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Male mate choice and male-male competition in the hermit crab *Pagurus nigrofascia*: importance of female quality

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Abstract

Male mate choice has recently been reported in some animals with male-male competition. In the laboratory, we examined whether males choose their mates based on female quality that was indicated by body size and/or days to prenuptial molt, and the effects of female quality on male-male competition in the hermit crab *Pagurus nigrofascia.* We collected samples from April to May 2009 at an intertidal shore in Hokkaido, Japan (41°N, 140°E). When a male simultaneously encountered two receptive females in the mate choice experiment, males chose females which require less time to molt. When a male guarding a female with less time to molt was challenged by an intruder, the guarding male defended the female for a longer period and was more likely to win the contest. These results indicate that male *P. nigrofascia* use time to molt to discriminate between females.

Introduction

Mate choice and competition for mates are major processes of sexual selection, and the conventional perspective is that indiscriminate males compete for the attention of choosy females. Although this perspective is true in some animals, male mate choice has recently been reported in a wide range of animals where there is intense male-male competition (Hoefler 2007; Candolin and Salesto 2009; Wada et al. 2011). Males of such animals often prefer to mate with larger females due to their higher fecundity (Byrne and Rice 2006; Bel-Venner et al. 2008; Baldauf et al. 2009). In some crustaceans where males show precopulatory guarding behavior and compete for mates, males are known to have thresholds for female sexual receptivity (Manning 1980; Dick and Elwood 1989; Wada et al. 1999). Male mate choice and male-male competition potentially will have effects on each other, and some theoretical models predict that competitive dominance of males could lead to variation in the direction and strength of male mate choice (Fawcett and Johnstone 2003; Härdling et al. 2004; Härdling and Kokko 2005; Venner et al. 2010). Wada et al. (2011) demonstrated that inferior small males of the hermit crab, *Pagurus middendorffii*, choose not only larger females but also females that require less time to guard until prenuptial molting and/or spawning, while large superior males choose females based on their body size.

Outcomes of dyadic contests of animals are usually explained by differences between contestants in two factors, resource holding potential and perception of resource value (Parker 1974; Maynard-Smith 1982; Enquist and Leimar 1983). Resource holding potential is typically correlated with body size, ownership and/or physiological conditions (Arnott and Elwood 2009). Many empirical studies for male-male contests have focused on the difference in resource holding potential between competitors (Lailvaux et al. 2005; Prenter et al. 2006, 2008; Yasuda et

al. 2011). For example, larger males have been shown to be more likely to retain or successfully seize possession of (below as, takeover) nests and/or mates in a sand goby (Lindstöm 1992), a penguin (Renison et al. 2002) and a hermit crab (Yasuda et al. 2011). The perception of resource value can also differ between contestants especially in a resident-intruder situation since the resident has spent more time at the resource, and has already gathered more information about the resource that is being contested (Arnott & Elwood 2008). Intruders need to estimate the resource quality in some way, such as the distribution of resource quality in the population or any chemical features and/or appearance of the resource. One of the expected outcomes of contests where only the resident has the opportunity of estimating the resource quality in detail is that the resident's probability of winning should increase with the resource quality (Enquist and Leimar 1987).

Males have been shown to assess female quality (body size and time until molting and/or spawning) accurately in the freshwater amphipod *Gammarus pulex* (Dick and Elwood 1990) and the hermit crab *Pagurus middendorffii* (Wada et al. 2011). If males can assess the female characters and thereby select females with high quality, the quality may affect the outcome of male-male contests. However, the effect of female quality has been paid less attention in studies on male-male contest for mates (Austad 1983) perhaps because males have previously been assumed to be indiscriminate regarding female quality in species with intense male-male competition. In marine invertebrates, no studies, as far as we know, have examined whether female quality affects the outcome of male-male contests.

We here examine the following questions in the hermit crab *P. nigrofascia*; (1) whether males conduct mate choice depending on the female quality (i.e., body size and/or time until molting) and (2) whether the timing of takeover and the outcome of male-male competition is

affected by the female quality. Males of *P. middendorffii* show both contest competition and mate choice (Wada et al. 1999; Wada et al. 2011). Males of the genus *Pagurus* engage in precopulatory guarding behavior, grasping the rim of a female shell with its minor cheliped during the breeding season (Hazlett 1972; Elwood and Neil 1992; Goshima et al. 1998). When a solitary male encounters with another male that is guarding a female, contest competition usually occurs between the two males. If the intruder male is larger than the pairing male, takeover often occurs in male-male contest of *P. middendorffii*, *P. filholi* and *P. nigrofascia* (Wada et al. 1999; Yoshino et al. 2004; Yasuda et al. 2011). Female quality may affect the outcomes of male-male contests in *Pagurus* hermit crabs since the body size of females varies within populations and larger females have a higher fecundity in many *Pagurus* hermit crabs (Wada et al. 1995; Goshima et al. 1996; 1998; Wada et al. 2000). Males of *P. middendorffii* choose to guard potential mates on the basis of female body size and, as for small males, time until spawning (Wada et al. 2011). We thus regard the body size and time to molting as indicators of female quality in this study.

Materials and Methods

The mating season of *P. nigrofascia* is from late April to early June in our study site (Goshima et al. 1996). We collected precopulatory guarding pairs of *P. nigrofascia* during low tides from 24 April to 1 May 2009 at Kattoshi, southern Hokkaido, Japan (41°N, 140°E). Each pair was placed in a small vinyl pouch with some seawater in the field and brought back to the laboratory. After placing each pair in a small container (19 x 12 x 7 cm) with some natural seawater for about an hour, we checked whether each male was still guarding the female. Guarding males and the females were then separated. We excluded the males and females that

were no longer in guarding pairs because they were assumed to have already copulated. All trials were conducted within ten hours after sampling.

(1) Male mate choice

Before the mate choice experiment, males and females of guarding pairs, collected on 29 April and 1 May 2009, were kept individually in polystyrene cylinders (300 ml) containing seawater for a minimum period of 30 min. We randomly chose two males and two females to use in the following two experimental trials while we avoided assigning crabs to a trial that formed guarding pairs in the field. The two females were placed in a small container (19 x 12 x 7 cm) filled with natural seawater to a depth of about 3 cm. After the females became active in the container, we added a male and recorded which female the male guarded after 5 min. Then, we returned the male back to the cylinder, rinsed the container in natural seawater, and added another male after the two females in the container became active. Each male was used once in the experiment, whereas each female was used twice. We identified each crab in a trial on the basis of gastropod species and morphological features, such as size and color of shells occupied by the crab. After all trials, guarding pairs in the field were reconstructed in their small containers, and we assessed the time until molting of each female by checking the number of days until prenuptial molting (hereafter DAY), since all *P. nigrofascia* females molt just before copulating and spawning (Yoshii et al. 2009). We measured all crabs for shield length (the calcified anterior portion of carapace, hereafter SL) to the nearest 0.01 mm under a stereoscopic microscope after the females spawned. The number of trials was 54.

Data of mate choice was first analyzed with the generalized linear mixed model (GLMM), with a binomial error distribution and logit link function. The response variable was binary data

of whether a male guarded the small female or the large female (i.e., small female = 0, large female = 1). Explanatory variables were, 1) difference in SL between the large and small females ($DSL_{LF - SF}$), 2) difference in SL between the male and the large female ($DSL_{M - LF}$), 3) difference in dates until molting between the large and small females ($DD_{LF - SF}$). Factor of class, which was composed of two males and two females, was treated as a random effect in the GLMM. However, when we compared by using AIC between the GLMM and GLM, which was the model that removed the random effect from the GLMM, the index of GLMM (AIC = 60.16) was larger than that of GLM (AIC = 58.16), indicating that the latter model is better for explaining our data because the outcome of the two mate choices in a class was independent of each other. We then analyzed our data by GLM with a binomial error distribution and logit link function.

(2) Male-male competition

We conducted experiments of male-male contest competition in the laboratory by using precopulatory guarding pairs collected from 24 April to 1 May 2009 to examine the effect of female quality on the contest duration and the outcomes of contests. After the males of guarding pairs were divided into two groups (i.e., pairing group and intruder group, hereafter PG and IG, respectively), we randomly chose a male from each group for each trial. We placed a male of PG and his partner in the field into a small plastic container (19 x 12 x 7cm), and checked whether the male guarded the female. A male of IG was added in the container after the PG male guarded the female. We observed the behaviors of males for 15 minutes, and recorded when physical contest was initiated, whether and when takeover of the female occurred, and which male guarded the female after the observation period. Since we treated PG males as focal males in the following statistical analysis, when PG or IG males guarded females at the end of observation,

we recorded them as "win" or "defeat", respectively. If the physical contest continued after the 15 minutes, we recorded it as a "draw". We conducted 74 trials. After all trials, guarding pairs in the field were reconstructed and kept in polystyrene cylinders (300 ml), and each female was checked every day to record the number of days until molting (DAY). We also measured all crabs for SL to the nearest 0.01 mm under a stereoscopic microscope after the females molted and spawned.

To examine the effects of body sizes of PG and IG males and female quality on whether and when the takeover occurred, we used Cox's proportional hazards model. We included four explanatory variables, 1) SL of PG male (SL_{PG}), 2) SL of IG male (SL_{IG}), 3) SL of female (SL_F) and 4) DAY of female. The effect of the female quality on the outcomes of contests was analyzed by generalized linear model (GLM) with binomial error distribution and logit link function. The outcome of contest was treated as a response variable (i.e., win by PG male = 2, draw = 1, defeat = 0), and the explanatory variables were SL_{PG}, SL_{IG}, SL_F, and DAY. We used the free software R version 2.14.1 (R Development Core Team 2011) for all statistical analysis.

Results

(1) Male mate choice

Female and male SL ranged from 3.48 mm to 5.87 mm and from 4.78 mm to 6.87 mm, respectively, and DAY ranged from 0 to 5 days. The mean ± SD of absolute differences in SL and DAY between large females and small females were 0.63 ± 0.51 mm and 0.71 ± 1.09 days, respectively. Table 1 shows the results of the GLM analysis. The probability that the males chose the large females significantly increased with decreasing $DD_{LF - SF}$ (Fig. 1) although female size did not affect the male mate choice, indicating that the males of *P. nigrofascia* showed

preference for females with less time to molting, but not for larger females. All males chose their partner within three minutes after becoming active. After choosing a female all but two of the 53 males did not catch or guard the other female in the container. The males played an active role in mate choice when the males were the largest crab in the container. However, females were observed to reject the male's approach when the male and the female were approximately the same body size or the male was smaller than the female.

(2) Male-male competition

In the male-male contest experiments, SL of male contestants ranged from 4.77 mm to 6.87 mm, and the mean ± SD of absolute differences between contestants was 0.53 ± 0.41 mm. After beginning the experimental trial, IG males approached the pairs and a physical combat between the two males occurred within four minutes in all of 74 trials. The numbers of "wins" and "draws" were 34 and 18, respectively, and the takeover ("defeat") occurred in 22 trials. Days until molting affected whether and when the takeover occurred (Table 2). PG males defended their females against IG males for longer periods if the PG males were guarding females with fewer days to molting. However, the frequency and timing of takeover were not significantly affected by female body size. Similar results were found in the outcomes of contests (Table 3). PG males were more likely to win the contests when they guarded females with fewer days to molting (Fig. 2).

Discussion

Our results revealed that males of the hermit crab *P. nigrofascia* chose females based on the time until molting and the duration and outcome of the contest was also affected by the time

until molting of the female that the PG male guarded. Female body size did not affect the male mate choice in the hermit crab *P. nigrofascia*. However, males of *P. middendorffii* choose their mates based on female body size while the mate choice of small males is based on both body size and the time until spawning of females (Wada et al. 2011). Mating seasons of *P. nigrofascia* and *P. middendorffii* are limited from late April to early June and late October to early December, respectively (Wada et al. 1995; Goshima et al. 1996). Males are considered to choose females to maximize their reproductive success during the limited reproductive season. This might be achieved by mating with females with a shorter time until molting and spawning if males have a high encounter rate with receptive females, and/or if the difference in fecundity between females is small. Otherwise, in the opportunity for choosing two females simultaneously, males might gain by choosing the larger, more fecund females even if a longer guarding duration is needed to mate with the larger female. There may thus be differences in the availability of receptive female, such as density and body size distribution, between *P. nigrofascia* and *P. middendorffii*.

In this study, all IG males initiated physical combat in male-male contests. In *P. middendorffii*, some intruder males do not show physical combat when they are much smaller than the opponent pairing male (Yasuda et al. in press). The interspecific difference could be explained by the difference in the size range of males. While the body size of males that guard females in the field range from 2.10 mm to 7.10 mm in SL of *P. middendorffii* (Yasuda et al. in press), that of *P. nigrofascia* ranged from 4.77 mm to 6.87 mm in this study. In male-male contest experiments of the two species, the mean of absolute differences in SL between contestants in *P. middendorffii* and *P. nigrofascia* are 1.39 mm and 0.53 mm, respectively. Since the size range and the mean of absolute difference in *P. nigrofascia* is much smaller than those of

P. middendorffii, male-male contests of *P. nigrofascia* would be more likely to escalate due to the small difference in body size between contestants.

PG males were more likely to win than IG males when the PG males guarded females with less time until molting. Although residency or ownership has been shown to confer an advantage in aggressive behavior (Hack 1997; Kemp 2003; Kemp and Wiklund 2004), the effects were sometimes mediated through an interaction with resource quality (Buena and Walker 2008). Our results suggest that information asymmetry about female quality between the PG male and the IG male would affect the duration and the outcome of aggressive interactions among male hermit crabs. This is consistent with studies of several taxa that show resident males with information indicating a high resource value are more aggressive and tend to win more contests (Austad 1983; Otto 1989; Hack et al. 1997; Bridge et al. 2000; Humphries et al. 2006; Buena and Walker 2008). Also, as predicted by Enquist and Leimar (1987), we found that IG males win more contests when the female quality was low. IG males would show more aggression and fight over females with low quality than PG males.

Several studies have found that intruders gain information about the female quality as the contests progresses (Dick and Elwood 1990) and others suggest that intruders get little or no information about resource quality during contests (Bridge et al. 2000). Intruder males of *P. filholi* and *P. middendorffii* seem to be able to gain some information about female quality from visual and chemical cues in hermit crabs (Wada et al. 1999; Okamura and Goshima 2010; Wada et al. 2011; Yasuda et al. in press). However, our results of contest experiment in *P. nigrofascia* suggest that IG males might not gain sufficient information to accurately determine female quality from visual and chemical cues in the contest. This is surprising since these cues would appear to be readily accessible for IG male since in the mate choice experiment, males chose

their unguarded mate immediately, suggesting that guarding may enable the female quality to be partially obscured. Since PG males guarded the females in the field while IG males found the female after starting the experimental trial, information asymmetry may result from differences in duration for information gathering between PG males and IG males. It might also indicate a trade-off between information gathering about female quality and information gathering about the opponent. Although it might be easy to collect information about female without an opponent, in a contest it might be more advantageous to initially assess the opponent (Arnott and Elwood 2008). Alternatively, interference by the PG male may preclude the assessment of female receptivity by the IG male. Bridge et al. (2000) found that residents might prevent the intruder from gathering information in the orb-weaving spider. Further inclusive studies would be needed to understand the mating behavior of hermit crabs.

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Figure Captions

Fig. 1. Male mate choice based on difference in days until prenuptial molting between large and small females (DD_{LF-SF}) in *P. nigrofascia*. Although males chose large females when DD_{LF-SF} was 0, they chose small females when the large females required a longer period until prenuptial molting than small females. Logistic curve indicates the regression curve between male mate choice and DD_{LF-SF} estimated by generalized linear modeling. The coefficients of the solid line are shown in Table 1. Two variables, DSL_{M-LF} and DSL_{LF-SF}, were treated as constants in the regression curve and mean values in the experiment were substituted for the two variables. LF and SF indicate shield lengths of large and small females, respectively. The number of replicates was 54.

Fig. 2. Outcomes of male-male competition in the hermit crab *P. nigrofascia*. Y-axis is the outcome of the competition (PG male win = 2, draw = 1, lose = 0), and X-axis is the difference in body size (i.e., shield length) between PG and IG males. Likelihood of winning depends on the size difference and days until prenuptial molting of females, DAY, that PG males guarded at the start of the experimental trials. Three logistic curves represent the likelihood of the competition outcomes when the DAY was 0, 1, or 2, which were estimated by generalized linear model. The total number of replicates was 74.

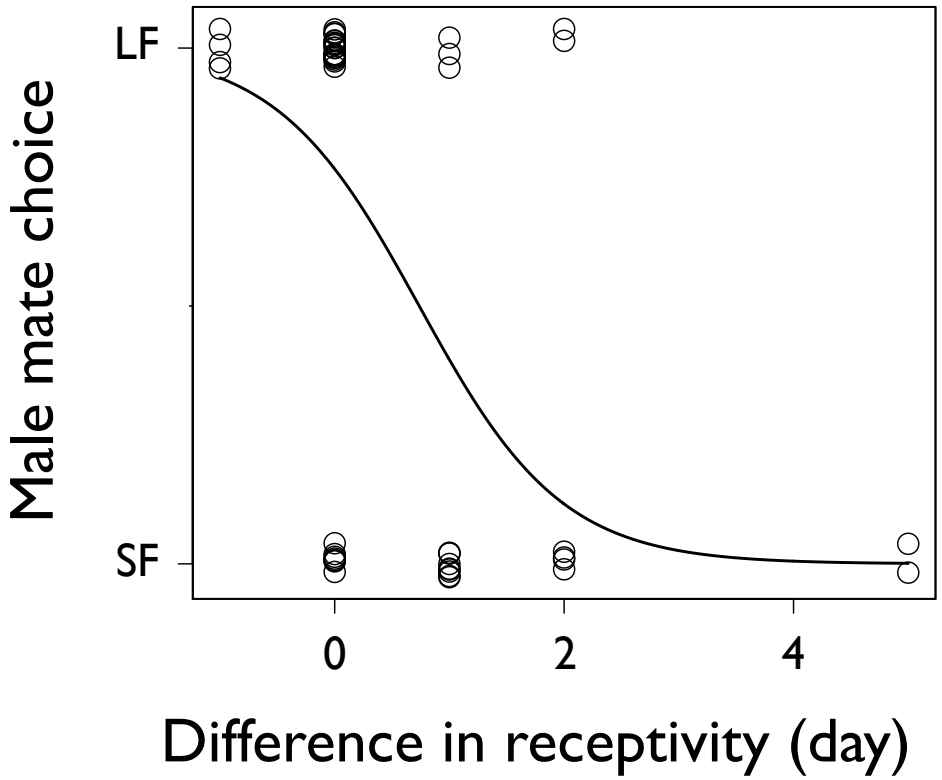

Fig. 1. Male mate choice based on difference in receptivity (i.e., days until prenuptial molting) between large and small females in *P. nigrofascia*. Although males chose large females when the receptivity difference between large and small females (DD_{LF-SF}) was 0, they chose small females when the large females took longer until prenuptial molting (i.e., lower receptivity) than small females. Logistic curve indicates the regression curve between male mate choice and DD_{LF-SF} estimated by generalized linear modeling. The coefficients of the solid line are shown in Table 1. Two variables, DSL_{M-LF} and DSL_{LF-SF}, were treated as constants in the regression curve and mean values in the experiment were substituted for the two variables. LF and SF indicate shield lengths of large and small females, respectively. The number of replicates was 54.

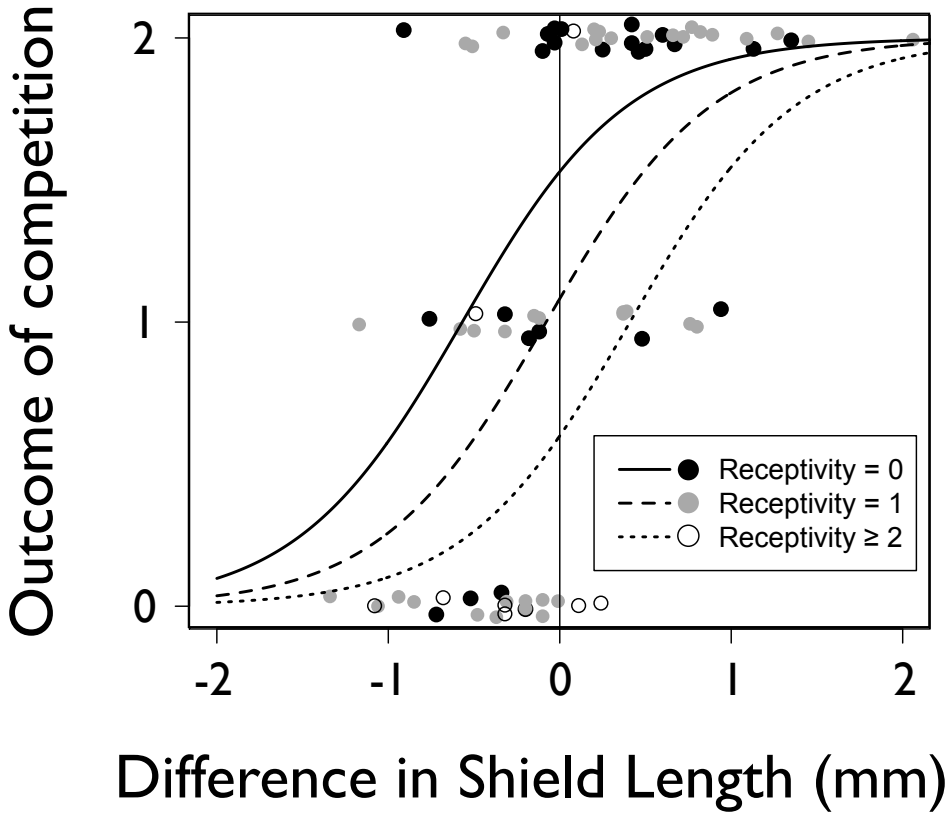

Fig. 2. Outcomes of male-male competition in the hermit crab *P. nigrofascia*. Y-axis is the outcome of the competition (PG male win = 2, draw = 1, lose = 0), and X-axis is the difference in body size (i.e., shield length) between PG and IG males. Likelihood of winning depends on the size difference and receptivity (i.e., days until prenuptial molting) of females, DAY, that PG males guarded at the start of the experimental trials. Three logistic curves represent the likelihood of the competition outcomes when the DAY was 0, 1, or 2, which were estimated by generalized linear model. The total number of replicates was 74.

Table 1. Results of generalized linear model on male mate choice of the hermit crab *Pagurus nigrofascia* . GLM with a binomial error distribution and logit link function to investigate the effects of difference in body size (shield length) between large and small females ($DSL_{LF - SF}$) and between a focal male and the large female ($DSL_{M - LF}$) and difference in time until spawning between the large and the small females ($DD_{LF - SF}$). Residual deviance was 50.2 on 47 degree of freedom. AIC was 58.161.

Explanatory variable	Estimate	Std. Error	*Z*	*P*
Intercept	-2.493	1.742	-1.431	0.152
$DD_{LF - SF}$	-1.660	0.535	-3.102	0.002
$DSL_{LF - SF}$	0.201	0.902	0.223	0.823
$DSL_{M - LF}$	2.434	1.027	2.370	0.018

Table 2. Results of Cox's proportional hazard model to analyze the effects of shield lengths of contestants (SLPG and SLIG) and female (SLF), and days until female prenuptial molting (DAY) on the frequency and duration of male-male contest in the hermit crab *Pagurus nigrofascia* .

Explanatory variable	Estimate	Std. Error	*Z*	*P*
SLPG	-2.397	0.594	-4.034	< 0.001
SLIG	-1.021	0.512	1.993	0.046
SLF	0.007	0.542	0.014	0.989
DAY	0.612	0.279	2.195	0.028

Table 3. Results of generalized linear model on outcomes of male-male contest of the hermit crab *Pagurus nigrofascia* . GLM with binomial error distribution and logit link function to investigate the effects of shield lengths of contestants (SLPG and SLIG) and female (SLF), and days until female prenuptial molting (DAY) on the contest outcomes. Residual deviance was 98.2 on 69 degrees of freedom. AIC was 133.17.

Explanatory variable	Estimate	Std. Error	*Z*	*P*
Intercept	-3.117	3.852	-0.809	0.418
SLPG	2.263	0.519	4.358	< 0.001
SLIG	-1.810	0.469	-3.863	< 0.001
SLF	0.273	0.449	0.607	0.544
DAY	-0.874	0.308	-2.840	0.005