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Factors affecting the interval between clutches in the hermit crab

Pagurus nigrivittatus

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Running head: Clutch interval of hermit crab

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ABSTRACT: Interval between reproductive events is an important factor for iteroparous animals because it determines the number of clutches throughout life. This study examined whether female size, clutch size, shell size and prenuptial molting affected the clutch interval in the hermit crab *Pagurus nigrivittatus*. Precopulatory guarding pairs of *P. nigrivittatus* were sampled in the field and kept in the laboratory until the female extruded eggs. The clutch interval of each female was assessed as one of two types of relatively "short" and "long" intervals by checking whether the guarded female had eggs and/or egg cases from the preceding brood or not when the guarding pair was collected. The clutch interval was longer in females with prenuptial molting than those without molting and these females usually grew larger at the prenuptial molt. This suggests that female *P. nigrivittatus* with a long interval might allocate energy into growth at the expense of the number of clutches during the current reproductive season. The allocation to growth is theoretically predicted to decrease with female size. Gastropod shell size is also known to affect the reproductive activity in hermit crabs. However, female size did not significantly affect the clutch interval in *P. nigrivittatus,* and the effect of gastropod shell size on clutch interval was not consistent with previous empirical studies. These results may be caused by differences in the gastropod species of shell occupied by the females of *P. nigrivittatus*.

INTRODUCTION

Reproduction carries costs, in terms of growth, survival and future reproduction, because reproduction entails energy and time that could be used for other functions. Reproductive costs have been considered to determine when animals should start to reproduce and how much energy they should devote to each reproductive event (Roff 1992; Stearns 1992). The costs would also affect how long interval individuals should take between successive clutches. The interval is an important determinant of life history evolution for iteroparous animals since it determines the number of clutches throughout their life. Recently, there has been growing interest in the interval between clutches in birds (Verhulst et al. 1997; Møller 2007), reptiles (Doughty and Shine 1998; Harris and Ludwig 2004), fishes (Rideout et al. 2005; Jørgensen et al. 2006) and insects (Forsman 2001). However, few studies have focused on the clutch interval in marine invertebrates although Henmi (2003) suggested a trade-off between clutch size and clutch interval, with considerations on feeding activity, among three fiddler crabs.

For iteroparous animals with indeterminate growth, a critical decision is the amount of energy and time to allocate between growth and reproduction after maturation (Heino and Kaitala 1999). Since clutch size increases with body size in many animals, growth should lead to a future increase in fecundity, although for the immediately ensuing clutch, growth may lead to a reduction in the resources allocated to reproduction. Thus in iteroparous animals with indeterminate growth, after maturation there is a trade-off between growth and the current clutch, even in the absence of survival costs of reproduction. The interval between successive clutches may affect the trade-off. For example, clutch interval would be related to the energetic constraints both in reproduction and growth, and a long interval may realize a larger clutch and/or higher growth rate than a short interval although the long interval will decrease the number of clutches throughout life. Harris and Ludwig (2004) reported that differences in the food level affected

clutch interval in a salamander, and that the female salamanders had higher growth rates when

they skip reproduction; i.e. long intervals between successive reproductive events. The clutch

interval is also related to another trade-off between the numbers of eggs in the successive

clutches (Forsman 2001; Møller 2007). Female grasshoppers producing relatively large clutches

show a greater decrease in the next clutch sizes, and they require a longer interval between these

successive clutches than those breeding small clutches (Forsman 2001). An increased clutch size,

in the latter of successive clutches, or a higher growth rate may be possible at the expense of an

increased clutch interval (Forsman 2001). Thus, considering the trade-off between current and

future reproduction, a female should optimize the clutch interval and, consequently, the number

and size of clutches within a reproductive season. The clutch interval may also depend on body

size. In crustaceans female size is frequently related with clutch size (Hazlett 1981; Goshima et al.

1998; Wada et al. 1995; Nakata and Goshima 2004; Nakata et al. 2004) and growth (Asakura

1992; Wada 2000). Large females breed earlier than small ones in some hermit crabs (Wada et al.

1996; Yoshino et al. 2002), suggesting that energetic and/or time allocation between growth and

reproduction might vary with female size. Therefore, we hypothesize that the clutch interval may

be affected by female size, clutch size and growth in iteroparous crustaceans with indeterminate

growth.

       The clutch interval and resource allocation between growth and reproduction may be

obscured under laboratory rearing condition. Since phenotypic trade-offs can be affected by

energetic and/or time constraints, frequency in detection of various trade-offs differs between

field conditions and "good" conditions in the laboratory (reviewed in Stearns 1992). Laboratory

conditions often include less foods variation, less physical rhythm, such as temperature and tidal

fluxes, than field conditions and no intra- and inter-specific interactions. Although these

environmental factors are also controlled in the laboratory, we need to investigate phenotypic

84   pattern of growth and reproduction in the field before detailed experiments in the laboratory.

85   However, it is difficult to investigate the clutch interval of marine animals in the field because it

86   is hard to observe the successive reproductive events of each individual. Copulation and

87   spawning in many species are short-term events that usually occur under concealment either

88   spatially or temporally and thus precluding direct observation. Especially, observations of

89   reproduction in rocky coastal animals are difficult because of the complex habitat, wave action

90   and tidal changes. It is also difficult to investigate the growth of mobile animals in the field.

91   Since crustaceans cannot readily be tagged and recaptured, the growth rate of individuals is hard

92   to measure with mark-recapture methods (e.g., Carroll 1982; Sharp et al. 2000).

93   Hermit crabs have advantageous characters to study the relationship between clutch

94   interval and growth in the field during a reproductive season. In the reproductive season *Pagurus*

95   hermit crabs show precopulatory guarding behavior in which males grasp the aperture of the shell

96   occupied by a mature female with their left chela during a period of up to several days (e.g.,

97   Hazlett 1972, 1975; Wada et al. 1999). Copulation must precede every clutch production (Hazlett

98   1968; 1996). In the copulation, males transfer and attach some spermatophores to the external

99   surface of the females (Tudge 1999). Females extrude eggs after copulation and fertilize their

100   eggs externally (Contreras-Garduño and Córdoba-Aguilar 2006). The clutch is protected on

101   female pleopods within the gastropod shells until larval hatching, and many *Pagurus* species

102   have several clutches during a reproductive season (Hazlett 1972; Wada 2001; Wada et al. 2000,

103   2005).

104   Clutch interval of each female can be assessed as two types of relatively "short" and

105   "long" intervals by checking whether the guarded female has the preceding eggs on their

106   pleopods or not when the precopulatory guarding pair is collected. The females of short and long

107   clutch interval can be defined as follows: short interval as females in precopulatory guarding

108   pairs that have well-developing eggs and/or empty egg capsules of the last clutch remaining on

109   the pleopods, and long interval as females that have clean pleopods because the empty egg

110   capsules were shed from the pleopods of the female after the last clutch hatching out (Wada et al.

111   2007). Clean pleopods of guarded female mean that (1) the female had rested from breeding for a

112   duration within the reproductive season, (2) this was the first clutch in the reproductive season, or

113   (3) this was the first clutch after maturity. Although (3) should not apply to long interval between

114   clutches as the proportion of virgin females in guarding pairs would be low in our sampling in

115   November (see Materials and Methods).

116   Guarded females sometimes perform a prenuptial molt just before copulation in many

117   *Pagurus* species (Hazlett 1968; Wada et al. 2007). It takes between a few minutes to a few days

118   from the prenuptial molt to copulation, and females extrude their eggs and attach them to their

119   pleopods within an hour after copulation (Hazlett 1968; S. Wada, personal observation).

120   Therefore, many *Pagurus* hermit crabs are iteroparous species with indeterminate growth, and the

121   females can be considered to allocate energy between growth and reproduction during a

122   reproductive season.

123   We examined whether female size, clutch size and prenuptial molting affect the clutch

124   interval in the hermit crab *Pagurus nigrivittatus*. We also investigated the effect of the gastropod

125   shell size on the clutch interval. Hermit crabs typically use gastropod shells to protect their soft

126   abdomen, and shells may be an important environmental factor in determining the allocation

127   between growth and reproduction of hermit crabs (Childress 1972; Fotheringham 1976; Bertness

128   1981a, b; Elwood et al. 1995; Yoshino et al. 2002; Hazlett et al. 2005). Ovigerous females are

129   found in smaller shells than non-ovigerous females in some hermit crabs (Bertness 1981a;

130   Hazlett et al. 2005). Bertness (1981a) suggested that females of hermit crabs might reduce growth

131   and result in allocating more time and energy to reproduction when they occupy small shells.

MATERIALS AND METHODS

Pagurus nigrivittatus Komai 2003 distributes in rocky shores in southern area of Japan, from the Boso Peninsula southward to Kyushu (Komai 2003). Females of *P. nigrivittatus* mature at the smallest size of sympatric congenerics, sometimes perform a prenuptial molt and spawn several clutches from October to June in the study site (Wada et al. 2005).

We sampled guarding pairs of *P. nigrivittatus* during low tides on a rocky intertidal area along coast of Hane-Cape (33°26'N 134°05'E), southern Shikoku, Japan. Sampling was carried out from November 2003 to March 2004. Frequencies of ovigerous females in *P. nigrivittatus* are over 80% from October to June in this area, and the incubation period in October is estimated as less than 20 days (Wada et al. 2005). Therefore, we considered that most females, collected in November, would have finished the first clutch of the reproductive season.

Each pair was placed in a vinyl pouch in the field and brought back to the laboratory. On return to the laboratory we turned over the female, and using a stereoscopic microscope when the female tried to right herself we observed the female's pleopods and checked whether the female of each pair had pleopods with well-developing eggs and/or empty egg capsules or had clean pleopods. Then, each pair was kept in a small container (14 x 9 x 7 cm height) or in a polystyrene cylinder (200 ml) in the laboratory for a week or until the female extruded eggs. If the female did not extrude eggs during the one week period we returned the pair to the sea. Most females extruded eggs by 4 days after collection. We checked daily whether the females had molted or not, and observed the pleopods of females under a stereoscopic microscope to determine whether the females had extruded eggs or not. Pairs were not fed during the rearing period and the seawater was exchanged every two days.

After the females extruded eggs, we counted the number of eggs on the bottom of the

156   container, which had failed to attach to the pleopods, and measured the shell width of the

157   gastropod shell that the female occupied. We fixed the females in 5% seawater formalin, counted

158   the number of eggs attached to their pleopods and measured the shield length (the calcified

159   anterior portion of the cephalothorax) under a stereoscopic microscope. Clutch size was

160   calculated as the sum of the number of dislodged eggs and the number of eggs attached to the

161   pleopods. When a female molted, the shield length of the ecdysis was also measured as the

162   female size. However if the ecdysis was broken or eaten, we used the post-molt shield length for

163   female size.

164   We used a generalized linear mixed model (GLMM) to explore the relationship between

165   clutch interval and the four variables (clutch size, female size, shell size and prenuptial molting

166   (no molting = 0, molting =1)). Sampling date was fitted as a random effect in the model. The

167   clutch interval (long = 0 vs short = 1) was a binary variable, and we specified the error

168   distribution as binomial. Our definitions of relative short and long intervals are however affected

169   by the ovigerous period that varies with temperature (Wada et al. 2005) and to minimize any

170   affects of this, the sampling date was included as a random effect in the model. Since coefficients

171   of determination were low both between clutch size and female size and between shell size and

172   female size (R^2 = 0.16, 0.18, respectively; see Results), multicollinearity was not considered in

173   the analysis. We also examined whether the shield length of female increased or not after the

174   prenuptial molting using the Wilcoxon signed rank test. All statistical analyses were conducted

175   with free statistical software R 2.2.0 (R Development Core Team 2005).

176

177   **RESULTS**

178   We collected 416 guarding pairs of *P. nigrivittatus* during the sampling period, and 384

179   females of these pairs extruded eggs. The mean female size was 1.99 ($\pm$ 0.30SD) mm (min = 1.31,

180 max = 3.12). Clutch size and shell size were linearly regressed against female size (Table 1).

181 Although both regressions had significant positive slopes, the squared Pearson correlation

182 coefficients (i.e., R^2) for these regressions were low.

183 Since, in eleven of the 384 females, the eggs on the pleopods were firmly stuck together

184 and it was not possible to count the number of eggs, we used the 373 females for the following

185 analyses. The clutch interval was significantly related to prenuptial molting, clutch size and shell

186 size (Table 2). Females that carried out a prenuptial molt tended to have a long clutch interval.

187 When the clutch interval was short, clutch size and shell size were larger than those with a long

188 interval (Table 2, Fig. 1, 2). However, there was no significant effect of female size upon the

189 clutch interval (Table 2).

190 Although we observed 182 molts, for 80 ecdysis we were not able to measure the shield

191 length of ecdysis because the crabs ate and/or crushed the shield of carapace of the ecdysis.

192 Growth increment calculated as the difference between the shield lengths after and before

193 prenuptial molt showed a significantly positive value (Wilcoxon test, n = 102, V = 423, P <

194 0.0001). We observed one and five cases for short and long interval with a zero increment,

195 respectively, and eight cases for long interval with negative growth. However, growth increments

196 of 87 females that molted, irrespective of the clutch interval, showed positive values.

197

198 **DISCUSSION**

199 The clutch interval tended to be long when the females performed prenuptial molting in *P.*

200 *nigrivittatus*. On the other hand, many females of *P. nigrivittatus* increased in size at the

201 prenuptial molt. Clutch size was related with female size in this study and larger females

202 produced larger clutches although the regression coefficient was not high. These results suggest

203 that the females conducted the prenuptial molt to grow larger and, consequently, increase their

204   fecundity of future clutches. Prenuptial molts with zero or minus growth tended to be observed

205   when the clutch interval was long. These "non-positive" molts may allow the regeneration of

206   parts of the body or cleaning the exoskelton for protection from ectoparasites to achieve a higher

207   survival rate. We therefore suggest that females of *P. nigrivittatus* might allocate energy into

208   growth and/or survival at the expense of the number of clutches during the current reproductive

209   season. Wada et al. (2007) also found some non-positive molts in the hermit crab *P. minutus*.

210   Theoretical studies have often predicted that allocation to growth decreases with

211   increasing body size, which leads to S-shaped growth curves (e.g. Kozłowski and Uchmanski

212   1987). On the other hand, shell resources are considered to be an important factor in determining

213   the allocation between growth and reproduction in hermit crabs (Betness 1981a, b; Elwood et al.

214   1995; Yoshino et al. 2002; Hazlett et al. 2005). Bertness (1981a) suggested that crabs occupying

215   smaller shells than the optimal reproduce at smaller sizes, reproduce more frequently, have larger

216   clutches, and are unable to grow to larger sizes than crabs occupying optimal sized shells. Hazlett

217   et al. (2005) also demonstrated that females of *Clibanarius vittatus* occupying heavy shells (i.e.

218   larger than optimal size) tended to be not ovigerous and ovigerous females were in shells with

219   optimal size. They suggested that *C. vittatus* females might have a threshold based on the shell

220   size and when the shell size is larger than the threshold size of the females, breeding might be

221   delayed (i.e. long clutch interval) or reproduction is not carried out during the season.

222   Our results seem not to be consistent with these studies. Size of shell occupied by females

223   with a short interval was larger than that occupied by females with a long interval in *P.*

224   *nigrivittatus*. Females with a short interval had larger clutches than those with a long interval in *P.*

225   *nigrivittatus* although females with large clutches are expected to have lengthened the

226   reproductive interval, compared with females with small clutches. Furthermore, while both shell

227   size and clutch size were related to female size, female size did not affect the clutch interval. One

228   possible reason for these results is that gastropod species of shells occupied by females might

229   affect the reproductive activity of the females. Crabs in shells of different species can be

230   differently constrained in terms of available energy and its expenditure because of interspecific

231   differences in shell characters (i.e. shape and weight), and the clutch size has been shown to

232   differ between females occupying shells of different species even if they are of the same size

233   (Bertness 1981b; Elwood et al. 1995). For example, females of *P. bernhardus* in a less preferred

234   species of shell had fewer eggs per clutch and fewer clutches per reproductive season (Elwood et

235   al. 1995). Yoshino et al. (2002) demonstrated that the shell species affected the breeding pattern

236   and that breeding of females in *Reticunassa fraterculus* shells was delayed relative to breeding in

237   other shells although the delay might be due to small crab size. The effects of shell species on

238   female reproduction may be a cause of the low coefficient of determination values between

239   clutch size and female size and between shell size and female size in this study. If the shell

240   species composition for *P. nigrivittatus* differs according to female size, the difference in shell

241   utilization might lead to different energetic allocations between growth and reproduction and

242   might obscure the effect of female size on the clutch interval. Although we did not identify the

243   species of gastropod shell in this study, shell species might be an important factor affecting clutch

244   interval and other life history traits in hermit crabs.

245   Environmental conditions, such as food availability (Harris and Ludwig 2004; Jørgensen

246   et al. 2006) and temperature (Forsman 2001; Møller 2007), are known to affect the clutch interval

247   in some animals. For example, Jørgensen et al. (2006) demonstrated that Atlantic cod skipped

248   spawning more often when food availability was both increased (opportunities for better growth)

249   and decreased (too little energy for gonad development). Female grasshoppers maintained under

250   a warm condition were more likely to oviposit, laid their first clutch earlier, produced more

251   clutches and had shorter intervals between successive clutches than females under a cold

252 condition (Forsman 2001). Møller (2007) found that the duration of the interval between clutches

253 increased during 1971-2005 in a barn swallow because of temperature increase during spring.

254 Global climatic warming may change clutch intervals and consequently alter reproductive

255 potentials in many organisms. The effects of these environmental conditions on reproductive

256 performance of females should also be examined in marine invertebrates.

257 In conclusion, prenuptial molting, clutch size and shell size affected the clutch interval in

258 the hermit crab *P. nigrivittatus*. When females molt just before copulating and breeding, their

259 clutch interval tended to be long, suggesting that females might allocate energy into the

260 prenuptial molt to increase their growth rate and survival rate at the expense of the number of

261 clutches during the current reproductive season. Iteroparous species with indeterminate growth,

262 like hermit crabs, allocate time and energy into growth and reproduction after maturation and the

263 allocation pattern typically depends on the body size. However, female size did not affect the

264 clutch interval in this study, and the effects of clutch size and shell size on clutch interval seemed

265 to differ from some previous studies of hermit crabs. Gastropod species of shells occupied by the

266 females and other environmental conditions might be the cause these differing results. Further

267 field and laboratory investigations are needed to further detail these factors affecting the resource

268 allocation between growth and reproduction in hermit crabs.

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366

Figure captions

367 Fig. 1. A boxplot showing the distributions of clutch size for long and short clutch intervals in the

368 hermit crab *Pagurus nigrivittatus*. The numbers of females with long and short clutch

369 intervals were 305 and 68, respectively. The solid lines inside the boxes represent the

370 medians of the data. The left and right ends of the box represent, respectively, the 1st

371 quartile and 3rd quartile of the data. The horizontal dashed lines extending from each box

372 represent the data inside a range of 1.5 times the interquartile range from the box. The

373 vacant circles represent data points for individuals.

374 Fig. 2. A boxplot showing the distributions of gastropod shell width (mm) for long and short

375 clutch intervals in the hermit crab *Pagurus nigrivittatus*. The numbers of females with

376 long and short clutch intervals were 305 and 68, respectively. The solid lines inside the

377 boxes represent the medians of the data. The left and right ends of the box represent,

378 respectively, the 1st quartile and 3rd quartile of the data. The horizontal dashed lines

379 extending from each box represent the data inside a range of 1.5 times the interquartile

380 range from the box. The vacant circles represent data points for individuals.
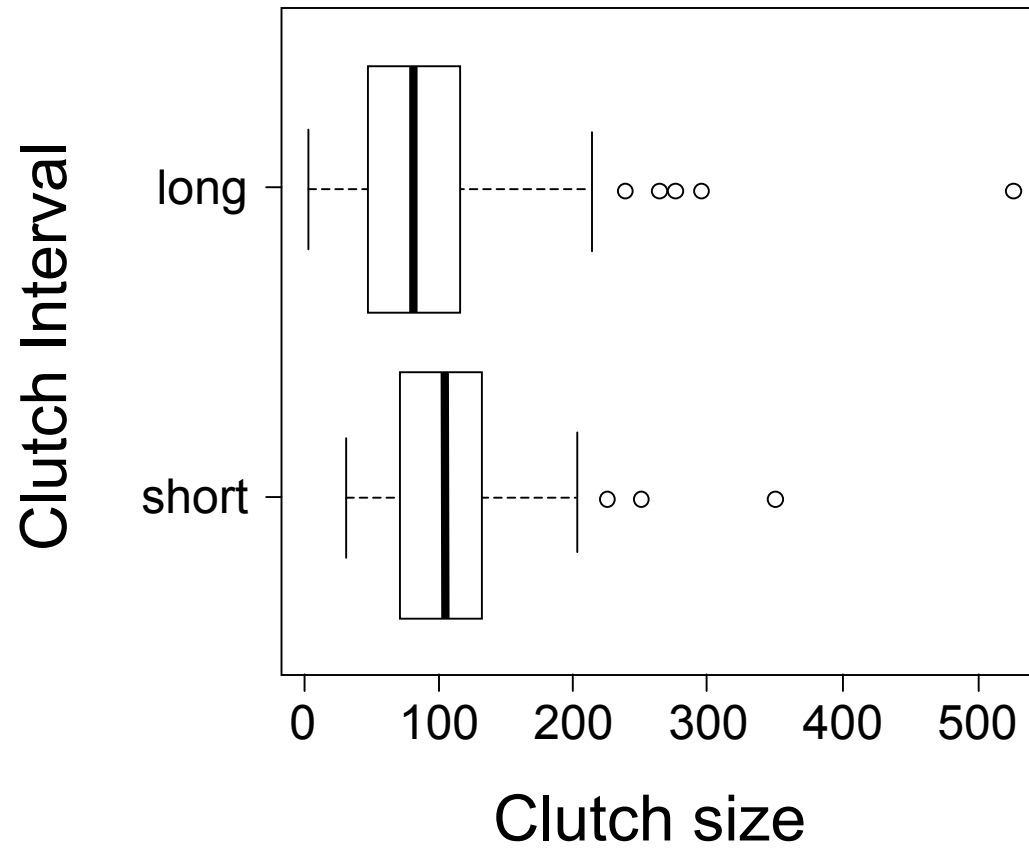
381
382

Fig. 1

Fig. 1. A boxplot showing the distributions of clutch size for long and short clutch intervals in the hermit crab *Pagurus nigrivittatus*. The numbers of females with long and short clutch intervals were 305 and 68, respectively. The solid lines inside the boxes represent the medians of the data. The bottom and top of the box represent, respectively, the 1st quartile and 3rd quartile of the data. The horizontal dashed lines extending from each box represent the data inside a range of 1.5 times the interquartile range from the box. The vacant circles represent data points for individuals.
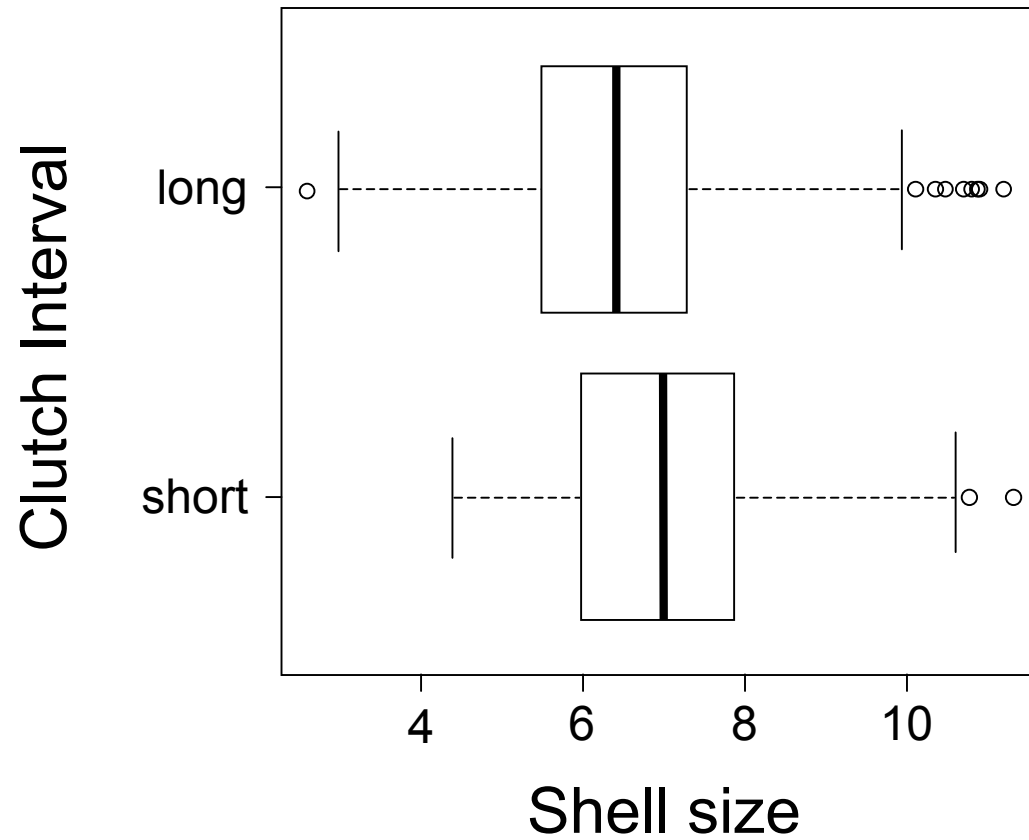
Fig. 2

Fig. 2. A boxplot showing the distributions of gastropod shell width for long and short clutch intervals in the hermit crab *Pagurus nigrivittatus*. The numbers of females with long and short clutch intervals were 305 and 68, respectively. The solid lines inside the boxes represent the medians of the data. The bottom and top of the box represent, respectively, the 1st quartile and 3rd quartile of the data. The horizontal dashed lines extending from each box represent the data inside a range of 1.5 times the interquartile range from the box. The vacant circles represent data points for individuals.

Table 1. Linear regressions of female size on clutch size and shell size in the hermit crab *Pagurus nigrivittatus*.

	Estimate	SE	t	P
(Clutch size)				
Intercept	-65.30	18.83	-3.47	<0.001
Female size	79.11	9.35	8.46	<0.001
Adjusted R^2	0.16			
$F_{1,371}$	71.58			
(Shell size)				
Intercept	2.27	0.49	4.64	<0.001
Female size	2.19	0.24	8.97	<0.001
Adjusted R^2	0.18			
$F_{1,371}$	80.52			

Table 2. Results of the fixed effects in generalized linear mixed model with binomial error distribution for clutch interval in the hermit crab *Pagurus nigrivittatus*. Sampling date was fitted as a random effect in the model. Clutch interval (long and short) and prenuptial molt (molting or not) were coded as two level categorical variables.

Fixed effect	Coefficient	SE	z	P
Intercept	-1.82	1.06	-1.72	0.085
Prenuptial molt	-0.99	0.30	-3.26	0.001
Female size	-0.74	0.55	-1.34	0.179
Clutch size	0.01	0.00	2.01	0.045
Shell size	0.23	0.11	2.10	0.036
Residual deviance	330			
df	367			