1   **Earwig preying on ambrosia beetle: Evaluating predatory process and prey preference**

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6   **Abstract**

7   Earwigs (Dermaptera), such as *Forficula auricularia* L., are important euryphagous predators for

8   a wide variety of prey and can markedly influence the populations of orchard pests. Most previous

9   studies on earwig feeding behavior have not used adult beetles of the prey species; few researchers

10 have focused on prey preference in earwigs. Some fragments of beetle exoskeleton and an earwig adult,

11 *Anisolabella marginalis* (Dohrn), were found in the same cage, where adults of ambrosia beetle,

12 *Euwallacea interjectus* (Blandford), were emerging from the logs of a fig tree infected with

13 *Ceratocystis* canker (fig wilt disease). Thus, *A. marginalis* was suspected of being a predator of

14 *E. interjectus*. To shed light on this issue, in the laboratory, we set up a test arena and observed and

15 recorded behavioral interactions between *A. marginalis* and *E. interjectus*. *E. interjectus* was collected

16 from the logs of fig trees and reared on an artificial diet, along with six different ambrosia beetle

17 species, which were collected from a trap (baited with ethanol) and a fallen maple tree. A series of

18 laboratory experiments demonstrated that *A. marginalis* is actually a predator of *E. interjectus* and

19 other species of ambrosia beetle, indicating its a potential for use in effective pest control in the field.

20 The predators frequently consume and tend to select their prey depending on prey size, rather than sex

21 and beetle species. Furthermore, earwigs have alternative predatory strategies for dealing with seven

22 different species, although they use their forceps to cut the body of most tested beetles.

23 **Keywords**: Anisolabididae, biological control, body size, natural enemy, predator-prey interactions,

24 Scolytinae

1 | INTRODUCTION

Most earwigs are known as euryphagous predators that capture a wide variety of prey (Burton & Burton, 2002). For example, European earwig, *Forficula auricularia* L. (Dermaptera: Forficulidae), has been reported to feeds on eggs and active stages of a wide range of Hemiptera, Lepidoptera, Coleoptera and Diptera in orchards (He et al., 2008; Logan et al., 2017). As a predator, *F. auricularia* can markedly influence the populations of orchard pests, such as woolly apple aphids (Carroll et al., 1985; Mueller et al., 1988; Nicholas et al., 2005; Cross et al., 2015; Dib et al., 2017). In addition, *Doru luteipes* (Scudder) (Dermaptera: Forficulidae) has been reported to prey on a stem borer (*Diatraea saccharalis* (Fabricius) (Lepidoptera: Crambidae)) and a leaf-chewing caterpillar (*Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae)) in Brazilian maize plants (Naranjo-Guevara et al., 2017), and *Anisolabis maritima* (Bonelli) (Dermaptera: Anisolabididae) appears to feed on driftline isopods and amphipods on the east coast of South Africa (Griffiths, 2018). However, few researchers have focused on forage ecology in earwig, and most of the previous studies on its feeding behavior used eggs, larvae and soft-bodied adults of prey species, as mentioned above. Prey preference is an important trait for evaluating different aspects of the feeding ecology of a predator, such as the trophic niche, and trophic adaptations for prey capture (Pekár et al., 2017; Nunes et al., 2019); therefore, the behavioral plasticity in facing different prey is a further key issue in characterizing its ecology.

The ambrosia beetle, *Euwallacea interjectus* (Blandford) (Coleoptera: Curculionidae: Scolytinae), is a secondary wood-boring pest of many tree species such as *Acer negundo* L. in US and *Populus deltoides* Marsh. in Argentina (Samuelson 1981; Landi et al. 2019; Aoki et al. 2019), and a vector of *Ceratocystis ficicola* Kajitani & Masuya (Kajitani, 1999; Kajitani & Masuya, 2011), which is a pathogenic fungus causing wilt disease in fig trees (*Ficus carica* L.) in Japan (Kajitani, 1999; Nitta et al., 2005; Kajii et al., 2013). This vector can promote development of wilt disease, and thus, increase the infestation and mortality rates of fig tree in the field (Morita et al., 2012). In integrated control systems, chemical insecticides have been used to reduce *E. interjectus* populations in fig orchards (Kajitani & Yamanaka, 2001). However, pesticides can have negative effects on the environment and biodiversity (Hong et al., 2009; Stavrinides & Mills, 2009). Specifically, they can affect non-target and beneficial species in unpredictable ways, such as through water contamination and runoff, or via the consumption of food with pesticide residues (Martinou et al., 2014). Earwigs have been shown to play

54   an important part in controlling orchard pests in the absence of chemical insecticides (Nicholas et al.,

55   2005; Cross et al., 2015; Dib et al., 2017). Adopting a non-polluting natural control strategy, and

56   thereby reducing the use of chemical insecticides, is likely to be beneficial to an orchard's other

57   inhabitants, including natural enemies of various pests, such as clerid beetle known as an important

58   predator on many species of bark beetle (Hansen, 1983; Tømmerås, 1988), the root-eating beetle

59   (*Rhizophagus grandis* Gyll.) on the great European spruce bark beetle (*Dendroctonus micans* Kugelann)

60   (Grégoire et al., 1985; Fielding et al., 1991), and other generalist predators (e.g. ladybirds, lacewings

61   and earwigs) (Nicholas et al., 1999). Therefore, there is a need to study the impact of various predators

62   and parasites on *E. interjectus* and other species of ambrosia beetle (Raffa & Dahlsten, 1995).

63   We obtained logs with many pinholes, which were assumably made by *E. interjectus*, of a fig tree

64   infected with *C. ficicola*, collected from Fukuyama, Hiroshima Prefecture, western Japan, and then

65   placed them in an out-door cage at the Higashiyama Campus of Nagoya University (Chikusa, Nagoya),

66   central Japan. On 6 May 2018, we simultaneously found some fragments of beetle exoskeleton and a

67   female earwig (Dermaptera) adult, *Anisolabella marginalis* (Dohrn), in the cage, where the adults of

68   *E. interjectus* were emerging from the logs. There are no reports that *A. marginalis* is a common

69   species in fig orchards and other cultivated areas. In addition, its ecological niche is unknown. Several

70   questions arose in this context: (a) Did the earwig *A. marginalis* prey on the ambrosia beetle

71   *E. interjectus*? (b) If it was a predator, how did it prey on it? (c) Can it prey on other ambrosia beetles?

72   In this context, we investigated the efficiency with which natural enemies prey on ambrosia beetles and

73   evaluate the prey preference of earwig.

74   **2 | METHODS**

75   2.1 | Earwigs and ambrosia beetles

76   At the start of the present study, a female *A. marginalis* earwig, discovered in the cage on 6 May 2018,

77   was initially used (AM1; see Table S1). After the day, no other earwigs, including males, were found in

78   the cage until the end of the study. Considering that adult females are more aggressive predators than

79   males in a different earwig species, *Euborellia annulipes* (Lucus) (Dermaptera: Anisolabididae) (Moral

80   et al., 2017), two other female earwigs of the same species (*A. marginalis*), collected from the field soil

81   at the Nagoya University Campus on June 4, 2018, were also used (AM2 and AM3; see Table S1).

82   There appeared to be no difference in size among the three female earwigs (approximately 2 cm from

83   the head to the tip of the forceps). The single female earwig was kept in a 500 mL beaker (rest area), at

84   the bottom of which folded filter paper was placed. To avoid drying up, a suitable amount of distilled

85   water was added to the filter paper every day. Throughout the experimental period, no food was

86   supplied in the beaker. The indoor temperature and relative humidity were set at 25 °C and 40%−50%,

87   respectively, under natural photoperiodic condition.

88   Since we aimed to compare the feeding behavior of *A. marginalis* among prey with contrasting

89   morphologies, we chose ambrosia beetles with different body sizes. Thus, we used seven species of

90   ambrosia beetles in this experiment (Table 1). *E. interjectus* was collected from logs in a fig orchard in

91   Hiroshima Prefecture and reared on artificial diets with a two-layer structure (Mizuno & Kajimura,

92   2009) in the Forest Protection Laboratory of Nagoya University (Table 1). The other six species were

93   collected from a trap (baited with ethanol) approximately 2 m above the ground and a fallen maple tree

94   (*Acer saccharum* Marsh.), both of which were set up in Nagoya University Forest at Inabu, northeast

95   Aichi Prefecture, central Japan (Table 1). For all prey species, we used newly emerged or flying adult

96   individuals. Before use for each experiment, species, sex and status (alive or dead) of all prey were

97   recorded. For males (♂), only *E. interjectus* (♀&♂), *Scolytoplatypus mikado* (♀&♂), and *S. tycon*

98   (♀&♂) were the targets due to large numbers of available individuals.

99   [Insert Table 1 over here]

100   2.2 | Experimental design

101   This study was performed from 14 May to 1 August 2018, in the Forest Protection Laboratory of

102   Nagoya University (AM1: 96 replications; AM2: 129 replications; AM3: 70 replications; see Table S1).

103   The predation experiment was carried out from 9:00 am to 10:00 pm. Owing to the different numbers

104   of ambrosia beetles collected every day, the test time changed accordingly. The whole predatory

105   process was divided into pre-attacking and attacking durations. Pre-attacking duration was from the

106   start of movement until first contact, whereas attacking duration was from first contact until finishing

107   (leaving exoskeleton; Figures 1 and 2). In the present study, a no-choice test was conducted to assess

108   the potential responses (fundamental niche of food selection) of one earwig to one prey insect (one

109   individual of the tested beetle species, including *E. interjectus*). To evaluate adaptive prey preference

110   (realized niche of food selection), a choice test was established, whereby one earwig was presented

111   with two prey insects from different beetle species.

112 [Insert Figures 1 and 2 over here]

113   From 6 May to 11 May 2018, we performed a preliminary experiment using three different kinds

114 of Petri dish (d = 3, 9, or ≈ 20 cm) as the test arena (AM1: 32 replications; see Table S1). The

115 maximum pre-attacking duration was set to 12 hr. From this preliminary work, we decided that a 9 cm

116 Petri dish and a pre-attacking duration of 1 hr were reasonable in this experiment.

117   For the predation experiments, two cross lines were drawn in trisection of diameter in the center

118 of the filter paper (d = 9 cm) with a pencil (Figure 2). Then, the drawn filter paper was placed in the

119 9 cm Petri dish. *A. marginalis* and a randomly selected ambrosia beetle(s) were moved into the

120 prepared arena and covered with a small Petri dish (d = 3 cm) separately and then released at the same

121 time. The behavioral interactions between them were observed and recorded by a digital video recorder

122 (HDR-CX590V; Sony). The edited video was made using iJianJi Version 3.0 software (IJianJi

123 Corporation, 2017). After a daylong test, the earwig was returned to the artificial beaker nest.

124   If the prey was not attacked and eaten in a time interval of 60 min after release or was ignored by

125 the earwig, the trial was considered to have involved unsuccessful capture, the prey was removed, and

126 the next prey was introduced (Figure 1). The procedure was repeated until the earwig captured the

127 offered prey. For the sake of keeping earwig in a state of starvation, after a daylong successful capture,

128 an interval of at least 1 day was set before the next test day.

129 2.3 | Statistical analyses

130 Statistical analyses were performed using the SPSS version 19.0 software (IBM Corporation, 2010)

131 and R 3.6.0 (R Core Team, 2019). Data except for those from the choice test are presented as

132 mean ± standard deviation. Kruskal–Wallis test was used to evaluate the differences in pre-attack

133 duration and attack duration among tests including different beetle species (alive; n ≥ 5) (Figures 3 and

134 4). We used generalized linear mixed models (GLMMs) to assess the relative importance of body size

135 among them because it contributes the most to the variation of attacking duration and percentage of

136 beetles consumed. Body size, the max body length in Table 1 (e.g., XG♀: 2.6 mm; XC♀: 2.7 mm;

137 XB♀: 3.0 mm), was entered in the model as a fixed effect. Because ambrosia beetles were preyed by

138 different individuals of the predator (earwig♀, 3), the predator was included as a random factor in the

139 model to avoid any variable influence of predator in pseudo replicates. The initial model was described

140 using the equation: *y = x_size + (1|predator)* fit using maximum likelihood (Laplace Approximation)

141   using the Lme4 package in the R (Bates et al., 2014). To examine whether handling time decreased as

142   the number of replications increased, a correlation analysis between attack duration and the number of

143   replications was conducted with a Spearman's correlation using the ggpubr package in R (Ferrari et al.,

144   2005; De Winter et al., 2016). EI♀ and SM♀ were used in the correlation because they had many

145   replications (Figure 4). Comparisons of percentages of beetles consumed according to the success or

146   failure of predation (i.e., a binary variable; eaten = 1 *vs.* not eaten = 0) at baseline were performed for

147   male *vs.* female and alive *vs.* dead with the Mann–Whitney U test. Fisher's exact test was used to

148   analyze the frequency of beetles consumed between two types of prey of different species in the choice

149   test.

150   [Insert Figures 3 and 4 over here]

151   **3 | RESULTS**

152   A total of 295 adults of the ambrosia beetles were used in the present study (Table 1). On the basis of

153   our observations, the predatory process by which earwigs pursue ambrosia beetles consists of the

154   following four steps: (a) walking or staying put, (b) touching the beetle body with its antenna, (c)

155   cutting it with its forceps and (d) eating the contents with its mouth organs, after which it searches for

156   new prey after leaving fragments of exoskeleton behind (Figure 2; see also Appendix S1). However, all

157   of the steps do not necessarily occur. For example, when earwigs preyed on *E. interjectus* (♂), "cutting

158   it with forceps" did not occur. The remains of exoskeleton fragments of ambrosia beetles were often

159   left after the attack, whereas the whole soft body of *E. interjectus* (♂) was completely eaten by earwigs.

160   Besides, an unsuccessful predatory process was also observed; specifically, a few *Xylosandrus brevis*

161   (♀; 3), *E. interjectus* (♀; 3), and *S. mikado* (♀&♂; 8) were touched and cut by earwigs, but the

162   contents of the dismembered beetle bodies were not eaten and instead ignored.

163   For predator and prey in this experiment, the opportunity for contact determines the occurrence of

164   the behavioral interactions between them. Thus, when an earwig accidentally encounters an ambrosia

165   beetle, it contacts it, cuts it, and then eats it. In the no-choice test (one predator to one prey), the median

166   pre-attacking duration was not significantly different among beetle species (Figure 3). Conversely,

167   GLMMs showed that the attacking duration of the earwig was dependent on body size (Table 2).

168   Therefore, the median attacking duration was significantly different among beetle species (Figure 4),

169   which shows the effect of body size (and other factors, such as body resistance and chemical defenses)

170   on handling. The correlation analysis indicated that attack duration was not related to the number of

171   replications (EI♀: AM1, 25 replications, $p = 0.25 > .05$, Rs = 0.24; SM♀: AM1, 18 replications, $p =$

172    $0.22 > .05$, Rs = 0.31).

173   In the no-choice test, *E. interjectus* (♀&♂), *S. mikado* (♀&♂), and *S. tycon* (♀&♂) were used to

174   examine the influence of sex on the predatory rate. All results for the three species showed that sex did

175   not significantly affect the percentage of beetles consumed between females and males (Figure 5). The

176   survival condition, alive or dead, which rely on the movements, such as the chance of encounter, had

177   inconsistent effects on the percentage of beetles consumed. In *E. interjectus* (♀) and *Euwallacea*

178   *validus* (♀), alive beetles were significantly predated on at a higher rate than dead ones. By contrast,

179   the rate did not differ significantly between alive and dead beetles in other species such as *S. mikado*

180   (♀&♂) and *S. tycon* (♀&♂) (Figure 6).

181   [Insert Table 2, Figures 5 and 6 over here]

182   In the choice test (one predator to two preys of different species), two pairs of beetle species,

183   *E. interjectus* (♀)–*X. brevis* (♀) and *E. interjectus* (♀)–*S. mikado* (♀&♂), were offered to the earwig.

184   Figure 7 shows that the order of prey preference was as follows: *X. brevis* (♀) < *E. interjectus* (♀) and

185   *E. interjectus* (♀) < *S. mikado* (♀&♂). In the no-choice test, GLMMs showed that the percentage of

186   beetles consumed (alive) was not significantly different among the whole of the beetle species (AIC =

187   426.5, $Pr(>|z|) = 0.9145 > 0.05$); however, the beetles consumed (alive) was dependent on the body

188   size among *X. brevis* (♀), *E. interjectus* (♀) and *S. mikado* (♀&♂) (Table 2). These results confirm that

189   the particular beetle species significantly influenced the percentage of beetles consumed, suggesting a

190   preference for larger prey.

191   [Insert Figure 7 over here]

192   **4 | DISCUSSION**

193   The series of experiments presented here provide data that support an examination of the hypothesis

194   about predation by earwig. The findings show that *A. marginalis* is actually a predator of *E. interjectus*

195   and other species of ambrosia beetle. This is the first reported case of an earwig preying on an ambrosia

196   beetle. The data presented here indicate that the common species of earwig can be an effective enemy

197   of ambrosia beetles to eat and cut its body, at least in the laboratory, selecting its prey in a manner

198   dependent on prey size, rather than sex and beetle species.

199   According to our observations, earwigs can occasionally attack *E. interjectus* (♂) without forceps

200   and eat the whole body together with the exoskeleton. In addition, the mean duration of attack of

201   *E. interjectus* (♂) (6 min) was the shortest among all the tested species except for *Xylosandrus*

202   *germanus* (♀) (5.57 min) (Figure 4), and the percentage of beetles consumed of *E. interjectus* (♂) was

203   higher than for *E. interjectus* (♀), regardless of whether they were alive or dead (Figure 6). We assume

204   that the soft exoskeleton of *E. interjectus* (♂) provided hardly any protection against an earwig's attack,

205   just like in apple aphids (Carroll et al., 1985; Cross et al., 2015; Dib et al., 2017). Given the particular

206   targeting of *E. interjectus* (♂) as prey, applying a pest control strategy that involves causing an

207   imbalance in the sex ratio (Robinson, 1983; Berec & Bernhauerová, 2016) could be a theoretical

208   solution for decreasing the population size of this species. However, this is probably impracticable

209   because *E. interjectus* has a female-biased sex ratio by nature and male adults mate with female adults

210   before emerging from their tunnels (nests) in fig trees.

211   The relative body sizes of predator and prey play a major role in their relationship in many animal

212   species (Travis et al., 1985; Körner et al., 2017). Figure 6 shows that the percentages of beetles

213   consumed of alive *X. brevis* (♀), *E. interjectus* (♀), and *S. mikado* (♀) and (♂) were 55.6%, 83.1%,

214   51.9%, and 64.7% in the no-choice test, respectively. However, Figure 7 shows that *X. brevis* (♀) and

215   *S. mikado* (♀&♂) were eaten at rates of 16% (4/25) and 100% (4/4) by earwigs because of their

216   smaller and larger body sizes in the choice test, respectively. The difference in prey preference between

217   the non-choice test and the choice test reveals the potential aggressiveness and adaptability of earwig.

218   Specifically, if one predatory earwig is focused on one type of prey, it will instinctively eat or leave the

219   prey. In contrast to this response, if one predatory earwig is focused on two types of prey of different

220   species, it would choose the larger of the two. This principle of behavioral ecology can apply in the

221   case of *E. interjectus* (♀) as shown in Figure 7. Thus, earwigs have alternative predatory strategies,

222   enabling them to gain energy efficiently from prey with diverse characteristics (Mukherjee & Heithaus,

223   2013).

224   Compared with other ambrosia beetle predators (e.g. clerid beetles and root-eating beetles)

225   (Hansen, 1983; Grégoire et al., 1985; Tømmerås, 1988; Fielding et al., 1991; Kenis et al.,

226   2004; Wegensteiner et al., 2015; Khanday et al., 2018) in the wild, the inconvenient truth is that

227   *A. marginalis* cannot fly and instead lives in chambers in debris, crevices, or soil at a depth of 2.5 cm

228   (Burton & Burton, 2002; Nishikawa, 2009), whereas ambrosia beetles inhabit host trees and make short

229   flights to new trees (Ranger et al., 2016). These conflicting habits would be expected to reduce the

230   opportunity for contact between earwigs and ambrosia beetles. However, in this study, a maple tree

231   felled by humans and a fig tree infested with *E. interjectus* were used as sites for collecting ambrosia

232   beetles, both of which may give earwigs occasion to encounter the beetles. First, when maple trees are

233   cut down and fall to the ground, many ambrosia beetles land on them (Maser & Trappe, 1984); earwigs

234   can thus easily encounter beetles on the ground and prey on them. Second, fig trees are often attacked

235   by adult *E. interjectus* in the lower trunk near the ground (Kajii et al., 2013), which also provides

236   earwigs with a good opportunity to encounter this prey. Other natural phenomena could also

237   tend to increase this rate of encounters. For example, after a storm or strong winds, broken branches of

238   trees are strewn on the ground, becoming suitable for boring by beetles and providing an opportunity

239   for earwigs and beetles to encounter each other. In fact, earwigs were sometimes found on tree trunk

240   and in the trap hanging from the tree branches at Nagoya University Forest (our personal observation).

241   In conclusion, our results show that *A. marginalis* is a euryphagous species (generalist) since it

242   consumes ambrosia beetles of seven different species, using alternative predatory strategies based on

243   the relative body size of the beetles. Further studies in the field should explore whether *A. marginalis*

244   has as high a predation efficiency as in the experimental conditions here and how it increases

245   its opportunities to encounter beetles.

246

258 **CONFLICT OF INTEREST STATEMENT**

259 There was no conflict of interest regarding the preparation and submission of this manuscript.

260 **AUTHOR CONTRIBUTION**

261 HK conceived the research. HK and ZRJ discussed and designed the research. ZRJ conducted the

262 experiments and wrote the manuscript. HK supervised and reviewed the research and manuscript.

263 **DATA AVAILABILITY STATEMENT**

264 The data that support the findings of this study are available from the corresponding author upon

265 reasonable request.

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406   **SUPPORTING INFORMATION**

407   Additional supporting information may be found online in the Supporting Information section.

408   Appendix S1. Predatory processes in the present study.

409   Table S1. The number of ambrosia beetles provided for earwig individuals on each date.

410

TABLE 1 Information on the ambrosia beetles used in this experiment

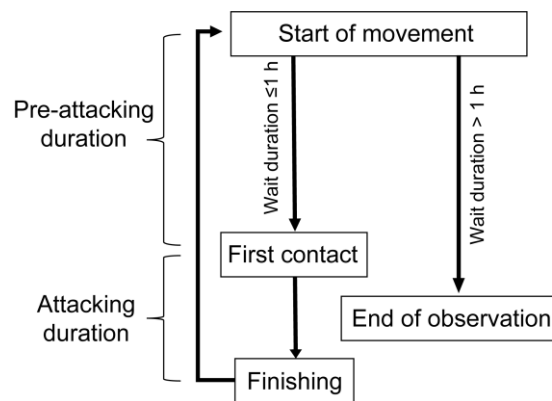| Beetle species	Abbreviation	Sex	Body length (mm)[a]	Collection methods	N	
					No choice/choice	AM1/AM2/AM3
Xylosandrus germanus	XG	♀	2.0–2.6	Trap	13/0	0/13/0
Xylosandrus crassiusculus	XC	♀	2.4–2.7	Maple trees or Trap	6/0	0/6/0
Xylosandrus brevis	XB	♀	2.5–3.0	Maple trees or Trap	21/25	0/28/18
Euwallacea interjectus	EI	♂	2.6–3.0	Rearing artificial diets	8/0	3/5/0
E. interjectus		♀	3.4–3.8	Fig trees or Rearing artificial diets	79/29	31/29/48
Scolytoplatypus mikado	SM	♂	2.9–3.8	Maple trees or Trap	36/1	30/6/1
S. mikado		♀	2.7–4.0	Maple trees or Trap	42/3	32/10/3
Euwallacea validus	EV	♀	3.5–4.1	Trap	6/0	0/6/0
Scolytoplatypus tycon	ST	♂	3.6–4.0	Maple trees or Trap	9/0	0/9/0
S. tycon		♀	3.3–4.5	Maple trees or Trap	17/0	0/17/0
Total					237/58	96/129/70

[a]Hayashi et al., 1984.

412
413

414 **TABLE 2** Summaries of GLMMs with predator as random variable and attacking duration or
415 percentage of beetles consumed as target variable

Parametric coefficients	Estimate/ [a]Variance	Std. Error/ [a]Std. Dev.	Z-value	$Pr(>|z|)$
Attacking duration (AIC = 872.7)				
Fixed effects				
Intercept	−0.01476	0.46382	−0.032	0.975
Body size	0.50924	0.06280	8.109	< 0.001
Random effect				
Predator[a]	0.4655	0.6823	—	—
Percentage of beetles consumed (AIC = 227.3)				
Fixed effects				
Intercept	0.6023	0.3854	1.563	0.118
Body size[b]	0.4829	0.1296	3.725	< 0.001
Random effect				
Predator[a]	0.1417	0.3764	—	—

416 [a]Estimate for the random effect of predator.
417 [b]*X. brevis* (♀), *E. interjectus* (♀) and *S. mikado* (♀&♂).
418

Figure 1 Layout of the predatory processes between predator and prey

419
420 **Figure 1** Layout of the predatory processes between predator and prey

421
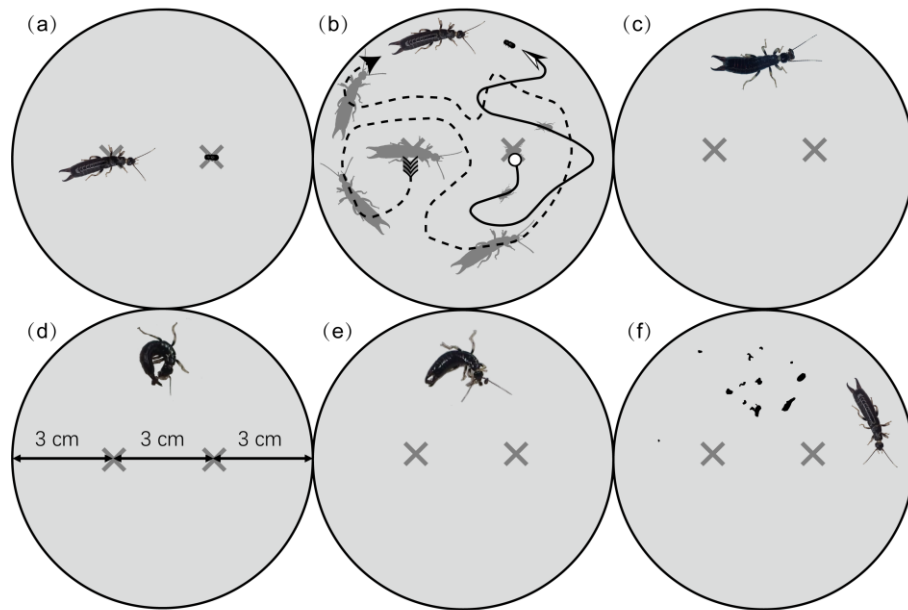
422
423 **Figure 2** Process of earwig preying on ambrosia beetle.
424 (a), Simultaneous release of predator and prey; (b), walking or staying put; (c), touching the beetle
425 body with antenna; (d), cutting it with forceps; (e), eating the contents with mouth organs; (f), finishing
426 (leaving exoskeleton after completion of predation)
427

428
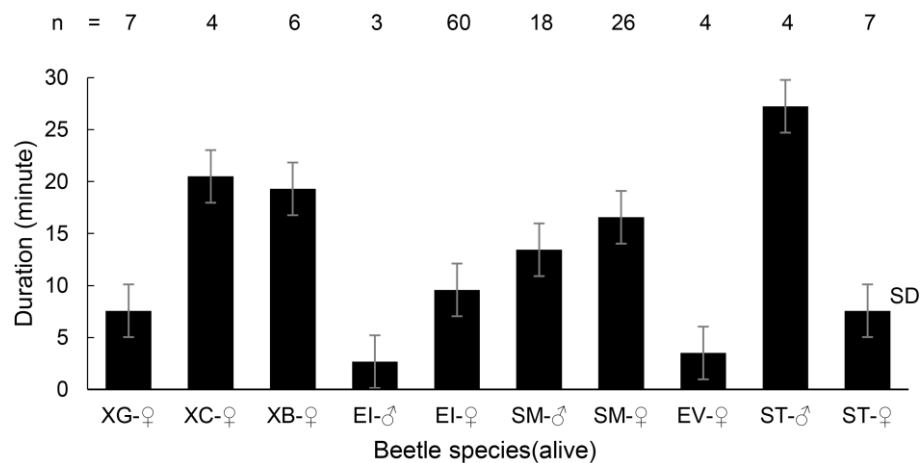
429 **Figure 3** Pre-attack duration in each beetle species in the no-choice test (total n = 139).

430 The overall difference in medians among the species (n ≥ 5) is not significant at $P > .05$ using

431 Kruskal–Wallis test. SD, standard deviation

432
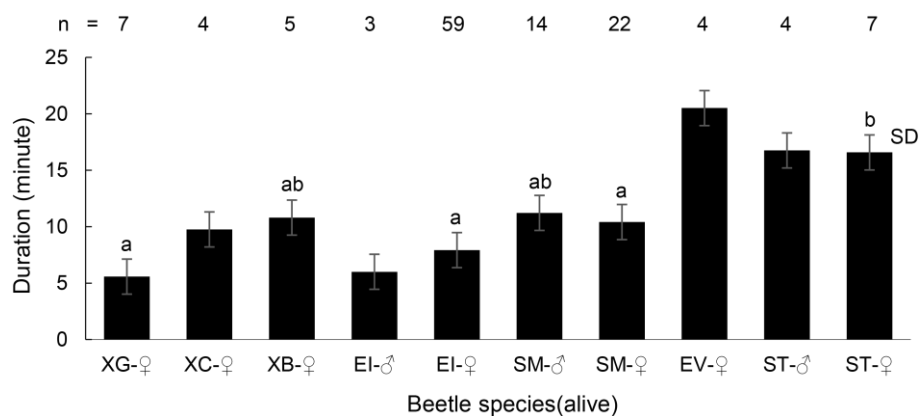
433
434 **Figure 4** Attack duration in each beetle species in the no-choice test (total n = 129).

435 The overall difference in medians among the species (n ≥ 5) is significant at $P < .01$ using

436 Kruskal–Wallis test. Means with different letters (a, b) are significantly different at the 1% level. SD,

437 standard deviation.

438
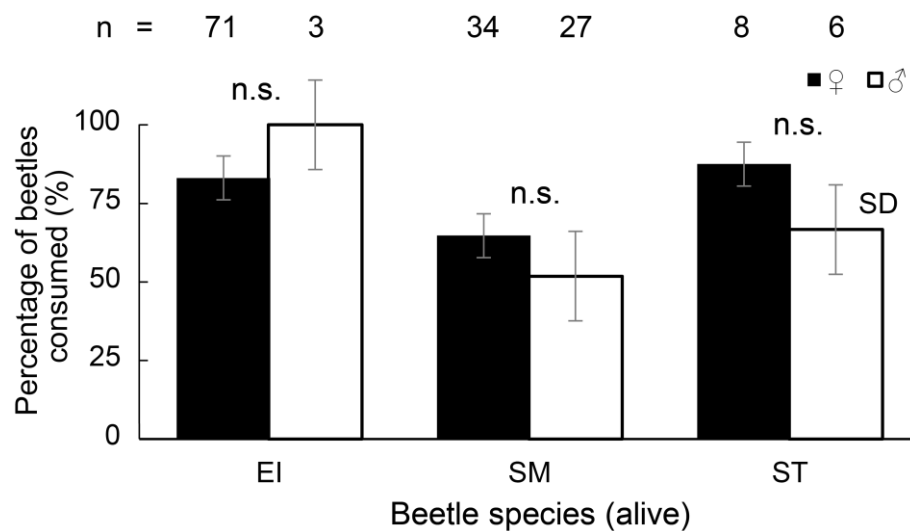
439
440 **Figure 5** Percentage of male and female beetles consumed in each beetle species in the no-choice test
441 (total n = 149).
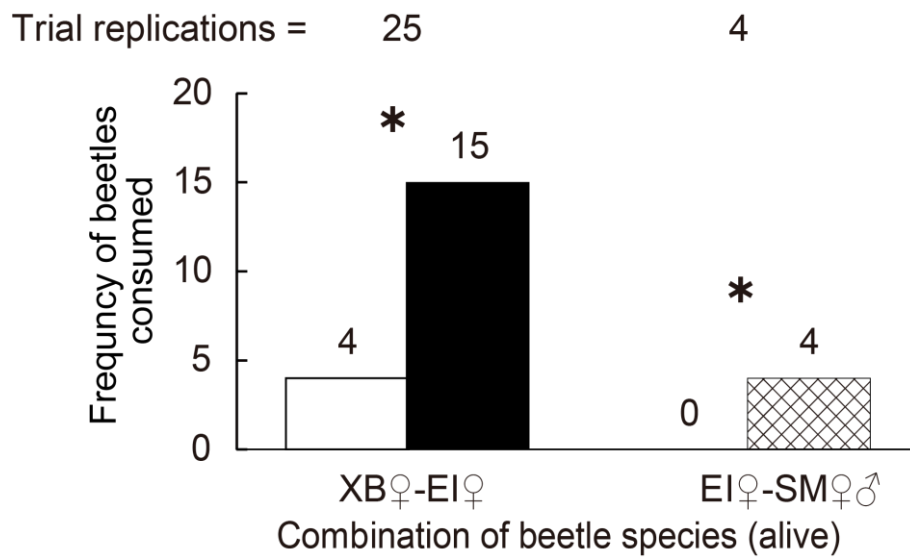442 n.s., not significant at $P > .05$ using Mann–Whitney U test; SD, standard deviation
443

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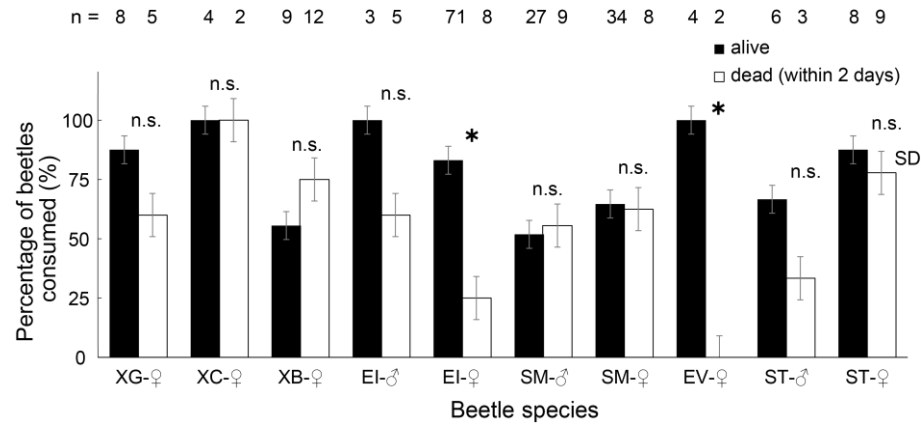
Figure 6 Percentage of alive or dead (within 2 days) cases of beetles consumed in each beetle species
in the no-choice test (total n = 237).

*: Statistically significant at $P < .05$ using Mann–Whitney U test; n.s., not significant at $P > .05$ using
Mann–Whitney U test; SD, standard deviation

450

451
452 **Figure 7** Prey preference between two different species in the choice test (total n = 58).

453 *: Significant at $P < .01$ using Fisher's exact test