Title: Previous mating experience increases fighting success during male-male contests in the hermit crab *Pagurus nigrofascia*

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Abstract

Prior social experience often affects subsequent competitive interactions and their outcomes. Although the effects of prior contest experience have been widely examined, effects of mating experience remain less well examined. We examined, in males of the hermit crab *Pagurus nigrofascia*, whether males successively copulated with more than one female, and whether males with copulation experience differed in their subsequent contest behaviors and probability of winning in male-male contests compared to males without copulation experience. The copulation experience of intruders was manipulated and the contest behaviors compared between mated and unmated groups. Males mated with several females regardless of the male body size. Compared with unmated intruders, intruders with mating experience succeeded more often in taking over females and did so within a shorter period particularly when the male-male contests occurred over females with a long time to molt. These results suggest that mated males of *P. nigrofascia* overestimate the female quality and/or enhance the competitive performance similar to the 'winner effect' that is a positive feedback from prior winning experience to future contests.

Keywords

copulation experience; competitive ability; male mating success; *Pagurus* hermit crab

Introduction

Males of many species engage in contests for females during the reproductive season (Andersson 1994). Since body and/or weapon sizes determine the fighting ability of contestants, many studies have focused on such physical attributes to understand decision making by contestants and the consequences of contests (e.g., Arnott and Elwood 2009; Hardy and Briffa 2013). Effects of prior experience on contest behaviors have also attracted much attention. For example, although larger males are typically dominant over smaller males in male-male contests, they do not fight with smaller males after they have lost a contest against other males in a snake (Schuett 1997). Both winning and losing experiences affect the aggression and outcomes in subsequent contests of rats over food (Lehner et al. 2011). Prior contest experience of males has been similarly demonstrated to affect subsequent contest behavior and/or the fighting success in various taxa (Hsu and Wolf 1999; Hsu et al. 2006; Rutte et al. 2006; Kasumovic et al. 2010; Okada and Miyatake 2010). The outcome of previous contests appears to form the basis of the evaluation of their own competitive ability.

Mating experience can also have either positive or negative effects on the process and outcomes of subsequent male-male contests. For example, male crickets become less aggressive and more likely to lose contests when they have previously paired with females (Brown et al. 2006, 2007) and copulated with them (Judge et al. 2010). Such negative effects of mating on the subsequent contest would be caused by the energetic costs of mating (Judge et al. 2010) and/or might be affected by a shortage of sperm due to mating (van Son and Thiel 2006; Sainte-Marie 2007; Sato and Goshima 2007). Furthermore, as perceived value of a mating opportunity would be expected to be lower in mated males than males that had not mated recently, such mating experience potentially impacts subsequent competitive performance for mating opportunities (e.g., subjective resource value; Arnott and Elwood 2008). On the other hand, other studies have shown that the probability of winning increases after sexual experience (i.e., exposure to female) including copulation (e.g., Suga 2006; Killian and Allen 2008; Pérez-Staples et al. 2010; Guevara-Fiore et al. 2012). However, there are only a limited number of studies examining how mating experience affects male-male contests in crustaceans (Kendall and Wolcott 1999), despite considerable research into male-male contests in this taxon (Briffa 2013). This study therefore examines the effect of copulation experience on the subsequent male-male contests in the hermit crab *Pagurus nigrofascia*.

Males of *Pagurus* hermit crabs show precopulatory guarding behavior, in which they grasp the aperture of the gastropod shell occupied by a mature female with the left cheliped over periods of several days (Hazlett 1968; Goshima et al. 1998). Male-male contests occur between guarding and solitary males, and larger males are more likely to win the contests in *P. filholi* (Okamura and Goshima 2010; Tanikawa et al. 2012), *P. middendorffii* (Wada et al. 1999) and *P. nigrofascia* (Yasuda et al. 2011). Although the intensity of contest behavior is affected by the experience of agonistic encounters in *Pagurus* hermit crabs (Gherardi and Tiedemann 2004a, b; Yasuda et al. 2014), no studies have examined the effects of copulation on contest behavior in hermit crabs. We hypothesized that males with copulation experience may be less likely to win the subsequent male-male contests in *P. nigrofascia* if they have a limited capacity for successive copulations due to the high energetic costs of guarding and/or shortage of sperm, and consequently have a lower perceived value of a new mating opportunity. On the other hand, if males of this species have a capacity for successive mating, copulation experience may not negatively affect the subsequent contest. We therefore first examined whether males successively copulate with females in *P. nigrofascia* since no studies have directly examined if males of this species are able to copulate with several females during a reproductive season. We then examined whether males with copulation experience differ in contest behaviors and the probability of winning from non-copulated males during male-male contests in *P. nigrofascia*.

Methods

We collected precopulatory guarding pairs of *Pagurus nigrofascia* from the intertidal rocky shore during April 26 to May 13, 2013 at Kattoshi, southern Hokkaido, Japan (41°44’N, 140°36’E). The mating season of this species is from late April to early June in our study site (Goshima et al. 1996), and females of this species always molt just before copulating and spawning (Suzuki et al. 2012). Since we could not know and standardize the prior mating experience of each male in the field, we collected a substantial number of samples (see below) to accommodate the variation of experience in the field. The rearing procedure in the following experiments was conducted under 15 °C, 12L: 12D and without food. After the experiments, we measured crabs for shield length (calcified anterior portion of the cephalothorax; hereafter, SL) as body size to the nearest 0.01 mm under a stereomicroscope. All statistical analyses were performed using R version 3.0.1 (R Core Team 2013).

Experiment 1: are males able to mate with more than one female in *P. nigrofascia*?

We collected guarding pairs of *P. nigrofascia*, placed them in a small vinyl pouch with seawater in the field, and brought them back to the laboratory on 8 to 10 May 2013. After we checked that males were intact (i.e., they had all appendages) and were still guarding females in the laboratory, each of the 33 guarding pairs were separately put into a plastic container (14.3 x 10.8 x 7.2 cm) with seawater 3 cm deep. Females of the remaining pairs were separated from the males, and were kept individually in a plastic cup (300 ml) until molting as stock females. We used the females which had molted as receptive females in the following procedure. All males that had guarded receptive females in the field were returned to the study site.

All pairs were observed at 12 hour intervals, and whether each male guarded the female or not were recorded. If the male did not guard the female, we confirmed if the female had spawned and if so removed the female from the container. We then introduced another receptive female into the container. Subsequently, to examine whether males are able to mate with multiple females during 24 hours, if males mated with the introduced female, we repeated this procedure. Maximum number of females mating with a male was therefore three: a male initially mated with a female that had been guarded in the field, and then mated with up to 2 receptive females introduced from the stock in each 12 hour interval.

Since all males mated with at least 2 females (see Results), we examined the effect of male body size on whether males mated with 3 females or not during the rearing period (i.e., 24 hours). Generalized linear model (GLM) with a binomial error distribution was used for the analysis. The response variable was whether males mated 3 times of not (i.e., yes = 1, no = 0), and the explanatory variable was SL in male. To examine the effects of a third female, SL of the third female was also treated as an explanatory variable in this analysis.

Experiment 2: how does prior copulation experience affect male-male contests?

We collected 90 guarding pairs between 26 April and 13 May 2013. After checking the guarding in the laboratory, each pair was maintained in a plastic container (14.3 x 10.8 x 7.2 cm). All individuals were maintained under 15 °C, 12L: 12D and without food. A day after collection, we checked whether the male was still guarding or not. When the male did not guard the female and the female had spawned, we regarded the males as a male with copulation experience (mated male; N = 45), whereas when the male guarded the female, we regarded the male as male without copulation experience (unmated male; N = 45). Then, we collected new guarding pairs from our study site to conduct the experiments of male-male contest between a maintained male and a pair collected on the date of the trial.

In this experiment, we randomly chose ‘intruder’ from either mated or unmated males and a pair from guarding pairs collected on the date of trial. Owner male and the guarded female in the field were placed in a small container (19.5 x 12.0 x 7.0 cm) with seawater 3 cm deep. After confirming that the owner male had initiated guarding the female, an intruder was then placed in the container. We used the video function built into digital cameras (Pentax, WG2) to record the interaction between contestants from the time of introducing the intruder.

All experimental trials were conducted within 6 hours of collection of the guarding pairs. All crabs were used only once and no crabs were injured or lost their appendages during contests. Each owner and his guarded partner were then placed in a small plastic container (14.3 x 10.8 x 7.2 cm) to re-construct the guarding pair and checked twice each day until the prenuptial molting of the female.

We observed the recordings for up to 15 minutes by focusing on the behavior of the intruder starting from when the intruder initiated movement. All intruders escalated the contests to the grappling behavior (for details of this behavior, see Yasuda et al. 2012). Since takeover of a female is only observed during this behavior (Yasuda et al. 2012), we recorded whether and when the intruder succeeded in taking over a female from the owner male. After the 15 minute observation period, we recorded the contest outcomes based on which male guarded the female. If the contest had not finished by the end of the observation, we recorded it as a draw.

To examine whether and how copulation experience affects subsequent male-male contests, we used a model selection approach based on the Akaike's information criterion (AIC). We compared AIC values among all possible models, and the model with the lowest AIC value was considered the most parsimonious (Akaike 1983). To examine whether copulation experience affected whether and when the intruder tookover the female guarded by the opponent during male-male contests, we used a Cox's proportional hazard model (Cox 1972). The response variable was the duration until the takeover (seconds). The explanatory variables in the initial model were (1) group of intruder (i.e., mated = 1, unmated = 0), (2) the difference in SL between intruder and owner (DSL_{I-O}), (3) SL of the female guarded by owner

(SL_F), and (4) the number of days until the prenuptial molting of the female guarded by owner (DAY). Since female quality affected the process and the outcomes of male-male contest in *P. nigrofascia* (Suzuki et al. 2012), (5) the interaction between group and SL_F and (6) the interaction between group and DAY were also treated as explanatory variables in the initial model. To examine the effect of copulation experience on the outcomes of male-male contests, we then used GLM with a binomial error distribution. The response variable was the outcome of contest (i.e., intruder win = 2, draw = 1, owner win = 0), and the explanatory variables were the same as above (i.e., (1) – (6)) in the initial model.

Results

Experiment 1: are males able to mate with more than one female in *P. nigrofascia*?

After mating with the female that was guarded in the field, all males immediately guarded an introduced receptive female (N = 33). Some males initiated mating with the introduced female within 5 minutes. In the rearing period after the initial mating, 24 males mated with 2 additional females (i.e., total of 3 females) and 9 males mated with one additional female (i.e., total of 2 females), respectively. Whether males copulated with 3 females or not was not affected either by male body size (GLM; z = -0.807, P = 0.420) or body size of the third female (z = -1.439, P = 0.150).

Experiment 2: how does prior copulation experience affect male-male contests?

Results of the top 5 models in each model selection are shown in Table 1. Whether and when takeover occurred was best described by the model with experimental group, size difference between contestants ($DSL_{I\text{-}O}$) and the number of days until the prenuptial molting (DAY) (Table 1). Mated intruders (N = 45) were more likely to takeover the female guarded by owners within a shorter period than unmated males (N = 45; Fig. 1). The duration until takeover also shortened as intruders were larger in SL than their opponents, and as the female required more days until the prenuptial molting (Table 1).

The outcome of male-male contests was best described by the model with group of intruders, $DSL_{I\text{-}O}$, DAY and the interaction between group and DAY (Table 1). Mated intruders had a higher probability of winning than unmated intruders, especially when the contests occurred over a female with more days to molting (Fig. 2). The probability of winning by intruders also increased with increasing size difference in SL compared to their opponents (Table 1). Female size (SL_F), on the other hand, was not selected in either of the best models and showed a lower effect on the occurrence of takeover and the probability of winning than other variables (Table 1).

Discussion

Intruders actively engaged in subsequent male-male contests regardless of prior mating experience, and those with mating experience had a higher probability of winning than unmated intruders in *Pagurus nigrofascia*. Further, males that had recently copulated took over females in a shorter period than non-copulated ones. Such enhancement of competitive performance after sexual experience has been observed in both vertebrates (Guevara-Fiore et al. 2012) and invertebrates (Chamorro-Florescano and Favila 2008; Kralj-Fišer et al. 2011; Kou and Hsu 2013). For example, in the vole *Microtus ochrogaster*, males with mating experience more aggressively respond to an intruder compared with males that cohabited with a female without mating or that were housed alone without female exposure (Wang et al. 1997). At the end of male-male contests, recently mated males in the blue crab *Callinectes sapidus* succeed in stable pairing with females more often than unmated males (Kendall and Wolcott 1999). Although there are relatively few studies to directly examine the effects of mating experience on contest behavior (Judge et al. 2010), the positive effects due to this experience on the subsequent male-male contests seems to occur in diverse taxa.

The enhancement of competitive performance after copulation may be associated with the modification of self-assessment by mating experience itself. Estimation of own fighting ability is one of the key concepts concerning contest behavior (Payne and Pagel 1996, 1997; Taylor and Elwood 2003). This self-assessment is often modified by prior contest experience of each contestant (i.e., self-assessment hypothesis; Whitehouse 1997; Rutte et al. 2006): winning experience increases, whereas losing experience decreases the perception of fighting ability and the probability of winning in the subsequent contests (winner/loser effects; Hsu et al. 2006). Recent studies have also reported that several taxa show social feedback effects similar to winner/loser effects in the mating context. For example, in the finch

Taeniopygia guttata, males that failed to form a pair bond with females in the juvenile stage show a lower pairing success with other females during adulthood, suggesting a similar phenomenon to the loser effects in a mating context (Mariette et al. 2013). Males in the fly *Anastrepha ludens* achieve a higher mating success with increasing own mating experience (Pérez-Staples et al. 2010). Unlike other studies, prior experience and the subsequent event were not the same in this study (i.e., copulation and male-male contest). However, given an ultimate goal of male-male contests is to maximize lifetime mating success (Andersson 1994; Emlen 2008), the prior copulation experience itself might have a positive feedback on subsequent self-assessment in mated males similar to the winner effect. Recently mated males of *P. nigrofascia* would therefore improve self-assessment and behave as prior winners in subsequent male-male contests.

Males may also modify the assessment of female quality during the contests after copulation. Intruders of *P. nigrofascia* were more likely to succeed in taking over females when those females required more days until prenuptial molting. Suzuki et al. (2012) pointed out the advantages to owners when the contested female required less time to molting and suggested that intruders are unable to accurately assess female quality in this species. Our results are consistent with this study, and similar findings have been reported in other animals (e.g., Hack et al. 1997; Bridge et al. 2000; Arnott and Elwood 2008). Moreover, mated intruders showed a higher probability of winning than unmated intruders especially when contested females had low receptivity. This suggests that mated intruders overestimate female quality more than unmated ones. Individuals with winning experience are expected to raise the subjective value of a resource in future contests (Hsu et al. 2006), and our study suggests that males with mating experience show similar enhanced competitive performance. Taken together, such overestimation of female value by mated males of *P. nigrofascia* might be explained as a similar mechanism to the winner effect but induced by mating experience. Alternatively, since mated intruders copulated with their partner within 1 day from a field collection, females guarded by these males were expected to be relatively high value (i.e., less time to molt or already having finished molting) when the guarding pairs were collected. This perceived high value (short period to molt) of guarded females might cause the overestimation of contested females. The positive effect of overestimation of resources is also supported by theoretical modelling (Dugatkin and Dugatkin 2011). Regardless of the process, such modification of resource assessment would contribute to the enhanced fighting success in mated males of *P. nigrofascia*.

As above, both the fighting ability and the perception of resource quality in each contestant determine the contest process and the outcomes in male-male contests (Arnott and Elwood 2008, 2009; Hardy and Briffa 2013). Our study suggests that both of these components in males might be modified by prior mating experience in *P. nigrofascia*. Still unknown is the relative importance between the modified fighting ability and the assessment of female quality on contest behavior and the probability of winning in mated males. Further manipulations of prior experience are needed to evaluate this.

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Figure captions

Fig. 1 Cumulative occurrences of takeover in females guarded by owner males during male-male contests of *P. nigrofascia*. The curves are estimated by the best model based on AIC. Previously mated intruders showed a higher probability to takeover females with a shorter period than unmated intruders. Other variables, the difference in shield length (index of body size) between contestants and the number of days until prenuptial molting in females guarded by owners, are treated as average values in the curves.

Fig. 2 Outcomes of male-male contests in the hermit crab *P. nigrofascia*. Logistic regressions were estimated by the best model based on AIC. Previously mated intruders showed a higher probability of winning than unmated intruders especially when the contested female required more days to molting. Points at 0 to 2 are owner and intruder males win, respectively. DAY indicates the number of days until prenuptial molting in females guarded by owners. Difference in shield length (index of body size) between contestants is treated as average value in the regression curves.

Fig. 1

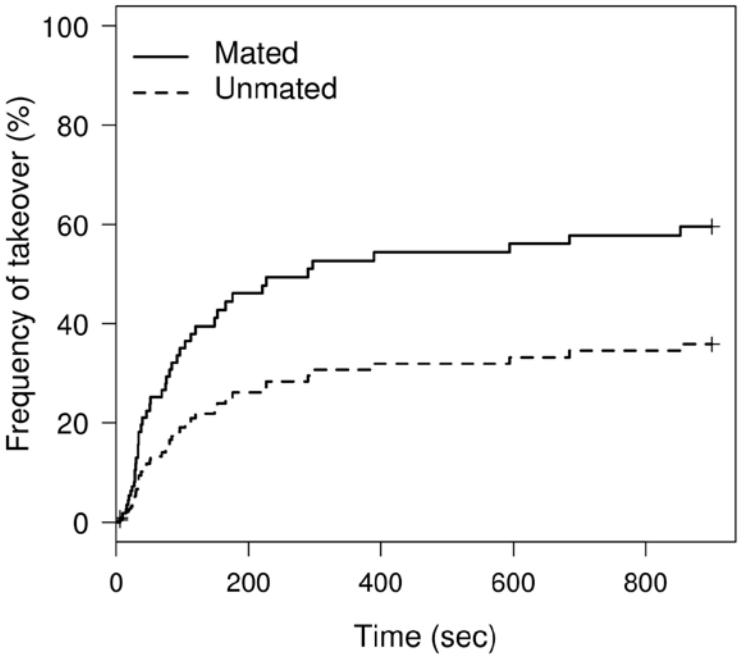
Mated
Unmated
Frequency of takeover (%)
Time (sec)
0
20
40
60
80
100
0
200
400
600
800

Fig. 2

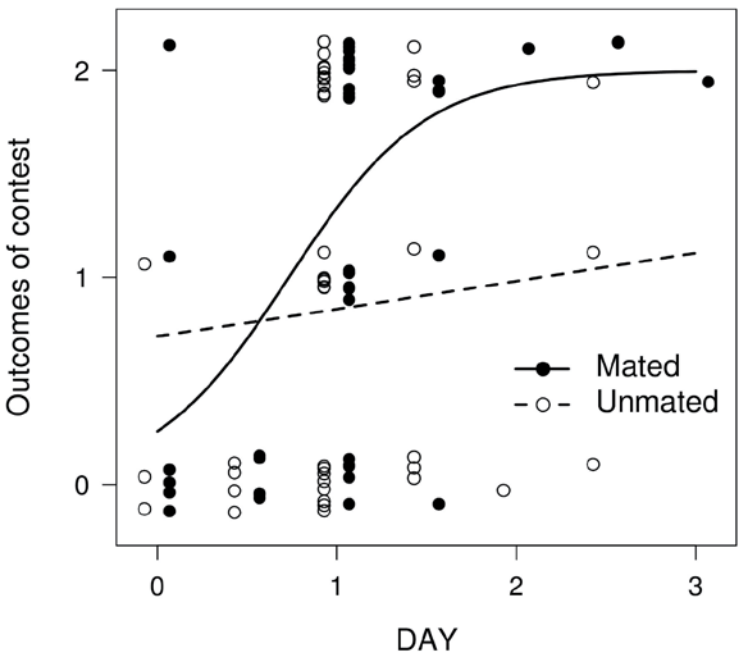

Table 1

Results of top 5 models selected based on Akaike's information criterion (AIC) analyzed by Cox's proportional hazard analysis and a generalized linear model (GLM) with a binomial error distribution

Model	Intercept	Group	$DSL_{I\text{-}O}$	SL_F	DAY	Group x SL_F	Group x DAY	*df*	AIC	Δ	weight
Whether and when intruders tookover the female from their opponents (*N* = 90)											
Cox's proportional hazard model											
1		0.712	1.245		0.528			3	337.6	0.00	0.227
2		0.738	1.214	-0.327	0.565			4	338.0	0.35	0.191
3		0.133	1.234		0.208		0.483	4	338.6	0.99	0.139
4		0.092	1.207	-0.347	0.195		0.539	5	338.8	1.21	0.124
5		0.650	1.214	-0.335	0.564	0.018		5	340.0	2.35	0.070
Contest outcomes of intruder (*N* = 90)											
Generalized linear model with binomial error distribution											
1	-0.678	-1.337	2.229		0.273		2.345	5	155.7	0.00	0.603

2	-1.235	-1.376	2.254	0.111	0.285		2.385	6	157.5	1.89	0.234
3	0.106	-4.985	2.305	-0.157	0.250	0.687	2.630	7	158.5	2.89	0.142
4	-1.833	0.989	2.022		1.329			4	163.3	7.69	0.013
5	-1.739	0.989	2.018	-0.018	1.323			5	165.3	9.69	0.005

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