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1 Male mate choice in hermit crabs: prudence by inferior males and simple preference by
2 superior males

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ABSTRACT

In species with both male-male competition and male mate choice, inferior males may make different mate choice decisions from superior males. Males of the intertidal hermit crab, *Pagurus middendorffii*, are known to conduct precopulatory guarding and to adjust the threshold for guarding according to social parameters, such as encounter rate with females, competitor size and sex ratio. Larger males are stronger in male-male competition during guarding in this species. We here tested whether male of *P. middendorffii* initially guarding a smaller female exchanged partners when the male encountered a larger receptive female, and whether large and small males chose potential mates on the basis of body size and/or time needed for guarding when a male simultaneously encounters two females. When a male guarding a smaller receptive female encountered a larger receptive female, the male assessed the larger female and exchanged his partner only in cases of a large difference in body size between the two females, suggesting that males of this species could choose their mates based on female quality even during guarding. When a male simultaneously encountered two receptive females, small males showed the prudent mate choice by balancing female traits between larger body size and shorter time until breeding, while large males showed preference for larger females. The distinct preference exhibited by males of different size classes is concluded to be an adaptive response to the size-dependent risk of losing the female during guarding.

Key words: crustacean, precopulatory guarding, prudent mate choice, sexual selection

31 INTRODUCTION

32 In species where the males engage in competition for mates, some theoretical models have
33 predicted that individual male mate preference will vary with their competitive dominance
34 (Fawcett and Johnstone 2003; Härdling et al. 2004; Härdling and Kokko 2005; Venner et al.
35 2010). Traditional mate choice studies have tended to assume that all individuals should prefer
36 the highest quality mate available in a population (reviewed in Parker 1983). If male
37 reproductive success increases by mating with large females because of their higher fecundity,
38 all males are considered to prefer large females as mates. Although this traditional idea is true in
39 some species (Hoefler 2007; Baldauf et al. 2009), recent theoretical models predict that
40 variation in competitive ability can generate variation in both the strength and the direction of
41 mate preference (Fawcett and Johnstone 2003; Härdling et al. 2004; Härdling and Kokko 2005;
42 Venner et al. 2010) and growing empirical evidence supports this prediction. For example,
43 males in poor condition showed indiscriminate mate choice under male-male competition in a
44 threespine stickleback (Candolin and Salesto 2009). Inferior (small) males of a spider preferred
45 small females while large males preferred large, more fecund females (Bel-Venner et al. 2008).

46 Body size of females is undoubtedly an important trait in male mate choice since
47 preference for large females could increase male fitness in many species where larger females
48 have higher fecundity (Byrne and Rice 2006; Bel-Venner et al. 2008; Baldauf et al. 2009).
49 However, considering female body size as the only indicator of female quality may
50 oversimplify the complex reality. Mate quality in female mate choice can be assessed through
51 various characters of males, such as visual and chemical characters (Andersson 1994; Candolin
52 2003). While female mate choice on the basis of multiple traits has received increased attention
53 (e.g., Backwell and Passmore 1996; Candolin 2003; Ward and McLennan 2009), there have
54 been relatively few attempts to examine whether males choose females on the basis of multiple
55 female traits (Roberts and Uetz 2005; Xu and Wang 2009), except in the context of mate choice

during precopulatory guarding behavior in crustaceans (Manning 1975; Thompson and Manning 1981; Elwood et al. 1987; Dick and Elwood 1989; Goshima et al. 1998, 2006; Franceschi et al. 2010). If male mate choice is conducted on the basis of multiple female traits, inferior males may choose their mate on the basis of different female traits from those used by superior males.

Males of *Pagurus* hermit crabs engage in precopulatory guarding behavior during their mating seasons, in which they grasp the aperture of the gastropod shells occupied by sexually mature females with their left (minor) chela, over a period of several days (Hazlett 1972; Elwood and Neil 1992; Wada et al. 1995). Males directly compete for females during guarding, and larger and/or owner males tend to be stronger competitors than smaller and/or unsuccessful challenger males (Wada et al. 1999; Goshima et al. 2006; Y. Suzuki et al. unpublished). Wada et al. (1999) demonstrated in a laboratory experiment that male *P. middendorffii* could assess females on the basis of time until spawning and adjust the threshold for guarding according to social factors, such as sex ratio, competitor size and encounter rate with females. Although long guarding duration would be beneficial for males to acquire their potential mates, there should be some costs associated with mate guarding, including loss of other mating opportunities (Wada et al. 1999) and restricted feeding during guarding (Yoshii et al. 2009). Energetic costs may also be substantial for males dragging the shells occupied by females, similar to the energy expenditure by males of *Gammarus* amphipods (Adams and Greenwood 1983; Robinson and Doyle 1985; Elwood and Dick 1990; but see Sparkes et al. 1996; Yoshii et al. 2009). On the other hand, female fecundity increases with body size in *P. middendorffii* (Wada et al. 1995). Large and small males of *P. middendorffii* may, therefore, make different decisions in determining their partners. Size assortative pairing is observed in this species (Wada et al. 1996), and there are no tendencies that larger females are more receptive, i.e., shorter time until spawning (S. Wada, unpublished), unlike some crustaceans (Manning 1975). Guarding males of *P. middendorffii* are usually nearly double the body length

of their partners (Wada et al. 1996), and females of this species do not actively resist male guarding attempts when the male is larger than the female (see Results).

Aims of this study are to examine (1) whether male *P. middendorffii* initially guarding smaller females exchange their partners when a male encounters a larger receptive female, and (2) whether large and small males choose females as potential mates on the basis of body size and/or time needed for guarding (time until spawning) when a male simultaneously encounters two females. Theoretical models implicitly assume that guarding males do not exchange partners even when they encounter females with higher quality than those they are guarding. However, males initially guarding smaller females have been observed to change their partners to later introduced larger females in the amphipod *G. pulex* (Dick 1992) and the hermit crab *P. filholi* (Goshima et al. 2006). Since no studies present statistical evidence for the hypothesis that males assess and choose better partners even while guarding females, we here test the hypothesis in experiment 1. We then examine mate choice by large and small male (experiment 2), and compare the strength and the direction of mate preferences between large and small males in Discussion.

MATERIALS AND METHODS

We collected precopulatory guarding pairs of *P. middendorffii* during low tides from 12 to 16 November 2008 at Kattoshi, southern Hokkaido, Japan (41°N, 140°E), since the mating season of this species is from late October to early December in our study site (Wada et al. 1995). Each pair was placed in a small vinyl pouch with some seawater in the field and brought back to the laboratory. After collecting pairs, we also filled several tanks (20 liter) with seawater in the field, took the tanks to the laboratory and used for our experiments. After placing each pair in a small container (19 × 12 × 7 cm) with some natural seawater for about an hour, we checked

whether the male still guarded the female. We excluded the males and females that were no longer in guarding pairs from the following procedures because they had already copulated. Mate choice experiments were conducted within five hours after sampling, and all crabs were measured for shield length (the calcified anterior portion of carapace, hereafter SL) to the nearest 0.01 mm under a stereoscopic microscope after the experiments. We used the statistical software, R version 2.9.0 (R Development Core Team, 2009) for all statistical analysis.

Experiment 1: can guarding males assess and choose another female?

Pairs collected on 16 November were used for the experiment. We first selected relatively large females (mean SL $\pm$ sd = 2.60 $\pm$ 0.48 mm, max. = 3.35 mm, min. = 1.63 mm) from samples, and placed them individually in a small container (19 x 12 x 7 cm) filling it with the natural seawater to a depth of about 3 cm. After the large solitary female started becoming active in the container, a guarding pair was then placed in the container. The female of the guarded pair (mean SL $\pm$ sd = 1.91 $\pm$ 0.27 mm, max. = 2.45 mm, min. = 1.41 mm) was always smaller than the solitary female in a container. We observed the behavior of the male crabs for five minutes and recorded whether the males showed assessment behavior, in which the male grasped the aperture of the shell occupied by the solitary female, with the apertures of their shells typically facing one another (Minouchi and Goshima, 1998), and whether the male exchanged their initial guarded partner with the later introduced large female. The number of replicates of this experiment was 21.

We analyzed the data with the generalized linear model (GLM) with binomial error distribution and logit link function. The response variable was the occurrence of three types of the male behavior in relation to the solitary large female (i.e., no action = 0, assess = 1, exchange = 2), and explanatory variable was the differences in SL between the solitary large

female and the smaller female of the initial guarding pair, which is hereafter expressed as

$DSL_{(LF - SF)}$.

Experiment 2: do males choose their mates on the basis of their body size, female body size and/or female receptivity?

Males and females of each guarding pair, collected on 12 and 14 November, were kept individually in polystyrene cylinders (300 ml) for a minimum period of thirty minutes before experiment 2. Two males and two females were randomly chosen as a class of two trials, excluding crabs that formed guarding pairs in the field, before the start of each experimental trial. We placed the two females in a small container (19 x 12 x 7 cm) filling it with natural seawater to a depth of about 3 cm. After the females started becoming active in the container, we added a male into the container and recorded which female the male guarded after five minutes. We also observed whether males showed assessment behavior of both females and/or guarded both females in rotation during the five minutes. Then, we returned the male back to the cylinder, rinsed the container in natural seawater, and added another male into the container after the two females in the container becoming active. Each male was thus used once in the experiment while each female was used twice for the two trials of each class in the experiment. Each crab in a trial occupied a gastropod shell that was identifiable on the basis of gastropod species and morphological features, such as size and color. Guarding pairs in the field were reconstructed in their small containers after the trial, and each female was checked for spawning every day to record the time until spawning. Although the number of replicates of this experiment was 71, the data were almost evenly divided into two categories, large males ($SL > 4.5$ mm, $N = 34$) and small males ($SL < 4.5$ mm, $N = 37$), for the following statistical consideration.

We first analyzed all of our data of experiment 2 with the generalized linear mixed

model (GLMM), with 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). We calculated three parameters as explanatory variables, differences in body size between the large and small females ($DSL_{(LF-SF)}$), differences between the male and the large female ($DSL_{(M-LF)}$), and differences in time until spawning 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, comparison by using Akaike's information criterion (AIC) between the GLMM and GLM, which was the model removed the random effect from the GLMM, showed the index of GLMM (AIC = 85.3) was larger than that of GLM (AIC = 83.3), 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 binomial error distribution and logit link function. Second, males were classified into two categories of large and small males to examine whether there are any differences in their behaviors related to mate choice between the categories. We thus analyzed two datasets by GLM and compared the estimates and significances of the three explanatory variables from two statistical models with each other. We also conducted binomial tests to compensate for our GLM analyses (see Results).

RESULTS

Experiment 1: can guarding males assess and choose another female?

Males initially guarding small females assessed the large females in 5 of 21 replicates, and exchanged their partners with the later introduced large females in 2 of 21 replicates. Significant relationship was found between the occurrence of these male responses and the size difference between the large and small females, $DSL_{(LF-SF)}$, and males assessed and exchanged their mates

only when $DSL_{(LF-SF)}$ was large (Table 1, Figure 1). The solitary large females and the initially guarded small females did not seem to resist the male's assessment behavior, and the males played an active role in mate choice.

Experiment 2: do males choose their mates on the basis of their body size, female body size and/or female receptivity?

Table 2 shows the results of the analysis with the GLM. The probability that the small males chose the large females increased with $DSL_{(LF-SF)}$ (Figure 2) and $DSL_{(M-LF)}$ (Figure 3), and/or with decreasing $DD_{(LF-SF)}$ (Figure 4). No explanatory factors significantly affected the probability that the large males chose the large females in the GLM (Table 2, Figure 5). On the other hand, while the small males guarded large females in 21 of 37 trials (binomial test, $P = 0.511$), the large males guarded large females in 26 of 34 trials (binomial test, $P = 0.003$), indicating that large males consistently had a strong preference for large females, irrespective of $DSL_{(LF-SF)}$ (Figure 5). Small males assessed both females in 4 of 37 trials and large males did in 8 of 34 trials. The males played an active role in mate choice when the males were larger than the large females. However, large females were observed to reject the male's approach when the male and the large female were approximately the same body size or the male was smaller than the large female.

DISCUSSION

We demonstrated here that small males showed a prudent mate choice based on multiple female traits in the hermit crab, *P. middendorffii*, while large males showed a simple preference for large females. Although small and large males did not show a difference in the direction of

preference for large females, the strength of the preference for large females seemed to be stronger in large males than that in small males. Mate preference of small males was not restricted to the preference for large females, but included the preference for short time until spawning. Small males would, therefore, balance their preferences for large females with the preference for receptive females (i.e., shorter time until spawning) in *P. middendorffii*. Some empirical studies have demonstrated that males, irrespective of their competitive dominance, assess both female size and time until molting and sequentially spawning in crustaceans (Manning 1975; Dick and Elwood 1989). To our knowledge, this is the first study to show empirical evidence that inferior (smaller) males choose their mates on the basis of different female traits from those used by superior (larger) males.

Why did the inferior small males show the prudent mate choice based on the multiple female traits in *P. middendorffii*? The high encounter rate with conspecifics and high opportunities for a successful takeover in our species may affect the behaviors related to male mate choice. *P. middendorffii* occurs in high density in our study site (206 crabs / m², calculated from Wada et al. 1995). Male-male competition for mates can be observed in the field and large size advantage in the competition has been demonstrated (Wada et al. 1999). It would benefit inferior small males to prefer mates requiring a shorter time until spawning under such a situation since the risk of losing the female during guarding would increase with guarding duration.

In contrast, large males should benefit to choose large females with high fecundity even when a relatively long time is needed to guard the large females, since their risks of losing the females would be lower than those of small males because of their competitive superiority. Wada et al. (1999) reported that when both large and small *P. middendorffii* males were kept with two females, large males always started guarding earlier than small males. Hume et al. (2002) demonstrated that large males tended to start guarding earlier than small males in the

amphipod *G. pulex*. Thus, the large males would be less discriminatory about female receptivity than small males in these species. This may result from the lower energetic costs for guarding in large males than in small males (Elwood and Dick 1990). Härdling and Kokko (2005) predicted in a theoretical model that inferior males should be more discriminating than superior males under the condition of a high encounter rate with other conspecifics and a high opportunity for a successful takeover.

Many theoretical models of precopulatory guarding assume that males adopt adjustable threshold tactics based either on female size (Fawcett and Johnstone 2003; Härdling et al. 2004) or female receptivity (Grafen and Ridley 1983; Yamamura 1987; Härdling and Kokko 2005). Wada et al. (1999) experimentally demonstrated that males of *P. middendorffii* used adjustable threshold tactics based on female receptivity. Our results further suggest that male *P. middendorffii* could also compare between two females and choose the better female when the male simultaneously encounters two mature females. Goshima et al. (2006) also reported that *P. filholi* males initially guarding females sometimes exchanged their partner with later introduced females. Males of these *Pagurus* species would therefore continue to search for better partners even while guarding females because they occur at high densities and consequently have a high encounter rate with females, and the comparison tactics should increase the male's reproductive success. While assessment and guarding behaviors in male isopods (Manning 1975; Jormalainen and Merilaita 1993) and amphipods (Adams and Greenwood 1983) are composed of holding their mates ventrally, *Pagurus* hermit crab male grasp the shell occupied by a female only with his minor cheliped. This guarding style of *Pagurus* may enable males easily to assess two females simultaneously since they can catch another female with using the major cheliped and/or hold the new female ventrally while simultaneously guarding the initial female. Dick (1992) also showed that males of *G. pulex* are able to hold and assess two females simultaneously and tend to retain new females of higher quality even if this means rejecting the original guarded females. If the comparison tactic, in

addition to adjustable threshold tactic, based on both female size and receptivity is assumed in theoretical modeling of precopulatory guarding, the predictions about mate choice of superior and inferior males might differ from the assumption of adjustable threshold tactics based on either female size or receptivity. Large males may be indiscriminate in relation to the threshold of receptivity for guarding, but may discriminate when comparing receptive females for body size with the initially guarded female. Similar comparison tactics of males were observed in the amphipod, *G. pulex* (Dick and Elwood 1989; Dick 1992).

Small males chose small females when the males were smaller than large females in our results. In the field males pairing with a female sized larger than the male are rare in *P. middendorffii* (Wada et al. 1996). A large female often rejected to be guarded by a smaller male than the female by thrusting the major cheliped forward and driving the smaller male away. Shorter guarding durations than the duration that males aim for might be favored by females in *P. middendorffii*, like in isopods and amphipods because of a number of potential costs of guarding (Jormalainen 1998). On the other hand, females of *P. filholi* induce indirect mate choice by extending their guarding duration to have more opportunity for male-male competition during guarding (Yamanoi et al. 2006; Okamura and Goshima 2010). Sexual conflict over guarding should affect the male mate choice in hermit crabs although we did not assess sexual conflict in this study. Male mate choice would therefore be related with male-male competition, sexual conflict and female mate choice, and further studies are needed to clarify the relationship between these processes of sexual selection.

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279 REFERENCES

280 Adams J, Greenwood PJ. 1983. Why are males bigger than females in precopula pairs of

281 *Gammarus pulex*? Behav Ecol Sociobiol. 13:239-241.

282 Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton University Press.

283 Backwell PRY, Passmore NI. 1996. Time constraints and multiple choice criteria in the

284 sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. Behav Ecol

285 Sociobiol. 38:407-416.

286 Baldauf SA, Kullmann H, Schroth SH, Thünken T, Bakker TCM. 2009. You can't always get

287 what you want: size assortative mating by mutual mate choice as a resolution of sexual

288 conflict. BMC Evol Biol. 9:129.

289 Bel-Venner MC, Dray S, Allaine D, Menu F, Venner S. 2008. Unexpected male choosiness for

290 mates in a spider. Proc R Soc Lond B Biol Sci. 275:77-82.

291 Byrne PG, Rice WR. 2006. Evidence for adaptive male mate choice in the fruit fly *Drosophila*

292 *melanogaster*. Proc R Soc B Biol Sci. 273:917-922.

293 Candolin U. 2003. The use of multiple cues in mate choice. Biol Rev. 78:575-595.

294 Candolin U, Salesto T. 2009. Does competition allow male mate choosiness in threespine

295 sticklebacks? Am Nat. 173:273-277.

296 Dick JT, Elwood RW. 1989. Assessments and decisions during mate choice in *Gammarus pulex*

297 (Amphipoda). Behaviour. 109:235-246.

- 298 Elwood RW, Gibson J, Neil S. 1987. The amorous *Gammarus*: size-assortative mating in *G.*
299 *pulex*. Anim Behav. 35:1-6.
- 300 Elwood RW, Neil SJ. 1992. Assessments and decisions. A study of information gathering by
301 hermit crabs. New York: Chapman and Hall.
- 302 Fawcett TW, Johnstone RA. 2003. Mate choice in the face of costly competition. Behav Ecol.
303 14:771-779.
- 304 Franceschi N, Lemaître J, Cézilly F, Bollache L. 2010. Size-assortative pairing in *Gammarus*
305 *pulex* (Crustacea: Amphipoda): a test of the prudent choice hypothesis. Anim Behav.
306 79:911-916.
- 307 Gibson RM, Langen TA. 1996. How do animals choose their mates? Trends Ecol Evol.
308 11:468-470.
- 309 Goshima S, Kawashima T, Wada S. 1998. Mate choice by males of the hermit crab *Pagurus*
310 *filholi* (Decapoda: Anomura: Paguridae): Do males assess ripeness and/or fecundity of
311 females? Ecol Res. 13:151-161.
- 312 Goshima S, Minouchi S, Yoshino K, Wada S. 2006. Size assortative mating by the hermit crab
313 *Pagurus filholi*. Crust Res, Special number. 6:87-94.
- 314 Grafen A, Ridley M. 1983. A model of mate guarding. J Theor Biol. 102:549-567.
- 315 Härdling R, Kokko H, Elwood RW. 2004. Priority versus brute force: when should males begin
316 guarding resources? Am Nat. 163:240-252.
- 317 Härdling R, Kokko H. 2005. The evolution of prudent choice. Evol Ecol Res. 7:697-715.
- 318 Hazlett BA. 1972. Shell fighting and sexual behavior in the hermit crab genera *Paguristes* and

319 *Calcinus*, with comments on *Pagurus*. Bull Mar Sci. 22:806–823.

320 Hoefler CD. 2007. Male mate choice and size-assortative pairing in a jumping spider, *Phidippus*
321 *clarus*. Anim Behav. 73:943-954.

322 Hume KD, Elwood RW, Dick JTA, Connaghan KM. 2002. Size-assortative pairing in
323 *Gammarus pulex* (Crustacea: Amphipoda): a test of the timing hypothesis. Anim
324 Behav. 64:239-244.

325 Jormalainen V. 1998. Precopulatory mate guarding in crustaceans: male competitive strategy
326 and intersexual conflict. Q Rev Biol. 73:275-304.

327 Jormalainen V, Merilaita S. 1993. Female resistance and precopulatory guarding in the isopod
328 *Idotea baltica* (Pallas). Behaviour. 125:219-231.

329 Manning JT. 1975. Male discrimination and investment in *Asellus aquaticus* (L.) and *A.*
330 *meridianus* Racovitsza (Crustacea: Isopoda). Behaviour. 55:1-14.

331 Minouchi S, Goshima S. 1998. Effect of male / female size ratio on mating behavior of the
332 hermit crab *Pagurus filholi* (Anomura: Paguridae) under experimental conditions. J
333 Crust Biol. 18:710-716.

334 Okamura S, Goshima S. 2010. Indirect female choice mediated by sex pheromones in the
335 hermit crab *Pagurus filholi*. J Ethol. 28:323-329.

336 Parker GA. 1983. Mate quality and mating decisions. In: Mate choice (ed. by P. Bateson), pp.
337 141-166. Cambridge: Cambridge University Press.

338 R Development Core Team. 2009. R: a language and environment for statistical computing
339 [Internet]. Vienna (Austria): R Foundation for Statistical Computing. Available from:
340 <http://www.R-project.org>.

- 341 Roberts JA, Uetz GW. 2005. Information content of female chemical signals in the wolf spider,
342 *Schizocosa ocreata*: male discrimination of reproductive state and receptivity. *Anim*
343 *Behav.* 70:217-223.
- 344 Robinson BW, Doyle RW. 1985. Trade-off between male reproduction (amplexus) and growth
345 in the amphipod *Gammarus lawrencianus*. *Biol Bull.* 168:482-488.
- 346 Sparkes TC, Keogh, PD, Pary AR. 1996. Energetic costs of mate guarding behavior in male
347 stream-dwelling isopods. *Oecologia.* 106:166-171.
- 348 Thompson DJ, Manning JT. 1981. Mate selection by *Asellus* (Crustacea: Isopoda). *Behaviour.*
349 78:178-186.
- 350 Venner S, Bernstein C, Dray S, Bel-Venner M. 2010. Make love not war: when should less
351 competitive males choose low-quality but defendable females? *Am Nat.* 175:650-661.
- 352 Wada S, Goshima S, Nakao S. 1995. Reproductive biology of the hermit crab *Pagurus*
353 *middendorffii* Brandt (Decapoda: Anomura: Paguridae). *Crust Res.* 24:23–32.
- 354 Wada S, Sonoda T, Goshima S. 1996. Temporal size covariation of mating pairs of the hermit
355 crab *Pagurus middendorffii* (Decapoda: Anomura: Paguridae) during a single breeding
356 season. *Crust Res.* 25:158-164.
- 357 Wada S, Tanaka K, Goshima S. 1999. Precopulatory mate guarding in the hermit crab *Pagurus*
358 *middendorffii* (Brandt) (Decapoda: Paguridae): effects of population parameters on
359 male guarding duration. *J Exp Mar Biol Ecol.* 239:289-298.
- 360 Ward JL, McLennan DA. 2009. Mate choice based on complex visual signals in the brook
361 stickleback, *Culaea inconstans*. *Behav Ecol.* 20:1323-1333.
- 362 Yamamura N. 1987. A model on correlation between precopulatory guarding and short

363 receptivity to copulation. J Theor Biol. 127:171-180.

364 Yamanoi T, Yoshino K, Kon K, Goshima S. 2006. Delayed copulation as a means of female
365 choice by the hermit crab *Pagurus filholi*. J Ethol. 24:213-218.

366 Yoshii K, Takeshita F, Wada S. 2009.Reproduction and growth in the hermit crab *Pagurus*
367 *nigrofascia* (Anomura: Crustacea) : Does males incur costs for molting in
368 precopulatory mate guarding? Jpn J Benthol. 64:25-31.

369 Xu J, Wang Q. 2009. Male moths undertake both pre- and in-copulation mate choice based on
370 female age and weight. Behav Ecol Sociobiol. 63:801-808.

371

Figure Captions

Figure 1. Mate replacement in *P. middendorffii* based on difference in body size between introduced larger females and initially guarding smaller females ($DSL_{(LF-SF)}$). The males initially guarding smaller females exchanged their partners with later introduced larger females, and the likelihood to choose the introduced female as a new guarding partner was significantly explained by the relative body size between the larger and smaller females. Solid curve indicates the estimated regression between male response and $DSL_{(LF-SF)}$ from experiment 1 by generalized linear modeling with a logit link function and binomial error distribution. Male response showed as, 0; not changing his partner, 1; holding the new large female, 2; guarding the new large female. The number of replicates was 21. The coefficient of the relationship is given in Table 1.

Figure 2. Male mate choice based on difference in body size between large and small females in small males of *P. middendorffii*. Small males chose large females when the size difference between large and small females ($DSL_{(LF-SF)}$) was larger. Solid curve indicates the regression curve between male mate choice and $DSL_{(LF-SF)}$ estimated by generalized linear modeling. The coefficients of the solid line are shown in Table 2. Two variables, $DSL_{(M-LF)}$ and $DD_{(LF-SF)}$, were treated as constants in the regression curve and mean values in experiment 2 were substituted for the two variables. LF and SF indicate large and small females, respectively. The number of replicates was 37.

Figure 3. Male mate choice based on difference in body size between males and large females in small males of *P. middendorffii*. Small males did not choose large females when the males were smaller than the large females. Solid curve indicates the regression curve between male mate choice and size difference between males and large females ($DSL_{(M-LF)}$) estimated by generalized linear modeling. The coefficients of the solid line are shown in Table 2. Two variables, $DSL_{(LF-SF)}$ and $DD_{(LF-SF)}$, were treated as constants in the regression curve and mean values in experiment 2 were substituted for the two variables. LF and SF indicate large and small females, respectively. The number of replicates was 37.

Figure 4. Male mate choice based on time until spawning in small males of *P. middendorffii*.

Small males chose small females when the time until spawning of small females was shorter than that of large females. Solid line indicates the regression curve between male mate choice and difference in time until spawning between the large and the small females ($DD_{(LF-SF)}$) estimated by generalized linear modeling. The coefficients of the solid line are shown in Table 2. Two variables, $DSL_{(LF-SF)}$ and $DSL_{(M-LF)}$, were treated as constants in the regression curve and mean values in experiment 2 were substituted for the two variables. LF and SF indicate large and small females, respectively. The number of replicates was 37.

Figure 5. Male mate choice based on female body size in large males of *P. middendorffii*.

Although all estimates from generalized linear modeling were not significant, males significantly chose large females in the binomial test ($P = 0.003$).

Table 1. Results of guarding male responses to solitary larger females in the hermit crab *Pagurus middendorffii*. Males initially guarding smaller females exchanged their partners with the later introduced larger females when there were large differences in body size between the larger and smaller females. GLM with binomial error distribution and logit link function to investigate the effects of differences in body size between large and small females ($DSL_{(LF-SF)}$). In bold are P values less than 0.05. Residual deviance was 18.8 on 19 df , and AIC was 26.92.

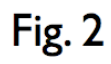
Explanatory variables	Estimate	SE	Z	P
Intercept	-6.514.	2.255	-2.889	0.004
$DSL_{(LF-SF)}$	5.936.	2.376	2.498	0.012

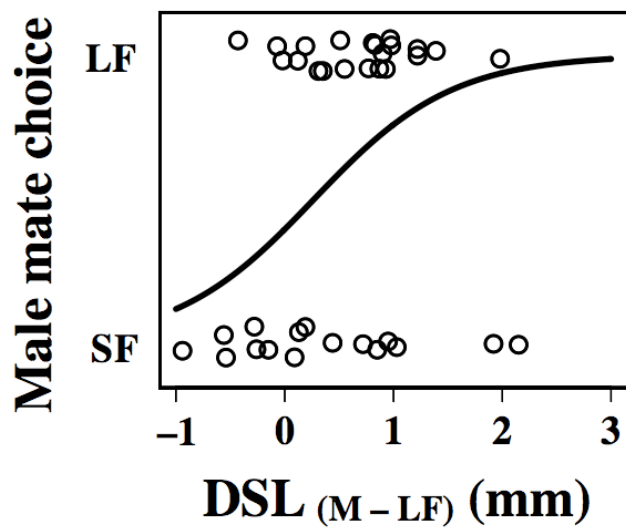
Table 2. Results of mate choice of small and large males in the hermit crab *Pagurus middendorffii*. GLM with binomial error distribution and logit link function to investigate the effects of differences in body size between large and small females ($DSL_{(LF-SF)}$) and between a focal male and the large female ($DSL_{(M-LF)}$) and difference in time until spawning between the large and the small females ($DD_{(LF-SF)}$). In bold are *P* values less than 0.05. Residual deviance of small and large males were 37.3 and 33.8 on 33 and 30 *df*, and AICs were 45.28 and 41.79, respectively.

Explanatory variables	Estimate	SE	Z	P
Small male				
Intercept	-1.315	0.825	-1.594	0.111
$DSL_{(LF-SF)}$	1.817	0.871	2.086	0.037
$DSL_{(M-LF)}$	1.566	0.745	2.103	0.036
$DD_{(LF-SF)}$	-1.157	0.538	-2.149	0.032
Large male				
Intercept	-0.358	2.895	-0.124	0.902
$DSL_{(LF-SF)}$	1.533	1.300	1.179	0.239
$DSL_{(M-LF)}$	0.273	0.841	0.325	0.745
$DD_{(LF-SF)}$	-0.312	0.337	-0.925	0.355

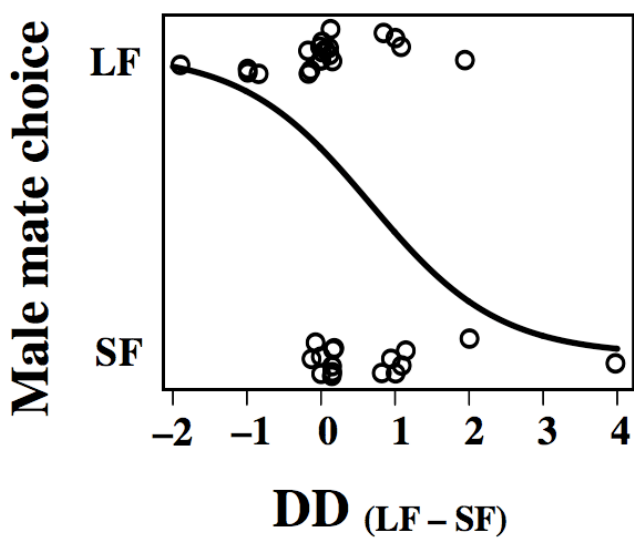


437





438 Fig. 3



439 Fig. 4

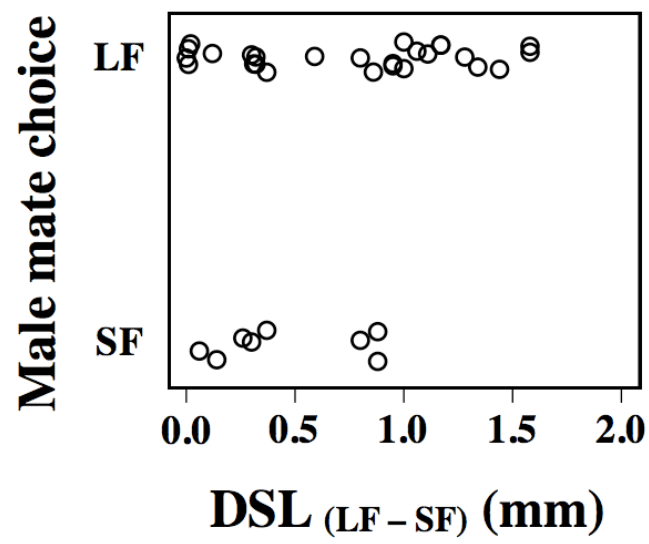


Fig. 5

From Wada S, Arashiro Y, Takeshita F, Shibata Y, 2010. Male mate choice in hermit crabs: prudence by inferior males and simple preference by superior males. *Behav Ecol* 19: 10.1093/beheco/arq183:

Mate characters being attractive to one individual may not be attractive to others. Across animals, males compete with one another over prospective mates. Superior and inferior males may have different preferences for a prospective mate in such animals. Males of many hermit crabs are known to engage in so called 'precopulatory guarding', where males grasp the gastropod shells housing sexually mature females with their minor chela, over the period until female breeding. Larger males are stronger in male-male competition during guarding in hermit crabs. In this study, we clarify that male hermit crabs are able to seek potentially more fecund mates even during guarding. We show that small, inferior males have a more prudent mate preference than large, superior males in the hermit crab. When a male encounters two mature females at the same time, small males choose their mates by balancing female characters between larger body size and length of time until breeding, while large males simply choose the larger females. The difference in mate preference exhibited by large and small males would be an adaptive response to the size-dependent risk of losing the female during guarding.