Biology

Biology fields

Okayama University   *Year* 2007

Ownership-dependent mating tactics of minor males of the beetle Librodor japonicus (Nitidulidae) with intra-sexual dimorphism of mandibles

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1   Title: Ownership dependent mating tactics of minor males of the beetle *Librodor japonicus*

2   (Nitidulidae) with intra-sexual dimorphism of mandibles

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10

11   Total text pages: 24

12

13   Numbers of tables: 4; Numbers of figures: 1

14

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18

19   **Abstract**

20   Intra-sexual dimorphism is found in the weapons of many male beetles. Different behavioral

21   tactics to access females between major and minor males, which adopt fighting and alternative

22   tactics, respectively, are thought to maintain the male dimorphism. In these species, major males

23   have enlarged weapons that they use in fights with rival males. Minor males also have small

24   weapons in some of these species, and it is unclear why these males possess weapons. We

25   examined the hypothesis that minor males might adopt a fighting tactic when their status was

26   relatively high, compared with other males (e.g., ownership of a territory). We observed the

27   behavioral tactics of major and minor males of the beetle *Librodor japonicus*, whose males have

28   a dimorphism of their mandibles. Major males fought for resources, whereas minor males

29   adopted two status-dependent tactics, fighting and sneaking, to access females, depending on

30   their ownership of a sap site. We suggest that ownership status-dependent mating tactics in

31   minor males may maintain the intra-sexual dimorphism in this beetle.

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33   **Key words** allometry · alternative phenotype · exaggerated trait · male-competition · status

34   dependent selection

Introduction

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36

37 Secondary sexual traits of male beetles such as horns and mandibles sometimes evolve into

38 enlarged weapons (Thornhill and Alcock 1983; Andersson 1994). These exaggerated traits are

39 often used when male beetles fight for limited resources such as food and mates (Eberhard 1979,

40 1980). Expression of weapons, or weapon sizes, varies extensively in populations, and thus

41 defining scaling relationships is an effective way to visualize this variation. These scaling

42 relationships are often non linear in six families of Coleoptera: Cerambycidae, Curculionidae,

43 Leiodidae, Lucanidae, Scarabaeidae and Staphylinidae (Emlen and Nijhout 2000; Eberhard et al.

44 2000; Hanley 2001; Miller and Wheeler, 2005; Tomkins et al. 2005). These relationships have

45 frequently attracted attention in studies of alternative phenotypes, and the major and the minor

46 males adopt strikingly different reproductive tactics based on their status (Eberhard 1982;

47 Thornhill and Alcock 1983; Gross 1996; Shuster and Wade 2003).

48 Generally, the minor males adopt strikingly different behavioral tactics, such as sneaking

49 (Moczek and Emlen 2000; Hunt and Simmons 2001) and using satellite tactics (Eberhard 1982),

50 compared to major males, which fight each other using their enlarged weapons to access

51 females (Thornhill and Alcock 1983; Gross 1996; Hunt and Simmons 2001). In dung beetles of

52 the genus *Onthophagus*, minor males ejaculated more sperm into females and displayed higher

53 maneuverability than major males did (Simmons et al. 1999; Moczek and Emlen 2000). In the

54 scarab beetle *Podischnus agenor*, minor males using satellite tactics arrive at mating sites earlier

55 in the season than major males, and this is thought to raise their probability of mating success

56 (Eberhard 1982). Although minor males first try to fight with their small or rudimentary weapon

57 in several species, they do not gain mating success by fighting because the weapon and body

58 size of larger males strongly affects the outcome of fights (Rasmussen 1994; Emlen 1997;

59 Moczek and Emlen 2000; Pomfret and Knell 2006). In *Onthophagus acuminatu*s and *O. taurus*,

60 minor males first try fighting and then switch to an alternative tactic when that fails (Moczek &

61 Emlen 2000; D. J. Emlen personal observation). Minor males of *Phanaeus difformis* also fight

62 first, and then adopt sneaking tactics later (Rasmussen 1994).

63 Minor males also have weapons, although their weapons are usually smaller than those of

64 major males in many species (Eberhard and Gutierrez 1991; Hanley 2001; Hongo 2003; Knell

65 et al. 2004; Pomfret and Knell 2006).If minor males adopted only non-combatative alternative

66 tactics, they would not be expected to continue to express weapons. This suggests that minor

67 males may sometimes adopt combatative tactics and succeed in fights. To date, only one study

68 has provided empirical support for this: minor males used their horns for fighting like major

69 males and occasionally defeated major males in the scarab beetle *Allomyrina dichotoma*, which

70 shows intra-sexual dimorphism (Hongo 2003).

71   In species with weapons, the fighting tactic should be disadvantageous to minor males

72   compared to major males. However, the ownership of resources (Davies 1978; Jackson and

73   Cooper 1991; Bridge et al. 2000) may alter the outcome of male interactions. Theoretical

74   (Enquist and Leimar 1987) and empirical (Bridge et al. 2000) studies have clarified that

75   asymmetry in the status or resource value of contestants can influence the outcome of fights. In

76   this case, a resident's advantage may permit some minor males to win contests against major

77   males. If true, then minor males may choose a tactic that yields higher fitness according to the

78   ownership status that they are facing. Thus, we propose a hypothesis that the status-dependent

79   choice of fighting or non-fighting tactics by minor males may explain the presence of

80   rudimentary weapons in these animals, which have different values in the secondary allometric

81   relation compared to major males in species with male dimorphism. We use both morphological

82   and detailed behavioral analyses of male-male interactions to examine this hypothesis.

83   The beetle *Librodor japonicus* (Coleoptera: Nitidulidae) is a good model animal to examine

84   the hypothesis. The sexually dimorphic enlarged mandibles are used when males fight for mates,

85   and copulation and male fighting occur readily both on banana slices in the lab, and on sap sites

86   in the field (Okada & Miyatake 2004). Using this beetle has made it possible to acquire

87   extensive combat behavioral data.

88   In the present study, we first statistically characterized male weapon dimorphism for this beetle.

89   We statistically determined a switching point between major and minor males, and used this

90   value to classify all individuals. Second, male interaction behaviors were quantitatively

91   analyzed incorporating the effects of ownership status and weapon size to clarify any behavioral

92   differences between major and minor males, and any differences in tactic that might exist within

93   the minor males. Based on these results, we discuss mechanisms for the maintenance of

94   intra-sexual dimorphism in mandibles of this beetle from ethological viewpoints.

95

96   **Materials and methods**

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98   Beetles

99

100   Adult beetles were collected in the field with banana traps: clear plastic bottles (500 ml)

101   containing fermented banana fruit (35 g). Several traps were placed on the trunks of *Quercus*

102   trees from April to November 2002 and 2003, near Handa-Yama Hill and Mt. Kinkou-Zan, in

103   the southern part of Okayama prefecture (133°54–58′E, 34°33–41′N). Primarily *Quercus glauca*,

104   *Q. serrata*, and *Q. variabilis* grow at these sites. The larvae grow at sap sites, and copulation

105   and male-male fighting occur at sap sites on *Q. variabilis* (Okada and Miyatake 2004). Adults

106   collected in the trap were brought to the laboratory and used for observations of behavior and

107   morphological analysis.

108

109   Observations of behavior

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111   Male interactions were observed using banana fruits as copulation and oviposition sites. A thin

112   circular slice (5 mm thick, 4 cm diameter) of banana fruit placed on filter paper (5 cm diameter)

113   in a plastic cup (7 cm diameter, 2.5 cm high) was used as the arena for combatant males. The

114   observations were made during the scotophase under red light at $25^{o}C$ and 60% relative

115   humidity.

116   One male (resident) and one female were placed in the cup described above, and the male

117   guarded the piece of banana. The next day, another male (intruder) was added to the cup, and he

118   tried to attack the resident male. Two-hundred fifty-two contests were staged in this manner,

119   and each was observed for 30 min. After the observation, all males were dehydrated and

120   preserved for measurement.

121

122   Morphological analysis

123

124   Prothorax and mandible length of 249 males were measured to the nearest 0.01 mm with a

125   dissecting microscopic monitoring system (VM-60 Olympus, Tokyo). We adopted the

126   non-linearity test of Eberhard and Gutierrez's model (1991) to verify the presence of

127   dimorphism. Then, Kotiaho and Tomkins's (2001) modified model was used to classify them

128   into major and minor males.

129   The non-linearity test (Eberhard and Gutierrez 1991) is as follows:

130
$$Y = \alpha_0 + \alpha_1 X + \alpha_2 X^2 + \varepsilon \quad (1)$$

131   where Y is the log to base e of mandible length, X is the log to base e of body size (prothorax

132   length), α_i is the regression coefficient, and ε is the error. If α_2 is significantly different from

133   zero, it is judged that the regression is nonlinear, and the original relationship of mandible

134   length to body size includes more than one linear relationship. In this case, further analysis was

135   performed.

136   To classify males into major and minor morphs, Kotiaho and Tomkins's modified model was

137   used. Their model is:

138
$$x = \beta_0 + \beta_1 y + \beta_2 (y - y^0) D + \beta_3 D + \varepsilon \quad (2)$$

139   where x and y are actual measurement values of body size and mandible length, respectively. y^0

140   is the proposed switch point, $D = 0$ if $y < y^0$, $D = 1$ if $y = y^0$ and $y > y^0$, β_i is the regression

141   coefficient and ε is the error. The switch point y^0 can be found by iterating the y^0 that gives the

142   best fit (highest R^2) for equation (2). If β_3 is significantly different from zero, the distribution of

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143   mandible length becomes discontinuous at the switch point y^0. If only β_2 is significantly

144   different from zero, the linear slope between mandible and prothorax lengths changes at the

145   switch point y^0. If either β_2 or β_3, or both are significant, the relationship between mandible and

146   prothorax lengths is statistically a dimorphism. Individuals that are larger than the switch point

147   (y^0) were classified as major males, and those smaller than the switch point were classified as

148   minor males.

149   In observation of combat between males, 252 contests could be grouped into four types of

150   encounter: major resident vs major intruder (MaR vs MaI), major resident vs minor intruder

151   (MaR vs MiI), minor resident vs major intruder (MiR vs MaI) and minor resident vs minor

152   intruder (MiR vs MiI).

153

154   Statistics

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156   The sequential Bonferroni method (Rice 1989) was applied after the chi-square test to compare

157   the frequencies of male interaction among of the four types of encounters. The chi-square test

158   was used to examine whether the resident or the intruder attacked first, and to compare the

159   frequencies of sneaking and fighting behaviors between major and minor males.

160   To examine which effects, mandible length or ownership status, affected the outcome of male

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161   interactions, multiple logistic regression analysis was used, with the outcome of the interaction

162   (winner = 1, loser = 0) as the dependant variable and mandible length of contestants and

163   ownership status (resident or intruder) as explanatory variables. Overall fit was assessed using

164   the likelihood ratio test statistic and significance with the Wald test (SAS Institute 1998).

165

166   **Results**

167

168   Male dimorphism

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170   Figure 1 shows the relationship between prothorax and mandible lengths in males and the

171   frequency distributions. The test for nonlinearity of the relationship between prothorax and

172   mandible lengths yielded a significant value of α_2 ($t = 2.699$, $P = 0.0074$). Therefore, further

173   analyses were conducted. In equation (2), coefficient β_3 was not significant ($t = 0.454$, $P =$

174   0.6503), but coefficient β_2 was ($\beta_2 = -0.305 \pm 0.048$, $t = -6.337$, $P < 0.0001$). This indicates

175   that the relationship between prothorax and mandible lengths is not discontinuous, but is a

176   dimorphism with a change in the slope at a switch point ($y^0 = 1.61$; $R^2 = 0.920$). Thus, males

177   with a mandible length longer than 1.61 mm were classified as major males and those with a

178   shorter mandible were classified as minor males (Fig. 1). Accordingly, 177 (71.1%) and 72

179   (28.9%) males were assigned major and minor status, respectively.

180

181   Male interactions

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183   Resident males guarded the banana slice as a copulation site, and intruder males approached the

184   resident to invade the banana slice. Male interactions were classified into two levels as follows:

185   1) non-fight, where neither male responded to the opponent with aggressive behavior, or 2) male

186   fight, where either a resident or an intruder male responded to the opponent with aggressive

187   behavior. In the male fight, several types of aggressive behaviors were observed: 1) Attack,

188   where one male responded to the opponent by aggressive behavior, including spreading the

189   mandibles and mounting the opponent. The attacking male bit or pushed his opponent with his

190   mandibles, but the attacked male showed little response. 2) Combat, where two males came into

191   bodily contact and attacked each other. Combat was further classified into three types: a) males

192   faced each other, interlocked their mandibles and shoved each other; b) males repeatedly

193   grabbed each other with the mandibles and pulled, trying to lift the rival off the substrate; c)

194   males opened their mandibles and bit each other. The male that attacked the opponent first was

195   defined as the attacker. The winner was considered the male that pushed his opponent out of the

196   fighting area and then chased him. The loser was the male that retreated from the fight site.

197   A total of 252 male-male interactions were observed. Table 1 shows the occurrence of

198   non-fight and male fight in the four types of male encounters. Male fights were observed

199   significantly more frequently in MaR vs MaI than in the other three types of encounters. Of 252

200   interactions, 88 resulted in a fight, and non-fights were observed in the remaining 164. Of the 88

201   fights in which an attack was observed, resident males were significantly more frequently the

202   attacker than intruder males in all four types of encounter (Table 2).

203

204   Effects of mandible length and ownership status on contests

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206   The outcome of the contest was decided in 88 male fights. The likelihood ratio test statistic by

207   multiple logistic regression analysis was significant, indicating that the regression model fitted

208   the data: mandible length and ownership status affected the probability of winning (Table 3).

209

210   Mating tactics of intruder

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212   Intruder males had two tactics: 1) intruders responded to the resident with aggressive behavior

213   by fighting (fighting tactic), and 2) intruders did not fight the resident but tried to copulate with

214   the female quickly (sneaking tactic). In the latter case, the intruder mounted the female

215   immediately after being introduced into the cup and tried to insert his genitalia into the female.

216   The frequency of sneaking was significantly higher in minor (14.4%, $n = 111$) than major (2.8%,

217      $n = 141$) intruders (Table 4, $\chi_1^2 = 11.393$, $P = 0.0007$). Sneaking behaviors by minor intruders

218   proceeded to copulation in only two cases (Table 4). No reaction was the case in which the

219   intruder male did not respond to a female in a non-fight. No difference was found in the

220   frequencies of no reaction between major and minor intruders (Table 4).

221   On the other hand, the frequency of fighting was significantly lower in minor (9.0%, $n = 111$)

222   than in major (34.8%, $n = 141$) intruders (Table 4, $\chi_1^2 = 22.953$, $P < 0.0001$). No response to

223   attack was the case in which an intruder male did not respond to a resident male and only the

224   resident male attacked the intruder male in a fight. No difference was found in the frequencies

225   of no response to attack between major and minor intruders (Table 4).

226

227   **Discussion**

228

229   Mandibles of *L. japonicus* males showed a continuous type of dimorphism with a switching

230   point dividing males into two morphs: major and minor. This type of dimorphism has been

231   observed in horned beetles, *Onthophagus binodis* (Simmons et al. 1999; Tomkins et al. 2005),

232   *Allomyrina dichotoma* (Hongo 2003), *Euoniticellus intermedius* (Pomfret and Knell 2006), and

233   stag beetles, *Lucanus* species. (Knell et al. 2004). This is the first report of male dimorphic

234   mandibles in Nitidulidae. However, male dimorphism in mandibles has been observed in three

235   families of Coleoptera: Lucanidae (Emlen and Nijhout 2000; Knell et al. 2004), Cerambycidae

236   (Goldsmith 1985) and Staphylinidae (Hanley 2001). Male dimorphism in weapons has been

237   identified in male-male interaction (Eberhard and Gutierrez 1991; Kotiaho and Tomkins 2001).

238   In *L. japonicus*, major males fought in many cases of male-male interactions. The frequency of

239   male fights in the contests between major resident vs major intruder was significantly higher

240   than those in other types of encounters (Table 1), and major intruders fought a resident more

241   aggressively than minor intruders did (Table 4). These data indicate that major males adopt

242   fighting tactics for accessing females regardless of whether they are the resident or the intruder.

243   On the other hand, minor males adopted fighting or sneaking tactics according to their

244   ownership status. Ownership status, i.e., being the resident of or intruder on a resource, was

245   important as the condition. Logistic regression showed that the probability of winning was

246   affected not only by mandible size but also by ownership status (Table 3). Resident males had a

247   greater tendency to attack than intruder males regardless of the morphs of contestants (Table 2).

248   Almost no minor intruder adopted fighting tactics (10 of 111 cases, Table 4), and minor males

249   seldom attacked opponents first when they were intruders (2 of 88 cases, Table 2). No minor

250   intruders won against major residents (0%, $n = 18$). When minor males were residents, however,

251   they were able to win against a major intruder in male fights for the territory in a few cases

252   (18.2%, *n* = 11). Otherwise, minor intruders adopted sneaking behavior to access females (16 of

253   111 case, Table 4), and succeeded in mating in 2 of 16 cases. On the other hand, no major

254   intruder succeeded in mating by the sneaking tactic (0 of 4 cases). The frequency of sneaking by

255   minor intruders was significantly higher than that by major intruders (Table 4). These results

256   indicate that minor males choose fighting and sneaking tactics according to their condition, that

257   is, ownership status. We consider that these status-dependent mating tactics in minor males may

258   maintain the mandible of minor male and the intra-sexual dimorphism in mandibles of the

259   beetle that morphologically divides them from major males.

260   In another species with male dimorphism, both major and minor males of *Allomyrina*

261   *dichotoma* used their horns to appraise the opponent's size (Hongo 2003). Hongo (2003)

262   suggested that even a minor male engages in male fights if he perceives that the size asymmetry

263   between his opponent and himself is small during this appraising behavior. Although some

264   minor males of *A. dichotoma* defeated major males in male fights, most minor males lost to

265   major males. No behavioral difference between major and minor males was observed in male

266   interactions of *A. dichotoma* (Hongo 2003). However, Siva-Jothy (1987) reported that minor

267   males arrived earlier at mating sites than major males and thus raised the probability of mating

268   success in *A. dichotoma*. Minor males of *A. dichotoma* also might choose competitive and

269   non-competitive tactics according to their condition.

15

270   In male-dimorphic beetles such as *Onthophagus acuminatu*s and *O. taurus*, minor males have

271   no weapon and major males have enlarged weapons (Emlen 1997; Moczek & Emlen 2000).

272   Emlen (1997) noted the behavioral difference between the male morphs as a difference in what they

273   did after losing a fight: major males moved on to another tunnel, and another contest, whereas minor

274   males stayed near the original tunnel and tried to slip back in later undetected. The minor males of

275   *Onthophagus acuminatu*s and *O. taurus* never defeated major males in fight because the

276   outcome of fights was influenced weapon and body size but not ownership (Emlen 1997;

277   Moczek & Emlen 2000; D. J. Emlen personal observation). The minor males would not be

278   expected to continue to express weapons, and this would explain the absence of horns in the

279   minor males of the *Onthophagus* species (D. J. Emlen personal communication).

280   In conclusion, the status-dependent mating tactics in minor males may maintain the

281   dichotomous difference in the morphs of males in *L. japonicus* and in the other beetles in which

282   both major and minor males have weapons.

283   As another possibility, mandibles of minor male of *L. japonicus* might be used for boring the

284   bark of *Quercus* oak trees. In the laboratory, males of *L. japonicus* bore branches of oak with

285   their mandibles (K. Okada personal observation). Several insects that feed on sap, such as

286   *Allomyrina dichotoma*, wound the barks of trees with their body parts and feed on sap exuding

287   from the wounds (Hongo 2006). It will be intriguing to examine the relationship between

288 bark-boring behavior in *L. japonicus* and the quantity of sap exuding from the wound.

289

290 **Acknowledgements**

291 We thank D.J. Emlen for valuable comments on the manuscript.

292

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Table 1. Frequencies of non-fight and male fight in each encounter

Encounter	n	Non-fight	Male fight	Multiple comparison
Ma R vs Ma I	97	46 (47.4)	51 (52.6)	A
Ma R vs Mi I	67	49 (73.1)	18 (26.9)	B
Mi R vs Ma I	44	33 (75.0)	11 (25.0)	B
Mi R vs Mi I	44	36 (71.8)	8 (18.2)	B
Total	252	164 (65.1)	88 (34.9)	

Values in parentheses are frequencies

The same letters indicate no significant difference between encounters at $P < 0.05$ by chi-square test; the

significance level was corrected by the squential Bonferroni method (Rice 1989).

Table 2. Numbers of attackers among resident and intruder males in each encounter

Encounter	n	Resident	Intruder	P^*
Ma R vs Ma I	51	36	15	< 0.05
Ma R vs Mi I	18	17	1	< 0.001
Mi R vs Ma I	11	9	2	< 0.05
Mi R vs Mi I	8	7	1	< 0.05
Total	88	69	19	< 0.001

[*]Resident males are attackers significantly more frequently than intruder males (chi-square test).

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Table 3. Results of logistic regression analysis on effects of outcome of fight

	Regression coefficient	Odds ratio	Wald χ^2	P
Mandible length	1.317	3.734	12.588	0.0004
Ownership status	1.209	3.350	13.489	0.0002
Likelihood ratio test statistic			15.797	<0.0001

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Table 4. Frequencies of no reaction, sneaking, fighting, and no response to attack by intruder males

	n	Non-fight ($n = 164$)		Male fight ($n = 88$)	
		No reation	Sneaking	Fighting	No response to attack
Major Intruder	141	75	4 (0)	49	13
Minor Intruder	111	69	16 (2)	10	16
χ^2		2.041	11.393	22.953	1.646
P		n.s.	< 0.001	< 0.0001	n.s.

Values in parentheses are the numbers of successful mating.

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Figure legends

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Fig. 1. The relationship between prothorax and mandible length, and their frequency

distributions in *L. japonicus.* The horizontal line is the switch point (1.61 mm) calculated from

Kotiaho and Tomkins's (2001) model. Circles located above the line were classified as major

males, and those below were minor males.

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