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1 **Title: Copy if dissatisfied, innovate if not: contrasting egg-laying decision making**  
2 **in an insect.**

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13  
14 **Abstract:**

15 The use of conspecific cues as social information in decision-making is widespread  
16 among animals, but because this social information is indirect it is error-prone. During  
17 resource acquisition, conspecific cues also indicate the presence of competitors;  
18 therefore, decision-makers are expected to utilize direct information from resources and  
19 modify their responses to social information accordingly. Here, we show that, in a  
20 non-social insect, unattractive egg-laying resources alter the behavioural response to  
21 conspecific cues from avoidance to preference, leading to resource sharing. Females of  
22 the adzuki bean beetle *Callosobruchus chinensis* avoid laying eggs onto beans that  
23 already have conspecific eggs. However, when we provided females with bean-sized  
24 clean glass beads with and without conspecific eggs, the females preferred to add their  
25 eggs onto the beads with eggs. The glass beads, once coated with water extracts of  
26 adzuki beans, enabled the females to behave as if they were provided with the beans:  
27 the females preferred bean-odoured glass beads to clean glass beads and they avoided  
28 the substrates with eggs. When females are provided with unattractive egg-laying  
29 substrates only, joining behavior (i.e. copying) might be advantageous, as it takes  
30 advantage of information about positive attributes of the substrate that the focal animal  
31 might have missed. Our results suggest that given only unsatisfactory options, the  
32 benefits of copying outweigh the costs of resource competition. Our study highlights the  
33 importance of integrating multiple information sources in animal decision-making.

34

35 **Keywords:**

36 Insect cognition, Oviposition, Scent-marking, Seed beetle, Information cascade

37

38 **Introduction**

39 For organisms to survive and reproduce, the acquisition of information about the  
40 environment, thereby reducing uncertainty, is crucial (Schmidt et al. 2011). Information  
41 can be acquired by individuals not only through their own trial and error but also from  
42 conspecific individuals (or their traces); such individuals may have already made  
43 decisions in the same situation (Danchin et al. 2004). It is advantageous for an  
44 individual to rely on such ‘social information’ when trial and error is costly (Dall et al.  
45 2005, Grüter and Leadbeater 2014) or when some benefit is gained from joining with,  
46 or avoiding, conspecifics (Prokopy and Roitberg 2001). Animals, ranging from humans  
47 to invertebrates (reviewed in Danchin et al. 2004; Grüter and Leadbeater 2014), have  
48 been shown to utilize, and benefit from, conspecific cues during decision-making in the  
49 contexts of predator avoidance (reviewed in Chivers and Smith 1998), foraging (birds,  
50 Ward and Zahavi 1973), habitat choice (birds, Betts et al. 2008; lizards, Stamps 1987),  
51 egg-laying substrate choice (insects, Fletcher and Miller 2008; Raitanen et al. 2013;  
52 Golden and Dukas 2014), and mate choice (reviewed in Nordell and Valone 1998;  
53 Westneat et al. 2000).

54

55 Despite the potential advantages accruing from the use of social information, for animal  
56 decision-makers that forage for resources, exclusive reliance on conspecific cues might  
57 be risky. Conspecific cues might reflect poor decisions (Giraldeau et al. 2002; Rieucan  
58 and Giraldeau 2011), and, even when they do not, the act of joining with conspecifics  
59 inevitably results in increased resource competition. Therefore, the information content  
60 of conspecific cues should be evaluated carefully and its importance relative to content  
61 derived from other information sources should be assessed. Even given identical social  
62 information, animals may use the information differently depending on the private  
63 information that is inherent in or acquired by themselves (Czaczkes et al. 2011; Wray et  
64 al. 2011). Previous studies found that animals copy others when private information is  
65 costly (bees, Saleh et al. 2006; fish, Webster and Laland 2008; reviewed in Rieucan  
66 Giraldeau 2011), undesirable (rats, Galef et al. 2008; bees, Wray et al. 2011; bees,

67 Grüter et al. 2013), unreliable (fish, Laland 2004; Rendell et al. 2010), outdated (fish,  
68 Laland 2004; Rendell et al. 2010), or uncertain (fish, Laland 2004; Rendell et al. 2010;  
69 rats, Galef et al. 2008; ants, Czaczkes and Beckwith 2018). These findings suggest that  
70 animals acquire information from multiple sources and integrate them so that they can  
71 make adaptive decisions (Grüter and Leadbeater 2014; Laland 2004).

72

73 In this study, we examined how the attractiveness to potential resources as private  
74 information affects how animals use conspecific cues as social information in their  
75 decision-making. During resource acquisition, the most reliable source of information is  
76 the resources themselves. We investigated egg-laying decisions made by females of the  
77 adzuki bean beetle, *Callosobruchus chinensis*. In laboratory-cultured conditions, the  
78 female beetles lay eggs on the surfaces of beans (Fig. 1) and the hatched larvae burrow  
79 into the beans to feed (Utida 1941). Because the larvae do not move to other beans, the  
80 amount of larval food is predetermined by the decision-making of their mothers. The  
81 females avoid laying eggs on beans when there are already conspecific eggs covered  
82 with scent-marking chemicals (Oshima et al. 1973; Utida 1941; Yamamoto 1990). In  
83 addition, their egg-laying decision is based on the odour (D-Catechin, Ueno et al. 1990)  
84 and curvature (Avidov et al. 1965; Ishii 1951) of the potential substrate. We prepared  
85 three different egg-laying substrates—namely, adzuki beans (*Vigna angularis*), clean  
86 glass beads that had a similar curvature to the beans but lacked odour (Avidov et al.  
87 1965; Ishii 1951), and glass beads coated with water extracts of adzuki beans, hereafter  
88 referred to as odoured glass beads (Credland and Wright 1988; Gokhale et al. 1990;  
89 Ueno et al. 1990). First, we confirmed that clean glass beads were less attractive than  
90 adzuki beans and odoured beads for the females to lay eggs. Next, we provided the  
91 females with only one of the above three substrate types and allowed them to choose  
92 between the substrates with and without eggs. We then examined how the attractiveness  
93 of resources affected how the females responded to the conspecific cue (the presence of  
94 conspecific eggs) in egg-laying decisions.

95

## 96 **Materials and methods**

97 *Insects.*

98 *Callosobruchus chinensis* is a pest beetle attacking stored legumes such as the adzuki  
99 bean *Vigna angularis* and the cowpea *V. unguiculata* (Fujii et al. 1990). Adult females

100 lay eggs on the surface of host beans or bean pods, and hatched larvae burrow into the  
101 bean in which they complete their development into adults. Adult *C. chinensis* can  
102 reproduce without any food supply, which makes this species an ideal model organism  
103 in laboratory studies of population and behavioral ecology (Yoshida 1990). We  
104 established a new laboratory strain (fkC16) of *C. chinensis* from at least 10 individuals  
105 (including adults and eggs) collected at the farm field of Kyoto University  
106 (N35.031294°, E135.787047°) in October 2016. The strain was maintained on adzuki  
107 beans (*Vigna angularis* “Toyomi-dainagon” cropped in Hokkaido, Japan; Hasebe Shoji)  
108 in plastic Petri dishes (Ø90 mm, height 15 mm) at 30 °C and 70% relative humidity  
109 under a 16:8-hour light:dark cycle. Beans were added every 1 to 3 weeks to make  
110 beetles’ generations continuous. We collected virgin beetles from the stock culture by  
111 putting beans (at one bean per well) in 24-well cell culture plates (IWAKI, Japan) just  
112 before adult emergence and then checking each well daily for adult females that had  
113 either emerged singly or were all the same sex. All beetles were kept individually in a  
114 plastic tube (1.5 mL, VIOLAMO) without beans in a room maintained at 20 °C until the  
115 experiments. Three to six hours prior to experiments, each virgin female was placed  
116 with a virgin male in a plastic tube at 25 °C for 1 hour to induce mating.

117

118 *Experiments.* The experiments were conducted at 25 °C in lighted conditions. We used  
119 adzuki beans (long axis: mean  $\pm$  SEM = 8.85  $\pm$  0.0654 mm; short axis: 7.05  $\pm$  0.0444  
120 mm;  $n$  = 30), transparent glass beads (diameter: 8.95  $\pm$  0.0145 mm;  $n$  = 30, washed with  
121 ethanol and distilled water, ING-GLASS, Japan) as egg-laying substrates. In order to  
122 make odoured glass beads, we placed 200 adzuki beans in a clean glass beaker and  
123 added 300 ml distilled water. After 24 h soaking with occasional agitation, the water  
124 solution was poured to another beaker. We added 200 glass beads to the liquid and after  
125 30 minutes soaking, the glass beads were removed and then were dried under reduced  
126 pressure. In the first experiment, we placed each pair of substrates (i.e. one bean and  
127 one clean bead, one bean and one odoured bead, or one clean bead and one odoured  
128 bead) into a plastic Petri dish (Ø35 mm, height 10 mm) (Fig. 2a). Then, the females  
129 were placed individually into the Petri dishes and allowed to lay eggs for 1 hour, after  
130 which we counted the eggs laid on both substrates. Subsequently, each female was  
131 transferred to a plastic tube with an adzuki bean to confirm her egg-laying ability; if she  
132 died without laying eggs in the tube, then her data were omitted from subsequent

133 analyses. In the second experiment, to prepare the substrates with conspecific eggs, we  
134 allowed 10 mated females (separately prepared) to lay eggs on 10 substrates of each  
135 type in a plastic Petri dish (Ø35 mm, height 10 mm) for 1 to 6 hours until we had  
136 enough substrates with eggs for the experiments. Clean substrates without eggs were  
137 used as negative controls. We placed four substrates (beans, clean beads or odoured  
138 beads) into a plastic Petri dish, one of which, called the focal substrate, had zero or  
139 more conspecific eggs, and was at a fixed position in the experimental arena (Fig. 2b).  
140 Then we allowed a female to lay eggs for 1 hour as described above and counted the  
141 eggs laid on each of the four substrates.

142

143 *Statistical Analyses.* We fitted generalized linear mixed models (GLMMs) to the egg  
144 distribution data of the experimental females. The GLMMs assumed a Poisson error  
145 distribution of the response variable with the log-link function (for the first experiment)  
146 or a binomial error distribution with the logit-link function (for the second experiment),  
147 and the following model was used:

148

149 First experiment:

150  $\#Eggs\ laid \sim \text{Substrate type} + (\text{female ID})$

151 Second experiment:

152  $\text{Egg's position (focal = 1 or not = 0)} \sim \#Initial\ eggs + (\#Initial\ eggs)^2 + (\text{female ID})$

153

154 In the second experiment, the effect of conspecific cue intensity (#Initial eggs) was  
155 evaluated sequentially up to its squared term. Individual differences (female ID) were  
156 included as a random effect (random intercept), and the maximum-likelihood estimation  
157 with Laplace approximation was used for the fitting. We used likelihood-ratio tests to  
158 evaluate the effect of adding the explanatory variables in the models. The tests were  
159 conducted separately for each type of substrate. All statistical analyses were conducted  
160 with R version 3.4.1 software (R Core Team 2017).

161

## 162 **Results**

163 In the first experiment, females obviously laid more eggs onto adzuki beans compared  
164 to clean glass beads and odoured glass beads (vs. clean beads: slope  $\pm$  SEM = 3.3322  $\pm$   
165 0.7196,  $\chi_1^2 = 63.006$ ,  $p < 0.0001$ ,  $n = 30$ , Fig. 3a; vs. odoured beads: slope  $\pm$  SEM =

166  $2.5177 \pm 0.3287$ ,  $\chi_1^2 = 114.62$ ,  $p < 0.0001$ ,  $n = 25$ , Fig. 3b), and females laid more eggs  
167 onto odoured glass beads than clean glass beads (slope  $\pm$  SEM =  $1.1109 \pm 0.2219$ ,  $\chi_1^2 =$   
168  $29.069$ ,  $p < 0.0001$ ,  $n = 26$ , Fig. 3c).

169

170 In the second experiment, females showed stronger avoidance of the focal adzuki beans  
171 when they had more conspecific eggs (slope  $\pm$  SEM =  $-0.4571 \pm 0.1221$ ,  $\chi_1^2 = 25.429$ ,  
172  $p < 0.0001$ ,  $n = 72$ ) (Fig. 4a). The effect of adding the squared term of conspecific cue  
173 intensity was not statistically significant ( $\chi_1^2 = 0.0261$ ,  $p = 0.8715$ ). The  
174 avoidance-inducing effect of the number of conspecific eggs was also observed in  
175 odoured glass beads with conspecific eggs (slope  $\pm$  SEM =  $-0.1124 \pm 0.0549$ ,  $\chi_1^2 =$   
176  $4.531$ ,  $p = 0.0333$ ,  $n = 66$ ) (Fig. 4b), with a non-significant effect of its squared term  
177 ( $\chi_1^2 = 0.5091$ ,  $p = 0.4755$ ). The avoidance-inducing effect was weaker in the odoured  
178 beads treatment than in the adzuki bean treatment, which was indicated by a statistically  
179 significant interaction between the number of conspecific eggs and the type of  
180 substrates (in the statistical analysis, data of adzuki bean and odoured glass bead  
181 treatments were combined and were coded by 0 and 1, respectively, and only the linear  
182 effects were considered; coefficient  $\pm$  SEM =  $0.2960 \pm 0.1127$ ,  $\chi_1^2 = 7.855$ ,  $p = 0.0051$ )  
183 (Fig. 4ab). In stark contrast, they showed an overall preference for focal clean glass  
184 beads with conspecific eggs (Fig. 4c). The strongest preference was for focal clean  
185 beads with a moderate number of conspecific eggs, as indicated by the statistically  
186 significant negative quadratic term of the regression (coefficient  $\pm$  SEM =  $-0.1914 \pm$   
187  $0.07166$ ,  $\chi_1^2 = 4.546$ ,  $p = 0.033$ ,  $n = 99$ ). An additional analysis that excluded the  
188 intensity of conspecific cues showed that the observed proportions of eggs on the focal  
189 substrate were overall significantly lower than the theoretical value of chance (= 0.25)  
190 when laid on adzuki beans (mean proportion = 0.149,  $G$ -test,  $G = 181.79$ , d.f. = 71,  $p <$   
191  $0.0001$ ) and on odoured glass beads (mean proportion = 0.178,  $G = 133.26$ , d.f. = 65,  $p$   
192  $< 0.0001$ ), whereas they were overall significantly higher than 0.25 when laid on clean  
193 glass beads (mean proportion = 0.633;  $G = 433.21$ , d.f. = 98,  $p < 0.0001$ ).

194

## 195 Discussion

196 In the first experiment, females obviously preferred adzuki beans to glass beads as  
197 egg-laying substrates (Fig. 3a), even when the glass beads were coated with bean  
198 extracts (Fig. 3b). These results strongly suggest that females indeed evaluate the

199 egg-laying substrate itself, and that the glass beads were less attractive substrates for  
200 beetles than adzuki beans. Moreover, they preferred odoured glass beads to clean glass  
201 beads (Fig. 3c), which suggests that the attractiveness was in part attributed to the  
202 water-soluble fraction of adzuki beans (see also Gokhale et al. 1990; Ueno et al. 1990).  
203 In the second experiment, females avoided laying eggs on beans with conspecific eggs  
204 (Fig. 4a), which confirms previous studies (e.g., Utida 1941; Yoshida et al. 1990). In  
205 stark contrast, however, when females are provided with clean glass beads with and  
206 without conspecific eggs, they preferred to add their eggs onto the beads with eggs (Fig.  
207 4c).

208  
209 As an important methodological control, the odoured glass beads successfully induced  
210 the females to show avoidance of the conspecific cue that was similar to what was  
211 observed in adzuki beans (Fig. 4b). The glass bead has long been used as an artificial  
212 egg-laying substrate in bean beetle research (e.g., Avidov et al. 1965; Credland and  
213 Wright 1988; Gokhale et al. 1990; Ishii 1951; Ueno et al. 1990). Our result could rule  
214 out the possibility that the artificial substrate itself automatically triggered a preference  
215 for moderate numbers of conspecific eggs or our artificial setup induced any kinds of  
216 irregular behaviors. Interestingly, the avoidance of conspecific eggs on odoured glass  
217 beads was weaker than those on adzuki beans (Fig. 4ab). This would commensurate  
218 with the odoured beads being less attractive than adzuki beans, reflecting an  
219 intermediate state between beans and clean beads.

220  
221 The contrast between avoidance and preference of the same social information on  
222 different resources might be generalized as a decision-making strategy consisting of two  
223 alternative tactics “copy if dissatisfied, innovate if not.” The former is already reported  
224 from rats (Galef et al. 2008) and honeybees (Grüter et al. 2013; Wray et al. 2011),  
225 where the decision of copying others is made when the payoff from private information  
226 is below an internal threshold reward level (reviewed in Grüter and Leadbeater 2014).  
227 Nevertheless, when combined with the latter “innovate if not,” i.e., keeping away from  
228 social information and finding their own ways for novel resources when the given  
229 resource is satisfactory, these contrasting decisions have an important implication for  
230 the adaptive significance of socially-mediated decision making as discussed below.

231



232 Because the larvae of this species do not move to other beans, when females lay  
233 multiple eggs onto the same bean, competition among the hatched conspecific larvae  
234 should be intense for this limited food resource. Beans already populated with  
235 conspecific eggs indicate the presence of competitors. Therefore, the tactic “innovate if  
236 not,” i.e., avoiding others during egg laying onto satisfactory resources, should be an  
237 evolutionary adaptation to avoid disadvantageous resource competition for the females’  
238 offspring. Note that avoiding others can also be interpreted as a part of social  
239 information use (Prokopy and Roitberg 2001). Given the cost of resource competition,  
240 there might be some benefits of taking the tactic “copy if dissatisfied” that outweigh the  
241 cost. Copying others, or laying eggs on substrates already with conspecific eggs, might  
242 benefit female *C. chinensis* in two ways. First, it might enable females to locate correct  
243 substrates more quickly than would be possible by trial and error (Dall et al. 2005);  
244 given the limited lifespan of the beetle, this might be an important benefit. Second,  
245 under information asymmetry between individuals, females that have poorer private  
246 information of resources might be more likely to lay eggs on appropriate resources  
247 when copying decisions of others, compared to relying on their own. Information  
248 asymmetry could be caused by accidental events such as olfactory dysfunction or by the  
249 degradation of information from resources (e.g., bean odour) over time.  
250 Resource-choice copying would then be beneficial despite the resource competition  
251 among facing their offspring.

252

253 Although our study used artificial clean glass beads as an unattractive egg-laying  
254 substrate, the clear behavioral change of females would suggest the existence of  
255 corresponding situations when they lay eggs in the field. In natural habitats of *C.*  
256 *chinensis*, laying eggs on bean pods might be one of the undesirable situations. In  
257 adzuki bean fields, the larval food is hidden in bean pods whose curvature and odour are  
258 different from, and possibly more changeable than, those of beans. Therefore, it might  
259 be more advantageous to prefer conspecific cues when laying eggs on bean pods as well  
260 as on the glass beads. A previous study reported that the distribution of eggs was  
261 clumped among bean pods in the field, while they showed uniform distribution among  
262 beans themselves (Shinoda 1989). More study is required to examine whether the  
263 clustering of eggs on bean pods is caused by beetles copying the behaviours of other  
264 females. More generally, patterns of social information use during egg laying might

265 vary among closely related species of the genus *Callosobruchus* (e.g., Messina and  
266 Karren 2003; Messina and Jones 2009; Parr et al. 1998) and even within *C. chinensis*  
267 depending on strains. The ecological covariates of varying social information use would  
268 be an interesting topic for future research.

269

270 The acquired private information such as familiarity with, or knowledge of, a resource  
271 is known to change the behavioural response of an animal to conspecific cues (Grüter  
272 and Leadbeater 2014; Kawaguchi et al. 2007). However, we observed contrasting  
273 responses in our experiments even though the females had no prior experience of the  
274 resources. This suggests that the avoidance and joining behaviours in *C. chinensis*  
275 would probably be an inherent (i.e., genetically encoded) behavioral response.  
276 Moreover, the observed behavioural change seemed drastic, even when compared with  
277 other reported resource-mediated behavioural changes that have occurred without  
278 learning (Heard 1994; Papaj and Messing 1996; Prokopy and Roitberg 2001), including  
279 behavioural changes in other bean beetles (Cope and Fox 2003), because these previous  
280 studies observed a change from a neutral response (neither preference nor avoidance) to  
281 one of avoidance or preference. The drastic change observed in our experiments  
282 suggests that the switch from avoidance to joining behaviour in *C. chinensis* may  
283 involve inherent mechanisms that have been shaped by complex evolutionary  
284 adaptation in response to resource attractiveness. Interestingly, we detected a  
285 statistically significant decrease in the number of eggs added to glass beads when an  
286 excessive number of conspecific eggs were presented together (Fig. 4c). This result also  
287 suggests that females are able to compare the costs and benefits of joining behavior (see  
288 also Fig. S1 in [Electronic supplementary material](#)). A previous study reported that *C.*  
289 *subinnotatus*, a closely related species of *C. chinensis*, does not rely on vision when  
290 assessing egg-laying substrate (Mbata 1994). Together with potential visual and  
291 numerical cognition of eggs on substrates, the cognitive ability of *C. chinensis* deserves  
292 further study.

293

294 The chemical basis of attractive conspecific cues, as well as the information acquired  
295 from the resources themselves, is left for future study. Because *C. chinensis* is a pest  
296 species, chemical egg-laying deterrents left by conspecific females have already been  
297 identified (Oshima et al. 1973; Yamamoto 1990) and constitute a mixture of fatty acids,

298 hydrocarbons and triglycerides secreted from their bodies. Of particular interest is  
299 whether these same chemicals would function as an attractant for egg-laying if they  
300 were put onto unattractive substrates. Our findings of copying behaviour on glass beads  
301 might open perspectives for a biologically safe way (i.e., clean glass beads or perhaps  
302 strongly odoured glass beads as decoys to attract egg laying females) to control bean  
303 beetles. In conclusion, our study provides a novel opportunity for further investigations  
304 of the underlying physiological, behavioural, cognitive and neural mechanisms  
305 underlying flexible decision-making by animals and their ability to integrate  
306 information from multiple sources.

307

308

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316

317 **Ethical approval:** All applicable international, national, and/or institutional  
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319 and use of animals were followed.

320

321 **Conflict of Interest:** The authors declare that they have no conflict of interest.

322

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459 **Figure legends**



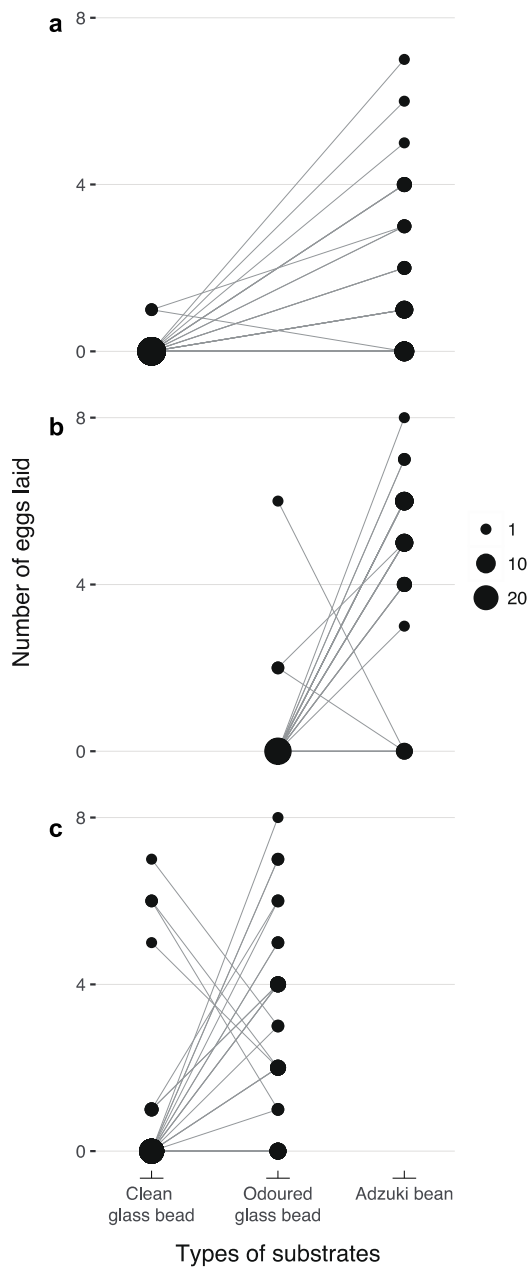
460

461 **Figure 1.** A female adzuki bean beetle *Callosobruchus chinensis* laying an egg on an  
462 adzuki bean (scale bar, 2 mm).



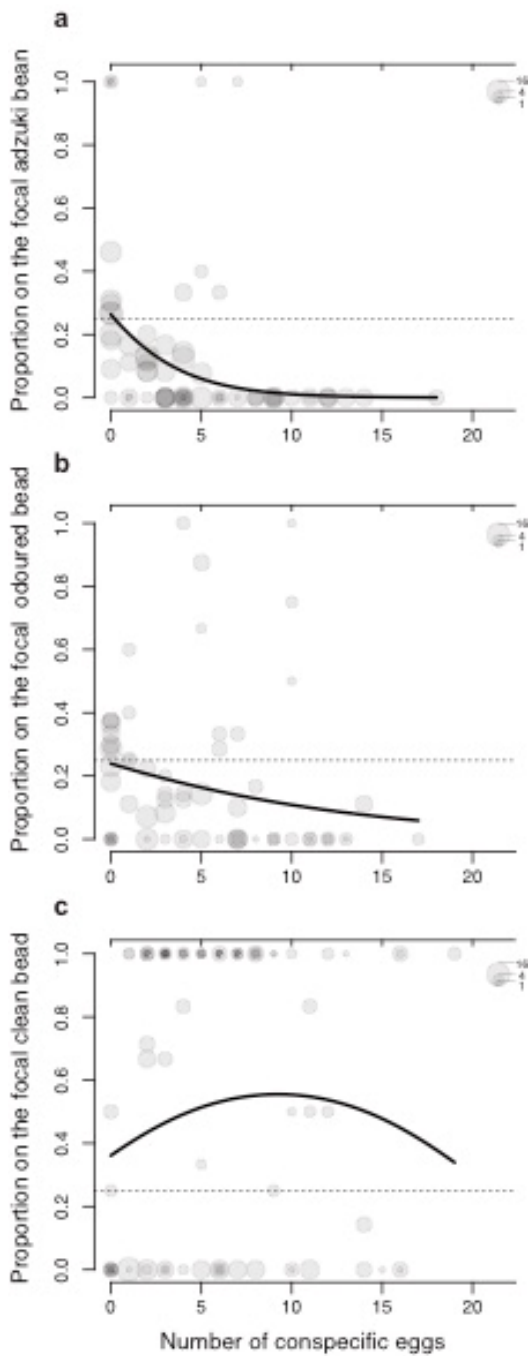
467 **Figure 2.** Snapshots of the experimental  
468 arena. (a) In the first experiment,  
469 egg-laying substrates of different types  
470 were paired and placed in a plastic Petri  
471 dish. (b, c) In the second experiment,  
472 four potential substrates (i.e., four beans,  
473 four clean beads, or four odoured beads)  
474 were placed in a Petri dish; among these  
475 substrates, only one (the focal substrate)  
476 had conspecific eggs (arrowheads; scale  
477 bar, 10 mm).

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488 **Figure 3.** (a–c) Total numbers of eggs  
 489 laid by females within 1 hour on each  
 490 pair of egg-laying substrates in the first  
 491 experiment. Each line connecting two  
 492 data points represents one female and  
 493 overlapping of the data points was  
 494 indicated by the size of the circle.

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503 **Figure 4.** Proportions of eggs laid on  
 504 the focal (a) adzuki bean, (b) odoured  
 505 glass bead, and (c) clean glass bead in  
 506 the second experiment. Each datapoint  
 507 (depicted by a circle) corresponds to a  
 508 result obtained from one female. The  
 509 size of the circle reflects the total  
 510 number of eggs laid by that female in 1  
 511 hour, and overlapping of the data points  
 512 was indicated by shading. GLMM-fitted  
 513 curves are shown together. The dotted  
 514 line indicates the proportion expected  
 515 given a random substrate choice (=   
 516 0.25).  
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