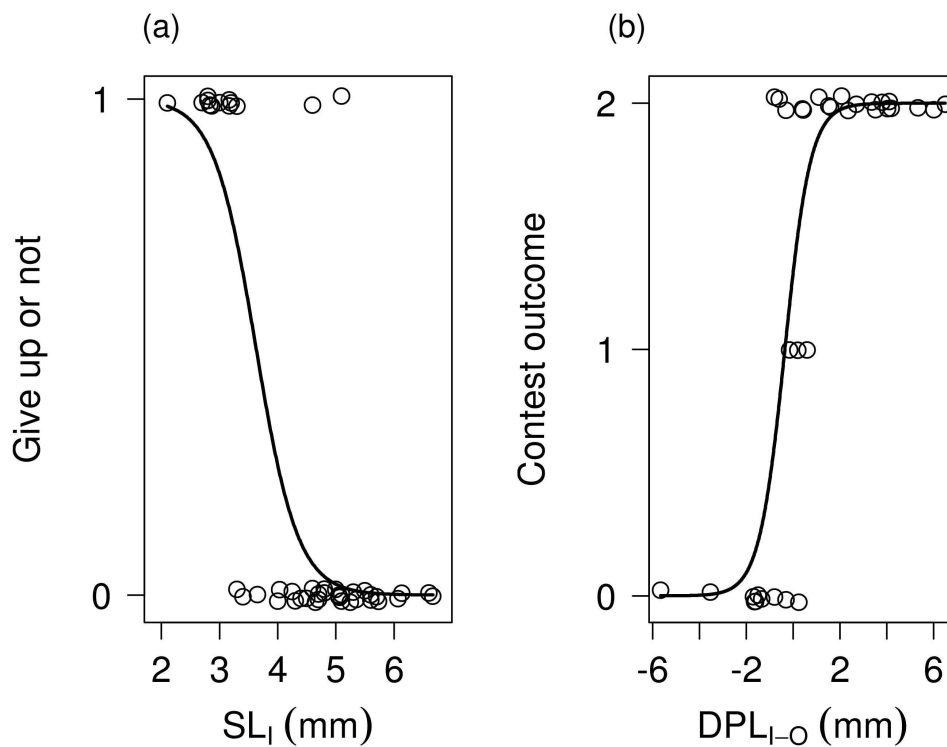
Figure 4-2 Logistic relationships of the best model based on AIC in which (a) intruder gives up the contest without escalation and (b) contest outcome after escalation in Exp-1. SL_I and $DPL_{I\text{-}O}$ indicate the shield length (index of body size) of the intruder and the difference in propodus length of major cheliped between the intruder and the owner in each contest, respectively. Points at 0 and 1 in (a) are intruders escalate or give up the contest, and 0 to 2 in (b) are owner and intruder males win or lose, respectively. Two variables, shield length and the number of days until spawning in females guarded by owners, are treated as mean values in the regression curves

Table 4-1 Results of model selection based on Akaike's information criterion (AIC) in Exp-1 analyzed by a generalized linear model (GLM) with the binomial error distribution and Cox's proportional hazard analysis

Model	N	AIC
Whether intruders give up the contest or not without escalation		
GLM with binomial error distribution		
PL_I, SL_F and DAY	46	34.600
SL_I, SL_F and DAY	46	30.766[**]
DPL_{I-O}, SL_F and DAY	46	34.311
DSL_{I-O}, SL_F and DAY	46	32.495
Escalation duration		
Cox's proportional hazard analysis		
PL_I, SL_F and DAY	33	168.26
SL_I, SL_F and DAY	33	166.85
PL_O, SL_F and DAY	33	168.47
SL_O, SL_F and DAY	33	168.88
$|DPL_{I-O}|$, SL_F and DAY	33	156.52[**]
$|DSL_{I-O}|$, SL_F and DAY	33	162.83
Contest outcome after escalation		
GLM with binomial error distribution		
PL_I, SL_F and DAY	33	75.674
SL_I, SL_F and DAY	33	77.150
PL_O, SL_F and DAY	33	76.215
SL_O, SL_F and DAY	33	78.269
DPL_{I-O}, SL_F and DAY	33	59.681[**]
DSL_{I-O}, SL_F and DAY	33	63.675

Asterisks (**) indicate the best fitted model (i.e. smallest AIC) in each analysis. PL_I, SL_I, PL_O and SL_O indicate the propodus length of major cheliped and shield length (index of body size) of intruder and owner, respectively. DPL_{I-O}, DSL_{I-O}, $|DPL_{I-O}|$ and $|DSL_{I-O}|$ indicate the relative and absolute value of differences between intruder and owner in each contest. SL_F and DAY indicate the shield length and the number of days until spawning of females guarded by owners in each trial, respectively

Table 4-2 Results of the best model in Exp-1 analyzed by a generalized linear model (GLM) with the binomial error distribution and Cox's proportional hazard analysis

	Estimate	SE	Z	P
Whether intruders give up contest or not without escalation ($N = 46$)				
GLM with binomial error distribution				
Intercept	5.414	6.287	0.861	0.389
SL_I	-0.276	0.088	-3.149	0.002
SL_F	0.128	0.228	0.562	0.574
DAY	0.090	0.595	1.506	0.132
Escalation duration ($N = 33$)				
Cox's proportional hazard analysis				
$|DPL_{I\text{-}O}|$	0.055	0.016	3.467	< 0.001
SL_F	0.118	0.121	0.980	0.327
DAY	0.194	0.197	0.988	0.323
Contest outcome ($N = 33$)				
GLM with binomial error distribution				
Intercept	2.314	5.348	0.433	0.665
$DPL_{I\text{-}O}$	0.082	0.023	3.529	< 0.001
SL_F	-0.089	0.225	-0.397	0.691
DAY	-0.075	0.285	-0.263	0.793

SL_I, $DPL_{I\text{-}O}$ and $|DPL_{I\text{-}O}|$ indicate the shield length (index of body size) of intruder, relative and absolute value in the difference in propodus length of major cheliped between intruder and owner in each contest, respectively. SL_F and DAY indicate the shield length and the number of days until spawning of females guarded by owners in each trial, respectively

Table 4-3 Results of model selection based on Akaike's information criterion (AIC) in Exp-2 analyzed by Cox's proportional hazard analysis and a generalized linear model (GLM) with the binomial error distribution

Model	N	AIC
Escalation duration		
Cox's proportional hazard analysis		
PL_I, SL_F and DAY	46	251.36
SL_I, SL_F and DAY	46	251.29
PL_O, SL_F and DAY	46	251.42
SL_O, SL_F and DAY	46	251.41
$|DPL_{I-O}|$, SL_F and DAY	46	246.91[**]
$|DSL_{I-O}|$, SL_F and DAY	46	249.01
Contest outcome after escalation		
GLM with binomial error distribution		
PL_I, SL_F and DAY	46	111.95
SL_I, SL_F and DAY	46	116.98
PL_O, SL_F and DAY	46	120.34
SL_O, SL_F and DAY	46	120.22
DPL_{I-O}, SL_F and DAY	46	76.931[**]
DSL_{I-O}, SL_F and DAY	46	96.010

Asterisks (**) indicate the best fitted model (i.e. smallest AIC) in each analysis. PL_I, SL_I, PL_O and SL_O indicate the propodus length of major cheliped and the shield length (index of body size) of intruder and owner, respectively. $|DPL_{I-O}|$, $|DSL_{I-O}|$, DPL_{I-O} and DSL_{I-O} indicate the absolute and the relative value of differences between intruder and owner in each contest. SL_F and DAY indicate the shield length and the number of days until spawning of females guarded by owners in each trial, respectively

Table 4-4 Results of the best model in Exp-2 analyzed by Cox's proportional hazard analysis and a generalized linear model (GLM) with the binomial error distribution

	Estimate	SE	Z	P
Escalation duration ($N = 46$)				
Cox's proportional hazard analysis				
$|DPL_{I-O}|$	0.062	0.029	2.166	0.030
SL_F	-0.087	0.059	-1.458	0.145
DAY	-0.242	0.148	-1.636	0.102
Contest outcome after escalation ($N = 46$)				
GLM with binomial error distribution				
Intercept	4.036	1.915	2.107	0.035
DPL_{I-O}	0.224	0.049	4.612	< 0.001
SL_F	-0.172	0.080	-2.142	0.032
DAY	0.177	0.274	0.644	0.519

$|DPL_{I-O}|$ and DPL_{I-O} indicate the absolute and the relative value of difference in propodus length of major cheliped between intruder and owner in each contest, respectively. SL_F and DAY indicate the shield length and the number of days until spawning of females guarded by owners in each trial, respectively

Chapter 5: Hermit crab, *Pagurus middendorffii* males avoid the escalation of contests with familiar winners

Introduction

Resource holding potential (RHP) in contestants determines contest winner (Chapter 1; Arnott & Elwood 2008, 2009; Hardy & Briffa 2013) and physical attributes of contestants (e.g. body and/or weapon size) are well known to correlate with RHP (Chapters 1, 2, 4). However, prior contest outcomes also have an important role in determining behavior during the contest and/or the outcomes (Hsu et al. 2006; Rutte et al. 2006). Since contestants would be able to use prior contest outcomes to self-assessment (Chapter 4) in relation to average RHP of other individuals in the population, contestants with prior experience may alter the self-assessment of their respective fighting abilities and change motivation in the contest (Whitehouse 1997; Rutte et al. 2006): prior winners are more likely to engage in and win subsequent contests (winner effect), whereas prior losers are more likely to be less aggressive and lose subsequent contests (loser effect). Such winner/loser effects have been reported in many taxa such as reptiles (Zucker & Murray 1996; Garcia et al. 2012), fishes (Hsu & Wolf 1999; Oliveira et al. 2009), insects (Okada & Miyatake 2010; Reaney et al. 2011), spiders (Kasumovic et al. 2009, 2010) and crustaceans (Moore 2007; Fujimoto et al. 2011).

The winner/loser effects differ in strength and manner between species although loser effects may be more common and usually longer lasting than winner effects (Hsu et al. 2006). For example, cricket males show loser effects during non-physical contests, whereas there are no loser effects if the contest escalates into aggressive behavior (Reaney et al. 2011). Winner effects are not found in physical or non-physical contests in this cricket (Reaney et al. 2011). Both winner and loser effects are of approximately the same magnitude in the jumping spider although loser effects last longer than winner effects (Kasumovic et al. 2010). The parasitoid wasp showed winner effects in fighting for hosts whereas a significant loser effect was not observed (Goubault & Decuignière 2012). Thus, effects of prior contests appear to be species specific, and the process and/or outcome of a contest still require further investigation (Mesterton-Gibbons 1999; Hsu et al. 2006).

When animals repeatedly encounter each other, they may memorize past outcomes of interactions with specific individuals and use the experience to modify subsequent interactions with the same individuals (van Doorn et al. 2003). For example, as a result of recognition, the levels of aggression for familiar neighbors are often lower than for strangers (i.e. 'dear enemy' effect; Temeles 1994). Recent studies have demonstrated the ability of individual recognition in invertebrates (Caldwell 1985; Karavanich & Atema 1998; D'Ettorre & Heinze 2005; Yurkovic et al. 2006; Tricarico et al. 2011) as well as vertebrates (López & Martín 2001; Jennings et al. 2004). The ability to distinguish between familiar and unfamiliar individuals may affect the strength and/or manner of winner/loser effects. When a dyadic dominance relationship between

two contestants has been determined by past contest(s), the contestants might behave as winner/loser in subsequent contests (Dugatkin & Earley 2004). Once a dominance relationship has been established, dominants and subordinates typically decrease the number of intense combat interactions as shown for example in the lizard (López & Martín 2001) and *Drosophila melanogaster* Meigen, 1830 (Yurkovic et al. 2006). Subordinates of the American lobster also avoid a second fight with familiar dominants but not with unfamiliar ones. They aggressively fight and often win during contests with the latter (Karavanich & Atema 1998).

There is also evidence that *Pagurus* hermit crabs recognize other individuals based on a previous encounter(s) and/or dominance relationship. Hazlett (1969) held four individuals of the hermit crab *P. bernhardus* in a tank for a week and then introduced an unfamiliar individual into the tank. The four crabs initiated intense aggressive interactions with the unfamiliar crab much more often than with the familiar ones. Gherardi and Tiedemann (2004a) showed that subordinate crabs of *P. longicarpus* were likely to initiate interactions with unfamiliar dominant crabs more often than familiar ones and escalated the fight only when the opponent was unfamiliar. Subordinate crabs in these species behaved as losers only when they faced familiar dominants. Strength and the manner of winner/loser effects may therefore differ depending on the familiarity with the opponent in male-male contests of hermit crabs.

Male-male contests of *Parugus middendorffii* are divided into two phases based on whether intruders initiate escalation of the contest with physical combat behavior (Chapter 4): initial contact phase (before escalation) and physical combat phase (after escalation). Intruders

of this species use self-assessment during the initial contact phase and mutual-assessment during the physical combat phase to decide their behaviors (Chapter 4), suggesting that they can use information from both their own and the opponent's RHP. They may thus show winner/loser effects in the subsequent male-male contest. Furthermore, if the males also distinguish a familiar opponent from an unfamiliar one, they may alter their contest behavior depending on both the previous contest outcomes and the familiarity with the opponent. These possibilities related to prior contest experience have been never investigated in the context of male-male contests in *Pagurus* hermit crabs including *P. middendorffii*.

Here I examined (1) whether winning or losing a contest causes any changes in the decision to escalate a subsequent contest, (2) whether males distinguish familiar opponents from unfamiliar ones in male-male contests and (3) how winner and/or loser effects are related to the familiarity with the opponent in *P. middendorffii*. To do this, I conducted two sequential trials of male-male contests in *P. middendorffii*, using three groups of males; I manipulated the contest experience and/or familiarity and compared male behaviors between the trials and/or between the groups.

Materials & Methods

I collected 178 precopulatory guarding pairs of *Pagurus middendorffii* from my study site

(Chapter 2) during 13-30 November 2012 (i.e. mating season; Chapter 3). After checking of

guarding, the male and female of each pair were separately introduced into plastic cups (300 ml).

All experimental trials were conducted within 6 h of collection.

Experimental design

The experiments involved two sequential trials of male-male contests. Guarding pairs were

divided into three experimental groups based on the type of second trial (see Fig. 5-1, Table 5-1)

and randomly assigned to the experimental sets in each group. Since intruders were focal males,

I chose one male from a guarding pair in each set as intruder and males in the remaining pairs as

owners (see below). Each intruder took part in two contests: after intruders lost in the first trial

(trial-1), they encountered a given owner in each group in the second trial (trial-2). In group-1,

losers encountered naïve owners with no trial-experience in trial-1. In group-2, losers

encountered unfamiliar owners that had won trial-1 (randomly chosen from other set). In

group-3, the losers again encountered the familiar (= same) owners from trial-1 (Fig. 5-1).

For each contest, I used three (group-1) or two (group-2 and -3) pairs as a set, which

were randomly assigned from guarding pairs collected on the same sampling day as each other

(group-1, $N = 24$ sets; group-2, $N = 27$ sets; group-3, $N = 26$ sets; see Table 5-1). Since males

with a larger size are more likely to win in *P. middendorffii* (Wada et al. 1999), the smallest

male of each set was chosen as the focal intruder male, whereas the largest male (group-2 and

-3) or two largest males (group-1) were used as the owner(s) in each experimental trial (Fig.

5-1). In trial-1, a pair was placed in a small plastic container of the same condition as previously

described (Chapter 2). The intruder was then placed in the container after the owner had

initiated guarding of the female. Since contests of *P. middendorffii* are typically settled within

10 min (Chapter 4), I recorded the outcomes of the male-male contests in trial-1 after 10 min

from when the intruder initiated movement. Since all intruders failed to takeover the female in

trial-1, I used all intruders for the subsequent trial (trial-2). I initiated trial-2 after an hour. The

experimental methods were the same as trial-1, with the losers in the three groups encountering

different types of owners as described above.

As Chapter 4, to compare the contest behaviors between trials or between groups, all

contests were recorded by using the video function of digital cameras (Pentax, Optio-W80 and

WG2) from the time of introducing the individuals. I observed these videos for 10 min to record

whether the contest was escalated based on the behavior of the intruders. The duration(s) of

physical combat behavior was also recorded in each video (see Chapter 4 for details). If

contestants did not perform combat behavior for more than 3 min, I defined the fight as settled

and recorded the contest outcomes, based on which male guarded the female. If the contest did

not finish by the end of the observation period, I recorded it as a 'draw'. Although all intruders

had lost the contests in trial-1, in trial-2 some of them succeeded in taking over the females

guarded by owners (i.e. win; Table 5-1). I therefore excluded from the following analysis the

data from contests in which the intruder won (group-1, $N = 1$ set; group-2, $N = 1$ set) so that all

intruders drew or lost. After the experiment, as an index of body size, the shield length (SL; see Chapter 2 for measurement) of all males and all females guarded by owners was measured to the nearest 0.01 mm under a stereomicroscope.

Analyses

To examine whether contestants altered their fighting behavior between the two trials, I used a model selection approach based on the Akaike's information criterion (AIC) focusing in the following analyses on both the prior contest outcomes and the familiarity with the opponent as well as Chapter 4. I separately used the data from group-1 and -2 and examined whether males showed winner/loser effects unrelated to the familiarity with the opponent by comparing the contest behavior between trials of each group. I then combined the data from group-2 and -3 to investigate the effects of the familiarity with the opponent.

To examine the factors affecting whether intruders escalated the contest to physical combat, I used a generalized linear mixed model (GLMM) with a binomial error distribution since all the males were used repeatedly in the two trials of the experiment. The response variable was whether intruders escalated to physical combat (Yes = 1, No = 0; group-1, $N = 46$ males; group-2, $N = 52$ males; group-2 and -3, $N = 104$ males). The explanatory variables were trial (trial-1 or -2) and the difference in SL between intruder and owner (DSL_{I-O}). In the analysis of group-2 and -3, I added a further explanatory variables in the model as follows; experimental

group (group-2 or -3) and the interaction between trial and group. Intruder ID was treated as a random effect in all the GLMMs.

I also used model selection based on AIC for the comparison of the contest duration after escalation between trials by using the sets of the contests that escalated to physical combat (group-1, $N = 24$ sets; group-2, $N = 29$ sets; group-2 and -3, $N = 46$ sets). Since the data from trial-2 included the unresolved contests (see Table 5-1), I used Cox's proportional hazard model as well as Chapter 4. The response variables were the duration of a series of escalations (sec). The explanatory variables were trial and DSL_{I-O}. In the analysis of group-2 and -3, I also considered experimental group and interaction between trial and group as explanatory variables.

Results

No loser effects in contests against naïve opponents

When intruders with experience of losing in trial-1 fought against naïve (i.e. no trial-experience) owners in trial-2 (group-1), the occurrence of escalation ($N = 46$) was best described by the models with an SL difference between intruders and owners (DSL_{I-O} model; Table 5-2). The duration of escalation ($N = 24$) was also best described by the model of SL difference between contestants (DSL_{I-O} model; Table 5-2). When the difference in SL between contestants

decreased, the occurrence of escalation increased (Fig. 5-2a) and the duration of escalation

became longer. Although intruders failed to takeover the female guarded by owner males in

trial-1, they actively fought naïve opponents in trial-2.

Winner/loser effects in contests between unfamiliar opponents

When intruders with experience of losing in trial-1 fought against an unfamiliar winner in trial-2

(group-2), the occurrence of escalation ($N = 52$) was best described by the model with the

number of the trial and DSL_{I-O} (Table 5-3) although the AIC difference between the best and the

second model was small ($\Delta AIC = 0.52$; Table 5-3). The occurrence of escalation increased with

decreasing SL difference but to a lesser extent in trial-2 than in trial-1 (Fig. 5-2b). The duration

of escalation ($N = 27$) was best described by the model with DSL_{I-O} (Table 5-3) and became

longer when the contestants had a similar SL as their opponents.

Loser effects in contests against familiar opponents

When intruders with experience of losing in trial-1 fought against the same owner as in trial-1

(group-3), both the occurrence of escalation ($N = 104$) and the duration of escalation ($N = 46$)

were best described by the full models (Table 5-4). In trial-2, the occurrence and the duration of

escalation in group-3 decreased more than in group-2 (Fig. 5-3a, b), indicating that losers

became less aggressive against familiar winners than unfamiliar winners. Results of the top of

five models are shown in Table 5-4. In group-3, intruders in trial-1 actively tried to takeover the

female guarded by owners. However, the intruders in trial-2 did not perform aggressive contest

behavior against the familiar opponent (Fig. 5-3a) and gave up soon even if they initiated

escalating the contest (Fig. 5-3b).

Discussion

In male-male contests for females, intruders of *Pagurus middendorffii* altered their contest

behavior according to prior contest outcomes only when the opponents were the same as in the

previous contest. Several spiders and insects show loser effects against naïve opponents during

contests (e.g. Kasumovic et al. 2009, 2010; Okada & Miyatake 2010; Reaney et al. 2011).

Okada & Miyatake (2010) suggested that this loser effect is based on modification of

self-assessment (Whitehouse 1997; Rutte et al. 2006). By contrast, although all intruders failed

to takeover the female (i.e. lost) in the first trial, after one hour, they showed a similar degree of

aggressiveness against naïve (i.e. no trial-experience) owners in the second trial (group-1). As

intruders decide whether to initiate or give up the contest based on an assessment of their own

RHP (Chapter 4), this result suggests that losing experience has no effect on self-assessment in

intruders of *P. middendorffii*.

My study demonstrated that losers in *P. middendorffii* can distinguish familiar winners without any physical combat. A conspicuous decrease in contest intensity was found in the male-male contests between familiar opponents. When intruders with losing experience encountered familiar owners (group-3), they were more likely to give up the contest without physical combat. Although a few intruders in group-3 escalated the contest in the second trial, they soon retreated from the familiar winner. Previous studies reported individual recognition in *Pagurus* hermit crabs (Hazlett 1969; Gherardi & Tiedemann 2004a, b) as well as other crustaceans (Caldwell 1985; Karavanich & Atema 1998; Rufino & Jones 2001). Therefore, information about the prior contest experience and the consequent opponent familiarity would allow intruders to make an immediate decision about a familiar opponent even in the pre-fight phase. What is unclear is how intruders distinguish familiar opponents before escalation. *Pagurus* hermit crabs display their major cheliped in shell fights and owners also aggressively use the major cheliped when intruders approach in male-male contests (Chapters 2, 4). The movement and/or any morphological characters of the major cheliped might therefore enable hermit crabs to distinguish familiar opponents from unfamiliar ones. Another hypothesis is that intruders may mark the opponents with something that the intruders can recognize next time. For example, Ivy et al. (2005) proposed that female crickets use self-referent chemical cues to avoid mating with the previous mates. Such chemical cues might be useful for short-term recognition of opponents.

Although many studies have reported individual recognition, the periods required for

establishing familiarization have varied between studies. For example, the period in my study

(10 min in trial-1) is shorter than in other studies (one day; Gherardi & Tiedemann 2004a, b;

one week; Hazlett 1969). This variation would be explained by the context of familiarization,

especially whether or not a physical fight occurs. Previous studies dealing with fights show

individual recognition within a short period (e.g. within 30 min; Karavanich & Atema 1998;

López & Martín 2001; Schneider et al. 2001) but not in other contexts (e.g. just seeing an

individual without physical contact for several days; Tricarico et al. 2011; White & Gowan

2013; rearing in the same tank for two weeks; Utne-Palm & Hart 2000). As individuals often

assess and/or make physical contact with each other during the contest (Arnott & Elwood 2009),

a fight would allow the contestants to get information that enable recognition of each other

relatively rapidly. Thus, the type of context could affect the period required for establishing

familiarization.

   P. middendorffii owners with winning experience may alter the contest behavior.

Model selection of the present study indicated that the probability of contest escalation

decreased in contests between owners with winning experience and unfamiliar losers (group-2)

although the ΔAIC was relatively small. This would be explained by the behaviors of both

intruders and owners. Although intruders of *P. middendorffii* decide whether to escalate the

contest based on self-assessment against the naïve and unfamiliar opponents (Chapter 4;

group-1), they would also alter their behaviors by detecting any cue (e.g. chemical cue) from

unfamiliar owners with winning experience (i.e. social cue; Rutte et al. 2006). Several

crustaceans use chemical cues to recognize prior contest experience with the opponent

(Obermeier & Schmitz 2003) and to communicate with each other (Bergman & Moore 2001).

Winner effect in crayfish is observed only if the opponent can perceive urine signals (Bergman

et al. 2003). Alternatively, *P. middendorffii* owners with winning experience may alter their

contest behavior against unfamiliar opponents based on self-assessment. Regardless of the

process, the potential winner effects would occur in male-male contests of *P. middendorffii*, and

they might also affect when familiar males encounter each other again (i.e. trial-2 of group-3)

although I did not focus on this in the present study. Although an intriguing possibility, I did not

directly test for a winner effect in *P. middendorffii* because owners with winning experience

encountered unfamiliar losers but not naïve intruders in this study. To investigate the winner

effect in this species, an experimental study of male-male contests between prior winners and

naïve intruders clearly needs to be conducted. After that, it might be possible to discuss more

closely how winner effects including winner cues influence individual recognition by losers in

this species.

Finally, I consider why the evolution of the loser effect in male-male contests is

contingent on individual recognition in *P. middendorffii*. Individual recognition would be

favored when individuals repeatedly encounter each other. The encounter rates with familiar and

unfamiliar opponents would depend on mobility and population density of the animals. Many

crustaceans, including hermit crabs, are primarily benthic with poor swimming ability (Duffy &

Thiel 2007), suggesting their mobility is low, and hence the encounter rate with the same

individuals would potentially be high (Karavanich & Atema 1998). In particular, just after the

contest, the encounter rate with the same contestants must be high. Population density, however,

would determine the encounter rate with unfamiliar opponents, and a high density of *P.*

middendorffii has been reported at my study site (Wada et al. 1995, 2011). Solitary *P.*

middendorffii, therefore, would often encounter both familiar and unfamiliar crabs. Furthermore,

since the mating season is limited to about one month in this species (Wada et al. 1995), solitary

male crabs are expected to have many opportunities for encountering the precopulatory

guarding males, including familiar and unfamiliar opponents, during this season. To examine the

relationship between these ecological features and individual recognition ability, further studies
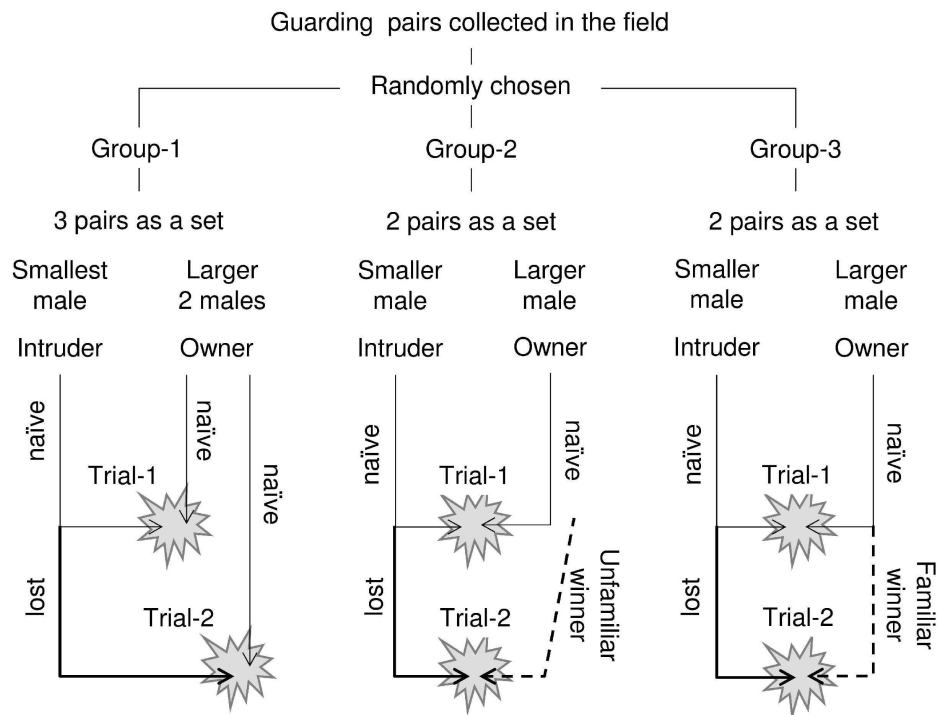
of various species are needed.

Figure 5-1 Summary of the experimental design. Guarding pairs were randomly assigned three groups (group-1, 2 and 3) which were differed the type of owner in the second trial. Smallest male from a guarding pair in each set was intruder and male(s) in the remaining pair were as owner male(s). Each intruder was in two contests: after intruders lost in the first trial (trial-1), they encountered a given owner in each group in the second trial (trial-2)
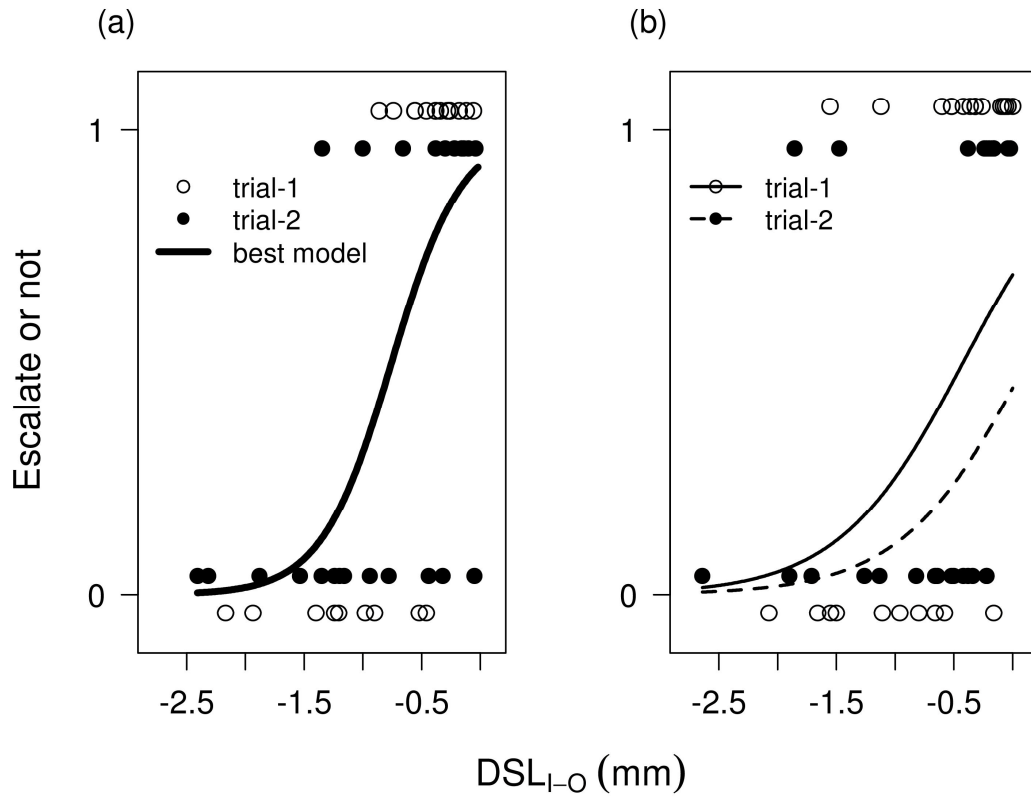
Figure 5-2 Logistic relationships of the best model based on AIC in which intruders with losing experience in the first trial (trial-1) encountered (a) a naïve opponent and (b) an unfamiliar winning opponent in the second trial (trial-2). DSL_{I-O} indicated the difference in the shield length (index of body size) between the intruder and the owner in each contest. Points at 0 and 1 are intruder gave up or escalated the contest
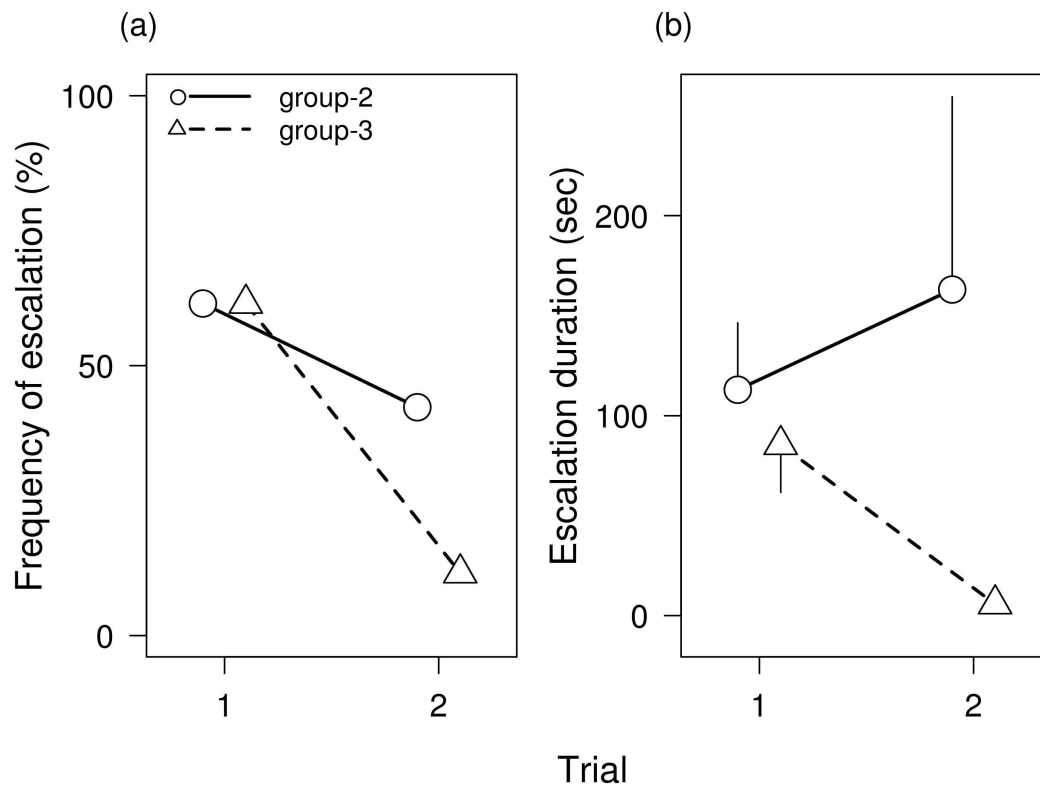
Figure 5-3 The changing trends in (a) the frequency of escalation and (b) the mean duration of escalation between two experimental groups. Intruders with losing experience encountered unfamiliar (group-2) or familiar (group-3) opponents with winning experience in the second trial. Standard errors of duration are given in (b). Interactions between trial and group were selected in best models, indicating that slopes differed from each other

Table 5-1 Summary of types of owner and contest processes in the three experimental groups of male-male contest in *Pagurus middendorffii*

Group	Type of owner in trial-2 for each intruder with losing experience	Replicate (sets)	Contest processes		Outcomes of intruder in trial 2		
			Number of escalations				
			Trial 1	Trial 2	Win	Draw	Lose
1	Unfamiliar naïve	24	15	11	1[*]	1	22
2	Unfamiliar winner in other set	27	17	12	1[*]	1	25
3	Familiar winner in the same set	26	16	3	0	0	26

Each group differs in the type of owners in the second trial (trial-2). All intruders lost in the first trial (trial-1; i.e. failed to takeover the female from their owner), and after one hour they encountered a given opponent in trial-2. Familiar and unfamiliar indicate that intruders encountered the owners or not in trial-1, respectively. Naïve indicates the owner had no trial-experience before trial-2. We excluded the data from the contests that the intruder won in trial-2 (*) in the following analysis

Table 5-2 Results of models selected based on Akaike's information criterion (AIC) in group-1 analyzed by a generalized linear mixed model (GLMM) with the binomial error distribution and Cox's proportional hazard analysis

Model	Intercept	Trial	DSL_{I-O}	df	AIC	Δ	weight
Whether intruders escalated the contest to physical combat or not ($N = 46$)							
GLMM with a binomial error distribution (random effect = intruder ID)							
1	2.532		3.407	3	46.4	0.00	0.665
2	2.763	-0.629	3.309	4	48.7	2.38	0.334
3	0.089			2	66.8	19.42	0.000
4	0.570	-0.957		3	66.9	19.59	0.000
Escalation duration ($N = 24$)							
Cox's proportional hazard analysis							
1			-2.149	1	103.4	0.00	0.697
2		0.049	-2.165	2	105.4	1.99	0.258
3				0	109.6	6.20	0.031
4		-0.207		1	111.3	7.96	0.013

Models are arranged in descending order of AIC, with model 1 the best model (smallest AIC) in this analysis. Values of intercept and coefficients of explanatory variables are shown on each line (blank cells indicate that the variable was not included in the model). DSL_{I-O} indicates the difference in shield length (index of body size) between intruder and owner in each contest. All listed for each model are: the degree of freedom (df); the AIC differential between the best model and the others (Δ); and the Akaike weight (weight)

Table 5-3　Results of models selected based on Akaike's information criterion (AIC) in group-2 analyzed by a generalized linear mixed model (GLMM) with the binomial error distribution and Cox's proportional hazard analysis

Model	Intercept	Trial	DSL_{I-O}	df	AIC	Δ	weight
Whether intruders escalated the contest to physical combat or not (N							
GLMM with a binomial error distribution (random effect = intruder ID)							
1	1.805	-1.011	1.881	4	66.5	0.00	0.558
2	1.209		1.735	3	67.0	0.52	0.430
3	0.549	-0.912		3	75.5	8.97	0.006
4	0.085			2	75.7	9.17	0.006
Escalation duration ($N = 27$)							
Cox's proportional hazard analysis							
1			-0.690	1	128.7	0.00	0.385
2				0	129.7	0.45	0.308
3		-0.230	-0.693	2	130.5	1.68	0.166
4		-0.262		1	130.1	2.02	0.140

Models are arranged in descending order of AIC, with model 1 the best model (smallest AIC) in this analysis. Values of intercept and coefficients of explanatory variables are shown on each line (blank cells indicate that the variable was not included in the model). DSL_{I-O} indicates the difference in shield length (index of body size) between intruder and owner in each contest. All listed for each model are; the degree of freedom (df), the AIC differential between the best model and the others (Δ); and the Akaike weight (weight)

Table 5-4 Results of models selected based on Akaike's information criterion (AIC) in combined data (group-2 and -3) analyzed by a generalized linear mixed model (GLMM) with the binomial error distribution and Cox's proportional hazard model

Model	Intercept	Trial	Group	DSL_{I-O}	Trial x Group	df	AIC	Δ	weight
Whether intruders escalate the contest to physical combat or not ($N = 104$)									
GLMM with a binomial error distribution (random effect = intruder ID)									
1	2.424	-3.231	-0.496	2.057	2.178	6	110.4	0.00	0.595
2	2.142	-1.944		2.025		4	112.1	1.77	0.245
3	1.858	-1.965	0.517	1.989		5	113.0	2.64	0.159
4	0.951			1.659		3	126.8	16.41	0.000
5	0.698		1.623	1.623		4	127.8	17.39	0.000
Escalation duration ($N = 46$)									
Cox's proportional hazard analysis									
1		1.798	1.548	-1.126	-2.021	4	257.2	0.00	0.476
2			-0.679	-0.978		2	258.4	1.18	0.264
3		0.146	0.744	-0.980		3	260.3	3.03	0.105
4				-0.903		1	260.7	3.50	0.083
5		-0.174		-0.912		2	262.5	5.22	0.035

Models are arranged in descending order of AIC, with model 1 the best model (smallest AIC) in this analysis. Values of intercept and coefficients of explanatory variables are shown in each line (blank cells indicate that the variable was not included in the model). DSL_{I-O} indicates the difference in shield length (index of body size) between intruder and owner in each contest. SL_F indicate the shield length of females guarded by owners. All listed for each model are: the degree of freedom (df); the AIC differential between the best model and the others (Δ); and the Akaike weight (weight)

Chapter 6: GENERAL DISCUSSION

Male-male contest is one of the most studied processes in sexual selection to explain the sexual

differences such as morphological traits and aggression behavior in various taxa (Chapter 1;

Andersson 1994). Many *Pagurus* hermit crabs show male-male contests during the

precopulatory mate guarding in the reproductive season (e.g. Wada et al. 1999; Yoshino et al.

2002; Contreras-Garduño & Córdoba-Aguilar 2006; Okamura & Goshima 2010; Suzuki et al.

2012; Tanikawa et al. 2012). Throughout my doctoral thesis, I conducted several experimental

studies of male-male contests to examine the assessment tactics for decision-making with

major cheliped use in two *Pagurus* hermit crabs, *P. nigrofascia* and *P. middendorffii*. In this

section, I discuss my results with the concept of sexual selection.

Assessment strategy during male-male contests in Pagurus *hermit crabs*

Intruders of *P. middendorffii* showed highly tactical decisions during male-male contests

(Chapters 4, 5). They switched both assessment tactics, self- to mutual-assessment, and also

switched index of RHP, body to major cheliped size, according to the phase transition of

male-male contests (Chapter 4). After losing, intruders of this species recognized the familiar

(i.e. same as the previous) and the unfamiliar (i.e. different) opponents during the pre-fight

phase, so they avoided the familiar winner without any physical combat (Chapter 5). Previous

studies have demonstrated that hermit crabs show complex assessment tactics during the

contest competitions for the gastropod shell in *P. bernhardus* (Chapter 4; Elwood & Neil 1992;

Briffa 2013) and individual recognition via the repeated encounter in *P. bernhardus* and *P.

longicalpus* (Chapter 5; Hazlett 1969; Gherardi & Tiedemann 2004a, b; Gherardi et al. 2005).

However, since no study has examined these in male-male contests, my study is the first report.

This study therefore provides further insights into decision strategy in *Pagurus* hermit crabs, or

the assessment tactics and individual recognition would evolve under sexual selection.

My results suggest that major cheliped in males of *P. middendorffii* would have

important functions as an index to assess his opponent's RHP and individual recognition

during male-male contests. This would be explained by the conspicuous moving and the

contribution of male major cheliped in the contests: owner males of *P. middendorffii* actively

use major cheliped as weapon even before the contest escalation (Chapter 4), and males with

larger major cheliped than opponents achieve a higher probability of winning (Chapter 4). It is

well known that males aggressively use major cheliped during the fighting and that size of

major cheliped determine winners in contest of several crustaceans (Barki et al. 1997; Sneddon

et al. 1997; Schroeder & Huber 2001; Morrell et al. 2005; Emlen 2008) including other hermit

crabs (*Diogenes nitidimanus*, Yoshino et al. 2011; *P. filholi*, Matsuo et al. in press). Some

animals also use major cheliped as morphological signals to assess RHP each other (Sneddon

et al. 1997; Mariappan et al. 2000; Morrell et al. 2005; Wilson et al. 2007; Yoshino et al. 2011).

In Chapter 2, I demonstrated the advantageous of presence and larger size in major cheliped of *P. nigrofascia*. Given these examples of other crustaceans, males of *P. nigrofascia* (and perhaps *P. filholi*) would also use major cheliped for decision-making related to contest behaviors, although I did not examine the decision process in this species.

Recently, several new approaches have been used to examine assessment strategy and RHP of each contestant during male-male contests. For example, although many studies have addressed one trait as assessment index (e.g. body size, Andersson 1994; Arnott & Elwood 2009; Hardy & Briffa 2013), multiple traits are used to assess opponent's RHP between two contest phases in chameleon (Ligon & McGraw 2013) as well as *P. middendorffii* (Chapter 4) and/or determine contest outcomes depending on life stage (Lailvaux et al. 2004). Also, to measure more accurate RHP, several authors have proposed an idea that it would be better to consider the interaction among multiple traits (i.e. whole-organism performance capacity; Lailvaux & Irschick 2006) rather than only one trait. Empirical studies support the importance of whole-organisms performance (Lailvaux et al. 2004; Hall et al. 2010) including hermit crab (Mowles et al. 2010) in determining contest winners. Although I revealed the effects of major cheliped on decision-making in male-male contests, further studies clearly would be needed to investigate the assessment strategy in males more comprehensively.

Sexual selection of male major cheliped in Pagurus *hermit crabs*

To discuss the evolutionary development of major cheliped, previous studies of *Pagurus* hermit crabs have focused on shell fights because contestants use major chelipeds as the assessment signals and defending weapons (Neil 1985; Elwood & Neil 1992; Elwood et al. 2006; Laidre 2009; Briffa 2013). However, shell fights are performed by both sexes (Yoshino & Goshima 2002; Briffa & Dallaway 2007), suggesting that shell fights could not explain why males have larger major chelipeds than females in these crabs (Yoshino & Goshima 2002; Briffa & Dallaway 2007; Doake et al. 2010). My results strongly suggest that major cheliped in *Pagurus* hermit crabs are sexually secreted traits (Chapter 2, 4). Sexual development of weaponry trait is sometimes discussed by its effectiveness during female choice in various taxa (Berglund et al. 1996; Tomkins & Simmons 1998; Emlen 2008) including crustaceans (e.g. fiddler crabs, Crane 1975; Murai & Backwell 2005; Reaney et al. 2008). In *Pagurus* hermit crabs, however, this hypothesis would not be appropriate because the precopulatory mate guarding is initiated by male approaching (Chapter 3). Male-male contests would thus be direct cause of the sexual size difference of major cheliped size in *Pagurus* hermit crabs as well as other crustaceans (Conlan 1991; Mariappan et al. 2000; Duffy & Thiel 2007; Emlen 2008; Baeza & Asorey 2012).

Sexual selection for male major cheliped is also observed in the regenerating process of this trait. In *P. middendorffii*, males largely and quickly regenerated their major cheliped at

the first molting after autotomy with reducing the body size growth (Chapter 3). Although I did

not examine the sexual difference in the regeneration process, recent study has reported that

males regenerate larger major cheliped than females after autotomy in *P. filholi* (Matsuo et al.

in press). Such sexual difference of regeneration is also demonstrated in shore crab (Juanes et

al. 2008). Major cheliped size is more reliable indicator of winning than body size during

male-male contest in both crabs (Sneddon et al. 1997; Matsuo et al. in press). These results

suggest that the selective advantage of major cheliped on male-male contests affect the general

activities especially energetic investment and/or allocation for major cheliped.

There are further topics to examine about sexual selection on male major cheliped.

For example, after intruders encountered their opponents guarding female, about 30 % of

intruders in *P. middendorffii* gave up the contest before escalation (Chapter 4). In *P. nigrofascia*,

on the other hand, almost all intruders escalated the contests to physical combat (i.e. grappling;

Suzuki et al. 2012) even if owners use major cheliped (Chapter 2). These results suggest that

there is interspecific difference in the effectiveness of major cheliped use by owner males to

avoid contest escalation. Therefore, the strength and/or direction of sexual selection on major

cheliped would differ between two *Pagurus* species. Moreover, energetic costs related cheliped

possession significantly increase with the size of major cheliped in crustaceans (Allen &

Levinton 2007; Wilson et al. 2009; Doake et al. 2010). This indicates that the degree of sexual

size dimorphisms in major cheliped would be limited by natural selection even if sexual

selection favors further trait exaggeration (Allen & Levinton 2007; Doake et al. 2010).

Other type of male-male competition in the field

Although I focused on the male-male contest competition, other processes of male-male competitions would also affect the male mating success in *Pagurus* hermit crabs. One of these would be male-male scramble competition where early search and location of the mates is critical for mating success (Andersson 1994). In my study area, solitary hermit crabs are typically found on the ground and/or under the boulders (Goshima et al. 1998; Yoshii et al. 2009) whereas the precopulatory guarding pairs are often observed on the seaweeds (e.g. Kawaminami & Goshima in press). This suggests that males move from usual fields (e.g. ground and under the boulders) to a given place after they initiate to guard, which would be considered as a type of scramble competition. If owner males on the seaweed are few encountering with intruders, they succeed in copulation with their guarded partner without any cost related with contests. Male mating success in hermit crabs therefore would be determined by complex selective pressure such as the combination of male-male scramble and contest competition.

Acknowledgements

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