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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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8   Short title: Male mate choice of hermit crab

9

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

INTRODUCTION

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

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

56   during precopulatory guarding behavior in crustaceans (Manning 1975; Thompson and

57   Manning 1981; Elwood et al. 1987; Dick and Elwood 1989; Goshima et al. 1998, 2006;

58   Franceschi et al. 2010). If male mate choice is conducted on the basis of multiple female traits,

59   inferior males may choose their mate on the basis of different female traits from those used by

60   superior males.

61   Males of *Pagurus* hermit crabs engage in precopulatory guarding behavior during

62   their mating seasons, in which they grasp the aperture of the gastropod shells occupied by

63   sexually mature females with their left (minor) chela, over a period of several days (Hazlett

64   1972; Elwood and Neil 1992; Wada et al. 1995). Males directly compete for females during

65   guarding, and larger and/or owner males tend to be stronger competitors than smaller and/or

66   unsuccessful challenger males (Wada et al. 1999; Goshima et al. 2006; Y. Suzuki et al.

67   unpublished). Wada et al. (1999) demonstrated in a laboratory experiment that male *P.*

68   *middendorffii* could assess females on the basis of time until spawning and adjust the threshold

69   for guarding according to social factors, such as sex ratio, competitor size and encounter rate

70   with females. Although long guarding duration would be beneficial for males to acquire their

71   potential mates, there should be some costs associated with mate guarding, including loss of

72   other mating opportunities (Wada et al. 1999) and restricted feeding during guarding (Yoshii et

73   al. 2009). Energetic costs may also be substantial for males dragging the shells occupied by

74   females, similar to the energy expenditure by males of *Gammarus* amphipods (Adams and

75   Greenwood 1983; Robinson and Doyle 1985; Elwood and Dick 1990; but see Sparkes et al.

76   1996; Yoshii et al. 2009). On the other hand, female fecundity increases with body size in *P.*

77   *middendorffii* (Wada et al. 1995). Large and small males of *P. middendorffii* may, therefore,

78   make different decisions in determining their partners. Size assortative pairing is observed in

79   this species (Wada et al. 1996), and there are no tendencies that larger females are more

80   receptive, i.e., shorter time until spawning (S. Wada, unpublished), unlike some crustaceans

81   (Manning 1975). Guarding males of *P. middendorffii* are usually nearly double the body length

82   of their partners (Wada et al. 1996), and females of this species do not actively resist male

83   guarding attempts when the male is larger than the female (see Results).

84   Aims of this study are to examine (1) whether male *P. middendorffii* initially

85   guarding smaller females exchange their partners when a male encounters a larger receptive

86   female, and (2) whether large and small males choose females as potential mates on the basis of

87   body size and/or time needed for guarding (time until spawning) when a male simultaneously

88   encounters two females. Theoretical models implicitly assume that guarding males do not

89   exchange partners even when they encounter females with higher quality than those they are

90   guarding. However, males initially guarding smaller females have been observed to change their

91   partners to later introduced larger females in the amphipod *G. pulex* (Dick 1992) and the hermit

92   crab *P. filholi* (Goshima et al. 2006). Since no studies present statistical evidence for the

93   hypothesis that males assess and choose better partners even while guarding females, we here

94   test the hypothesis in experiment 1. We then examine mate choice by large and small male

95   (experiment 2), and compare the strength and the direction of mate preferences between large

96   and small males in Discussion.

97

98   **MATERIALS AND METHODS**

99   We collected precopulatory guarding pairs of *P. middendorffii* during low tides from 12 to 16

100   November 2008 at Kattoshi, southern Hokkaido, Japan (41°N, 140°E), since the mating season

101   of this species is from late October to early December in our study site (Wada et al. 1995). Each

102   pair was placed in a small vinyl pouch with some seawater in the field and brought back to the

103   laboratory. After collecting pairs, we also filled several tanks (20 liter) with seawater in the

104   field, took the tanks to the laboratory and used for our experiments. After placing each pair in a

105   small container (19 x 12 x 7 cm) with some natural seawater for about an hour, we checked

106   whether the male still guarded the female. We excluded the males and females that were no

107   longer in guarding pairs from the following procedures because they had already copulated.

108   Mate choice experiments were conducted within five hours after sampling, and all crabs were

109   measured for shield length (the calcified anterior portion of carapace, hereafter SL) to the

110   nearest 0.01 mm under a stereoscopic microscope after the experiments. We used the statistical

111   software, R version 2.9.0 (R Development Core Team, 2009) for all statistical analysis.

112

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

114   Pairs collected on 16 November were used for the experiment. We first selected relatively large

115   females (mean SL ± sd = 2.60 ± 0.48 mm, max. = 3.35 mm, min. = 1.63 mm) from samples, and

116   placed them individually in a small container (19 x 12 x 7 cm) filling it with the natural

117   seawater to a depth of about 3 cm. After the large solitary female started becoming active in the

118   container, a guarding pair was then placed in the container. The female of the guarded pair

119   (mean SL ± sd = 1.91 ± 0.27 mm, max. = 2.45 mm, min. = 1.41 mm) was always smaller than

120   the solitary female in a container. We observed the behavior of the male crabs for five minutes

121   and recorded whether the males showed assessment behavior, in which the male grasped the

122   aperture of the shell occupied by the solitary female, with the apertures of their shells typically

123   facing one another (Minouchi and Goshima, 1998), and whether the male exchanged their initial

124   guarded partner with the later introduced large female. The number of replicates of this

125   experiment was 21.

126   We analyzed the data with the generalized linear model (GLM) with binomial error

127   distribution and logit link function. The response variable was the occurrence of three types of

128   the male behavior in relation to the solitary large female (i.e., no action = 0, assess = 1,

129   exchange = 2), and explanatory variable was the differences in SL between the solitary large

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

131    $DSL_{(LF - SF)}$.

132

133   **Experiment 2: do males choose their mates on the basis of their body size, female body size**

134   **and/or female receptivity?**

135   Males and females of each guarding pair, collected on 12 and 14 November, were kept

136   individually in polystyrene cylinders (300 ml) for a minimum period of thirty minutes before

137   experiment 2. Two males and two females were randomly chosen as a class of two trials,

138   excluding crabs that formed guarding pairs in the field, before the start of each experimental

139   trial. We placed the two females in a small container (19 x 12 x 7 cm) filling it with natural

140   seawater to a depth of about 3 cm. After the females started becoming active in the container,

141   we added a male into the container and recorded which female the male guarded after five

142   minutes. We also observed whether males showed assessment behavior of both females and/or

143   guarded both females in rotation during the five minutes. Then, we returned the male back to

144   the cylinder, rinsed the container in natural seawater, and added another male into the container

145   after the two females in the container becoming active. Each male was thus used once in the

146   experiment while each female was used twice for the two trials of each class in the experiment.

147   Each crab in a trial occupied a gastropod shell that was identifiable on the basis of gastropod

148   species and morphological features, such as size and color. Guarding pairs in the field were

149   reconstructed in their small containers after the trial, and each female was checked for spawning

150   every day to record the time until spawning. Although the number of replicates of this

151   experiment was 71, the data were almost evenly divided into two categories, large males (SL >

152   4.5 mm, $N = 34$) and small males (SL < 4.5 mm, $N = 37$), for the following statistical

153   consideration.

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

155   model (GLMM), with binomial error distribution and logit link function. The response variable

156   was binary data of whether a male guarded the small female or the large female (i.e., small

157   female = 0, large female = 1). We calculated three parameters as explanatory variables,

158   differences in body size between the large and small females ($DSL_{(LF-SF)}$), differences between

159   the male and the large female ($DSL_{(M-LF)}$), and differences in time until spawning between the

160   large and small females ($DD_{(LF-SF)}$). Factor of class, which was composed of two males and two

161   females, was treated as a random effect in the GLMM. However, comparison by using Akaike's

162   information criterion (AIC) between the GLMM and GLM, which was the model removed the

163   random effect from the GLMM, showed the index of GLMM (AIC = 85.3) was larger than that

164   of GLM (AIC = 83.3), indicating that the latter model is better for explaining our data because

165   the outcome of the two mate choices in a class was independent of each other. We then

166   analyzed our data by GLM with binomial error distribution and logit link function. Second,

167   males were classified into two categories of large and small males to examine whether there are

168   any differences in their behaviors related to mate choice between the categories. We thus

169   analyzed two datasets by GLM and compared the estimates and significances of the three

170   explanatory variables from two statistical models with each other. We also conducted binomial

171   tests to compensate for our GLM analyses (see Results).

172

173   **RESULTS**

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

175   Males initially guarding small females assessed the large females in 5 of 21 replicates, and

176   exchanged their partners with the later introduced large females in 2 of 21 replicates. Significant

177   relationship was found between the occurrence of these male responses and the size difference

178   between the large and small females, $DSL_{(LF-SF)}$, and males assessed and exchanged their mates

179   only when $DSL_{(LF-SF)}$ was large (Table 1, Figure 1). The solitary large females and the initially

180   guarded small females did not seem to resist the male's assessment behavior, and the males

181   played an active role in mate choice.

182

183   **Experiment 2: do males choose their mates on the basis of their body size, female body size**

184   **and/or female receptivity?**

185   Table 2 shows the results of the analysis with the GLM. The probability that the small males

186   chose the large females increased with $DSL_{(LF-SF)}$ (Figure 2) and $DSL_{(M-LF)}$ (Figure 3), and/or

187   with decreasing $DD_{(LF-SF)}$ (Figure 4). No explanatory factors significantly affected the

188   probability that the large males chose the large females in the GLM (Table 2, Figure 5). On the

189   other hand, while the small males guarded large females in 21 of 37 trials (binomial test, $P =$

190   0.511), the large males guarded large females in 26 of 34 trials (binomial test, $P = 0.003$),

191   indicating that large males consistently had a strong preference for large females, irrespective of

192    $DSL_{(LF-SF)}$ (Figure 5). Small males assessed both females in 4 of 37 trials and large males did in

193   8 of 34 trials. The males played an active role in mate choice when the males were larger than

194   the large females. However, large females were observed to reject the male's approach when the

195   male and the large female were approximately the same body size or the male was smaller than

196   the large female.

197

198   **DISCUSSION**

199   We demonstrated here that small males showed a prudent mate choice based on multiple female

200   traits in the hermit crab, *P. middendorffii*, while large males showed a simple preference for

201   large females. Although small and large males did not show a difference in the direction of

202   preference for large females, the strength of the preference for large females seemed to be

203   stronger in large males than that in small males. Mate preference of small males was not

204   restricted to the preference for large females, but included the preference for short time until

205   spawning. Small males would, therefore, balance their preferences for large females with the

206   preference for receptive females (i.e., shorter time until spawning) in *P. middendorffii*. Some

207   empirical studies have demonstrated that males, irrespective of their competitive dominance,

208   assess both female size and time until molting and sequentially spawning in crustaceans

209   (Manning 1975; Dick and Elwood 1989). To our knowledge, this is the first study to show

210   empirical evidence that inferior (smaller) males choose their mates on the basis of different

211   female traits from those used by superior (larger) males.

212   Why did the inferior small males show the prudent mate choice based on the multiple

213   female traits in *P. middendorffii*? The high encounter rate with conspecifics and high

214   opportunities for a successful takeover in our species may affect the behaviors related to male

215   mate choice. *P. middendorffii* occurs in high density in our study site (206 crabs / m^2, calculated

216   from Wada et al. 1995). Male-male competition for mates can be observed in the field and large

217   size advantage in the competition has been demonstrated (Wada et al. 1999). It would benefit

218   inferior small males to prefer mates requiring a shorter time until spawning under such a

219   situation since the risk of losing the female during guarding would increase with guarding

220   duration.

221   In contrast, large males should benefit to choose large females with high fecundity

222   even when a relatively long time is needed to guard the large females, since their risks of losing

223   the females would be lower than those of small males because of their competitive superiority.

224   Wada et al. (1999) reported that when both large and small *P. middendorffii* males were kept

225   with two females, large males always started guarding earlier than small males. Hume et al.

226   (2002) demonstrated that large males tended to start guarding earlier than small males in the

227 amphipod *G. pulex*. Thus, the large males would be less discriminatory about female receptivity

228 than small males in these species. This may result from the lower energetic costs for guarding in

229 large males than in small males (Elwood and Dick 1990). Härdling and Kokko (2005) predicted

230 in a theoretical model that inferior males should be more discriminating than superior males

231 under the condition of a high encounter rate with other conspecifics and a high opportunity for a

232 successful takeover.

233   Many theoretical models of precopulatory guarding assume that males adopt

234 adjustable threshold tactics based either on female size (Fawcett and Johnstone 2003; Härdling

235 et al. 2004) or female receptivity (Grafen and Ridley 1983; Yamamura 1987; Härdling and

236 Kokko 2005). Wada et al. (1999) experimentally demonstrated that males of *P. middendorffii*

237 used adjustable threshold tactics based on female receptivity. Our results further suggest that

238 male *P. middendorffii* could also compare between two females and choose the better female

239 when the male simultaneously encounters two mature females. Goshima et al. (2006) also

240 reported that *P. filholi* males initially guarding females sometimes exchanged their partner with

241 later introduced females. Males of these *Pagurus* species would therefore continue to search for

242 better partners even while guarding females because they occur at high densities and

243 consequently have a high encounter rate with females, and the comparison tactics should

244 increase the male's reproductive success. While assessment and guarding behaviors in male

245 isopods (Manning 1975; Jormalainen and Merilaita 1993) and amphipods (Adams and

246 Greenwood 1983) are composed of holding their mates ventrally, *Pagurus* hermit crab male

247 grasp the shell occupied by a female only with his minor cheliped. This guarding style of

248 *Pagurus* may enable males easily to assess two females simultaneously since they can catch

249 another female with using the major cheliped and/or hold the new female ventrally while

250 simultaneously guarding the initial female. Dick (1992) also showed that males of *G. pulex* are

251 able to hold and assess two females simultaneously and tend to retain new females of higher

252 quality even if this means rejecting the original guarded females. If the comparison tactic, in

253 addition to adjustable threshold tactic, based on both female size and receptivity is assumed in

254 theoretical modeling of precopulatory guarding, the predictions about mate choice of superior

255 and inferior males might differ from the assumption of adjustable threshold tactics based on

256 either female size or receptivity. Large males may be indiscriminate in relation to the threshold

257 of receptivity for guarding, but may discriminate when comparing receptive females for body

258 size with the initially guarded female. Similar comparison tactics of males were observed in the

259 amphipod, *G. pulex* (Dick and Elwood 1989; Dick 1992).

260   Small males chose small females when the males were smaller than large females in

261 our results. In the field males pairing with a female sized larger than the male are rare in *P.*

262 *middendorffii* (Wada et al. 1996). A large female often rejected to be guarded by a smaller male

263 than the female by thrusting the major cheliped forward and driving the smaller male away.

264 Shorter guarding durations than the duration that males aim for might be favored by females in

265 *P. middendorffii*, like in isopods and amphipods because of a number of potential costs of

266 guarding (Jormalainen 1998). On the other hand, females of *P. filholi* induce indirect mate

267 choice by extending their guarding duration to have more opportunity for male-male

268 competition during guarding (Yamanoi et al. 2006; Okamura and Goshima 2010). Sexual

269 conflict over guarding should affect the male mate choice in hermit crabs although we did not

270 assess sexual conflict in this study. Male mate choice would therefore be related with male-male

271 competition, sexual conflict and female mate choice, and further studies are needed to clarify

272 the relationship between these processes of sexual selection.

273

277   current laws of Japan.

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371

372   **Figure Captions**

373   Figure 1. Mate replacement in *P. middendorffii* based on difference in body size between

374   introduced larger females and initially guarding smaller females (DSL $_{(LF \text{-} SF)}$). The

375   males initially guarding smaller females exchanged their partners with later

376   introduced larger females, and the likelihood to choose the introduced female as a

377   new guarding partner was significantly explained by the relative body size between

378   the larger and smaller females. Solid curve indicates the estimated regression

379   between male response and DSL $_{(LF \text{-} SF)}$ from experiment 1 by generalized linear

380   modeling with a logit link function and binomial error distribution. Male response

381   showed as, 0; not changing his partner, 1; holding the new large female, 2; guarding

382   the new large female. The number of replicates was 21. The coefficient of the

383   relationship is given in Table 1.

384

385   Figure 2. Male mate choice based on difference in body size between large and small females in

386   small males of *P. middendorffii*. Small males chose large females when the size

387   difference between large and small females (DSL $_{(LF - SF)}$) was larger. Solid curve

388   indicates the regression curve between male mate choice and DSL $_{(LF - SF)}$ estimated

389   by generalized linear modeling. The coefficients of the solid line are shown in Table

390   2. Two variables, DSL $_{(M - LF)}$ and DD $_{(LF - SF)}$, were treated as constants in the

391   regression curve and mean values in experiment 2 were substituted for the two

392   variables. LF and SF indicate large and small females, respectively. The number of

393   replicates was 37.

394

395   Figure 3. Male mate choice based on difference in body size between males and large females

396   in small males of *P. middendorffii*. Small males did not choose large females when

397   the males were smaller than the large females. Solid curve indicates the regression

398   curve between male mate choice and size difference between males and large

399   females (DSL $_{(M - LF)}$) estimated by generalized linear modeling. The coefficients of

400   the solid line are shown in Table 2. Two variables, DSL $_{(LF - SF)}$ and DD $_{(LF - SF)}$, were

401   treated as constants in the regression curve and mean values in experiment 2 were

402   substituted for the two variables. LF and SF indicate large and small females,

403   respectively. The number of replicates was 37.

404

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

406   Small males chose small females when the time until spawning of small females was

407   shorter than that of large females. Solid line indicates the regression curve between

408   male mate choice and difference in time until spawning between the large and the

409   small females ($DD_{(LF-SF)}$) estimated by generalized linear modeling. The

410   coefficients of the solid line are shown in Table 2. Two variables, $DSL_{(LF-SF)}$ and

411          $DSL_{(M-LF)}$, were treated as constants in the regression curve and mean values in

412   experiment 2 were substituted for the two variables. LF and SF indicate large and

413   small females, respectively. The number of replicates was 37.

414

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

416   Although all estimates from generalized linear modeling were not significant, males

417   significantly chose large females in the binomial test ($P = 0.003$).

418

419 Table 1. Results of guarding male responses to solitary larger females in the hermit crab

420 *Pagurus middendorffii*. Males initially guarding smaller females exchanged their

421 partners with the later introduced larger females when there were large differences in

422 body size between the larger and smaller females. GLM with binomial error distribution

423 and logit link function to investigate the effects of differences in body size between

424 large and small females ($DSL_{(LF - SF)}$). In bold are *P* values less than 0.05. Residual

425 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

426

427 Table 2. Results of mate choice of small and large males in the hermit crab *Pagurus*

428 *middendorffii*. GLM with binomial error distribution and logit link function to

429 investigate the effects of differences in body size between large and small females

430 ($DSL_{(LF-SF)}$) and between a focal male and the large female ($DSL_{(M-LF)}$) and difference

431 in time until spawning between the large and the small females ($DD_{(LF-SF)}$). In bold are

432 *P* values less than 0.05. Residual deviance of small and large males were 37.3 and 33.8

433 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
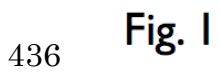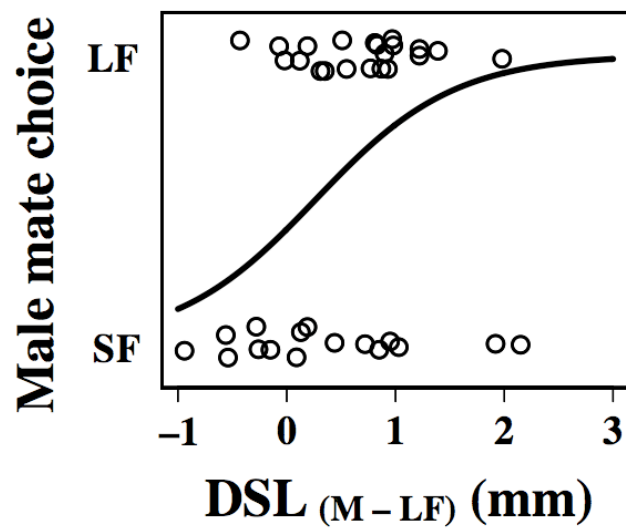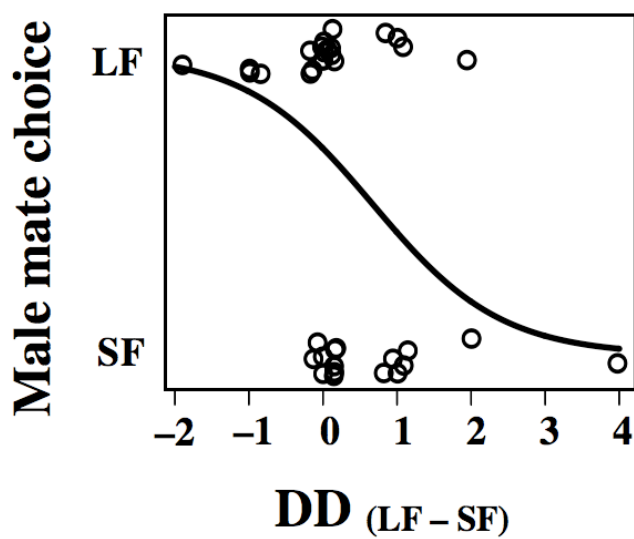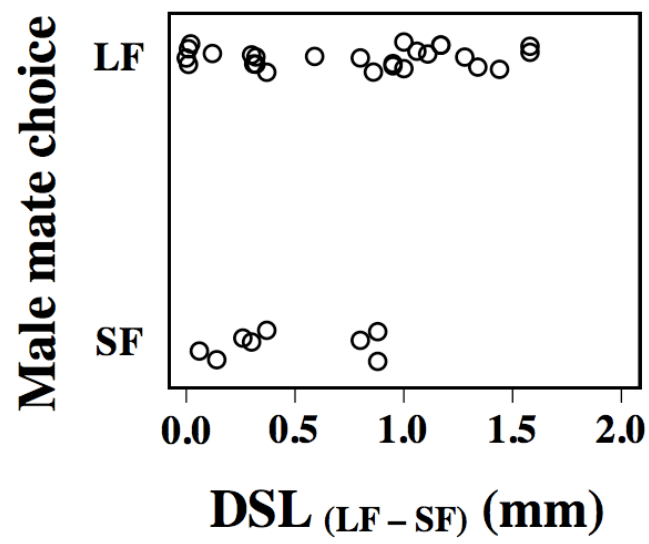
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Fig. 1

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Fig. 2

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Fig. 3

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Fig. 4

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Fig. 5

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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-mele 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.