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

Authors: Ryoga Otake, Shigeto Dobata

Author affiliation: Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University.

Corresponding author: Shigeto Dobata

Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University,
Kitashirakawa Oiwake-cho, Sakyo-ku, Kyoto 606-8502, Japan

Email: dobata@kais.kyoto-u.ac.jp

ORCID ID: 0000-0003-1586-6758

Abstract:

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

Keywords:

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

Introduction

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

Despite the potential advantages accruing from the use of social information, for animal decision-makers that forage for resources, exclusive reliance on conspecific cues might be risky. Conspecific cues might reflect poor decisions (Giraldeau et al. 2002; Rieucau and Giraldeau 2011), and, even when they do not, the act of joining with conspecifics inevitably results in increased resource competition. Therefore, the information content of conspecific cues should be evaluated carefully and its importance relative to content derived from other information sources should be assessed. Even given identical social information, animals may use the information differently depending on the private information that is inherent in or acquired by themselves (Czaczkes et al. 2011; Wray et al. 2011). Previous studies found that animals copy others when private information is costly (bees, Saleh et al. 2006; fish, Webster and Laland 2008; reviewed in Rieucau and Giraldeau 2011), undesirable (rats, Galef et al. 2008; bees, Wray et al. 2011; bees, Grüter et al. 2013), unreliable (fish, Laland 2004; Rendell et al. 2010), outdated (fish, Laland 2004; Rendell et al. 2010), or uncertain (fish, Laland 2004; Rendell et al. 2010; rats, Galef et al. 2008; ants, Czaczkes and Beckwith 2018). These findings suggest that animals acquire information from multiple sources and integrate them so that they can make adaptive decisions (Grüter and Leadbeater 2014; Laland 2004).

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

Materials and methods

Insects.

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

Experiments. The experiments were conducted at 25 °C in lighted conditions. We used adzuki beans (long axis: mean ± SEM = 8.85 ± 0.0654 mm; short axis: 7.05 ± 0.0444 mm; n = 30), transparent glass beads (diameter: 8.95 ± 0.0145 mm; n = 30, washed with ethanol and distilled water, ING-GLASS, Japan) as egg-laying substrates. In order to make odoured glass beads, we placed 200 adzuki beans in a clean glass beaker and added 300 ml distilled water. After 24 h soaking with occasional agitation, the water solution was poured to another beaker. We added 200 glass beads to the liquid and after 30 minutes soaking, the glass beads were removed and then were dried under reduced pressure. In the first experiment, we placed each pair of substrates (i.e. one bean and one clean bead, one bean and one odoured bead, or one clean bead and one odoured bead) into a plastic Petri dish (Ø35 mm, height 10 mm) (Fig. 2a). Then, the females were placed individually into the Petri dishes and allowed to lay eggs for 1 hour, after which we counted the eggs laid on both substrates. Subsequently, each female was transferred to a plastic tube with an adzuki bean to confirm her egg-laying ability; if she died without laying eggs in the tube, then her data were omitted from subsequent analyses. In the second experiment, to prepare the substrates with conspecific eggs, we allowed 10 mated females (separately prepared) to lay eggs on 10 substrates of each type in a plastic Petri dish (Ø35 mm, height 10 mm) for 1 to 6 hours until we had enough substrates with eggs for the experiments. Clean substrates without eggs were used as negative controls. We placed four substrates (beans, clean beads or odoured beads) into a plastic Petri dish, one of which, called the focal substrate, had zero or more conspecific eggs, and was at a fixed position in the experimental arena (Fig. 2b). Then we allowed a female to lay eggs for 1 hour as described above and counted the eggs laid on each of the four substrates.

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

First experiment:

#Eggs laid ~ Substrate type + (female ID)

Second experiment:

Egg's position (focal = 1 or not = 0) ~ #Initial eggs + (#Initial eggs)^2 + (female ID)

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

Results

In the first experiment, females obviously laid more eggs onto adzuki beans compared to clean glass beads and odoured glass beads (vs. clean beads: slope ± SEM = 3.3322 ± 0.7196, $\chi^2_1 = 63.006$, $p < 0.0001$, $n = 30$, Fig. 3a; vs. odoured beads: slope ± SEM =

2.5177 ± 0.3287, χ_1^2 = 114.62, *p* < 0.0001, *n* = 25, Fig. 3b), and females laid more eggs onto odoured glass beads than clean glass beads (slope ± SEM = 1.1109 ± 0.2219, χ_1^2 = 29.069, *p* < 0.0001, *n* = 26, Fig. 3c).

In the second experiment, females showed stronger avoidance of the focal adzuki beans when they had more conspecific eggs (slope ± SEM = −0.4571 ± 0.1221, χ_1^2 = 25.429, *p* < 0.0001, *n* = 72) (Fig. 4a). The effect of adding the squared term of conspecific cue intensity was not statistically significant (χ_1^2 = 0.0261, *p* = 0.8715). The avoidance-inducing effect of the number of conspecific eggs was also observed in odoured glass beads with conspecific eggs (slope ± SEM = −0.1124 ± 0.0549, χ_1^2 = 4.531, *p* = 0.0333, *n* = 66) (Fig. 4b), with a non-significant effect of its squared term (χ_1^2 = 0.5091, *p* = 0.4755). The avoidance-inducing effect was weaker in the odoured beads treatment than in the adzuki bean treatment, which was indicated by a statistically significant interaction between the number of conspecific eggs and the type of substrates (in the statistical analysis, data of adzuki bean and odoured glass bead treatments were combined and were coded by 0 and 1, respectively, and only the linear effects were considered; coefficient ± SEM = 0.2960 ± 0.1127, χ_1^2 = 7.855, *p* = 0.0051) (Fig. 4ab). In stark contrast, they showed an overall preference for focal clean glass beads with conspecific eggs (Fig. 4c). The strongest preference was for focal clean beads with a moderate number of conspecific eggs, as indicated by the statistically significant negative quadratic term of the regression (coefficient ± SEM = −0.1914 ± 0.07166, χ_1^2 = 4.546, *p* = 0.033, *n* = 99). An additional analysis that excluded the intensity of conspecific cues showed that the observed proportions of eggs on the focal substrate were overall significantly lower than the theoretical value of chance (= 0.25) when laid on adzuki beans (mean proportion = 0.149, *G*-test, *G* = 181.79, d.f. = 71, *p* < 0.0001) and on odoured glass beads (mean proportion = 0.178, *G* = 133.26, d.f. = 65, *p* < 0.0001), whereas they were overall significantly higher than 0.25 when laid on clean glass beads (mean proportion = 0.633; *G* = 433.21, d.f. = 98, *p* < 0.0001).

Discussion

In the first experiment, females obviously preferred adzuki beans to glass beads as egg-laying substrates (Fig. 3a), even when the glass beads were coated with bean extracts (Fig. 3b). These results strongly suggest that females indeed evaluate the egg-laying substrate itself, and that the glass beads were less attractive substrates for beetles than adzuki beans. Moreover, they preferred odoured glass beads to clean glass beads (Fig. 3c), which suggests that the attractiveness was in part attributed to the water-soluble fraction of adzuki beans (see also Gokhale et al. 1990; Ueno et al. 1990). In the second experiment, females avoided laying eggs on beans with conspecific eggs (Fig. 4a), which confirms previous studies (e.g., Utida 1941; Yoshida et al. 1990). In stark contrast, however, when females are provided with clean glass beads with and without conspecific eggs, they preferred to add their eggs onto the beads with eggs (Fig. 4c).

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

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

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

Although our study used artificial clean glass beads as an unattractive egg-laying substrate, the clear behavioral change of females would suggest the existence of corresponding situations when they lay eggs in the field. In natural habitats of *C. chinensis*, laying eggs on bean pods might be one of the undesirable situations. In adzuki bean fields, the larval food is hidden in bean pods whose curvature and odour are different from, and possibly more changeable than, those of beans. Therefore, it might be more advantageous to prefer conspecific cues when laying eggs on bean pods as well as on the glass beads. A previous study reported that the distribution of eggs was clumped among bean pods in the field, while they showed uniform distribution among beans themselves (Shinoda 1989). More study is required to examine whether the clustering of eggs on bean pods is caused by beetles copying the behaviours of other females. More generally, patterns of social information use during egg laying might vary among closely related species of the genus *Callosobruchus* (e.g., Messina and Karren 2003; Messina and Jones 2009; Parr et al. 1998) and even within *C. chinensis* depending on strains. The ecological covariates of varying social information use would be an interesting topic for future research.

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

The chemical basis of attractive conspecific cues, as well as the information acquired from the resources themselves, is left for future study. Because *C. chinensis* is a pest species, chemical egg-laying deterrents left by conspecific females have already been identified (Oshima et al. 1973; Yamamoto 1990) and constitute a mixture of fatty acids, hydrocarbons and triglycerides secreted from their bodies. Of particular interest is whether these same chemicals would function as an attractant for egg-laying if they were put onto unattractive substrates. Our findings of copying behaviour on glass beads might open perspectives for a biologically safe way (i.e., clean glass beads or perhaps strongly odoured glass beads as decoys to attract egg laying females) to control bean beetles. In conclusion, our study provides a novel opportunity for further investigations of the underlying physiological, behavioural, cognitive and neural mechanisms underlying flexible decision-making by animals and their ability to integrate information from multiple sources.

Acknowledgements: We thank Ken Cheng and three anonymous referees for constructive comments on earlier drafts. We also thank K. Matsuura, members of Laboratory of Insect Ecology, and Y. Toquenaga for their discussions and laboratory support.

Funding: This study was partly supported by the Japan Society for the Promotion of Science (15K18609 to S.D.).

Ethical approval: All applicable international, national, and/or institutional (Regulation on Animal Experimentation of Kyoto University) guidelines for the care and use of animals were followed.

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

References

Avidov Z, Berlinger MJ, Applebaum SW (1965) Physiological aspects of host specificity in the Bruchidae: III. Effect of curvature and surface area on oviposition of *Callosobruchus chinensis* L. Anim Behav **13**:178–180. https://doi.org/10.1016/0003-3472(65)90089-8

Betts MG, Hadley AS, Rodenhouse N, Nocera JJ (2008) Social information trumps vegetation structure in breeding-site selection by a migrant songbird. Proc R Soc B **275**:2257−2263. https://doi.org/10.1098/rspb.2008.0217

Chivers DP, Smith RJF (1998) Chemical alarm signalling in aquatic predator-prey systems: A review and prospectus. Écoscience **5**:338–352. https://doi.org/10.1080/11956860.1998.11682471

Cope JM, Fox CW (2003) Oviposition decisions in the seed beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae): effects of seed size on superparasitism. J Stored Prod Res **39**:355–365. https://doi.org/10.1016/S0022-474X(02)00028-0

Credland PF, Wright AW (1988) The effect of artificial substrates and host extracts on oviposition by *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae). J Stored Prod Res 1–8. https://doi.org/10.1016/0022-474X(88)90013-6

Czaczkes TJ, Beckwith JJ (2018) Information synergy: adding unambiguous quality information rescues social information use in ants. bioRxiv 1–18. https://doi.org/10.1101/219980

Czaczkes TJ, Gruter C, Jones SM, Ratnieks FLW (2011) Synergy between social and private information increases foraging efficiency in ants. Biol Lett **7**:521–524. https://doi.org/10.1098/rsbl.2011.0067

Dall S, Giraldeau L, Olsson O, Mcnamara J, Stephens D (2005) Information and its use by animals in evolutionary ecology. Trends Ecol Evol **20**:187–193. https://doi.org/10.1016/j.tree.2005.01.010

Danchin E, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: from noisy neighbors to cultural evolution. Science **305**:487–491. https://doi.org/10.1126/science.1098254

Fletcher RJ, Miller CW (2008) The type and timing of social information alters offspring production. Biol Lett **4**:482−485. https://doi.org/10.1098/rsbl.2008.0306

Fujii K, Gatehouse AMR, Johnson CD, Mitchel R, Yoshida T (eds.) (1990) Bruchids and Legumes: Economics, Ecology and Coevolution. Dordrecht: Springer Netherlands. Kluwer Academic Publishers. https://doi.org/10.1007/978-94-009-2005-7_1

Galef BG, Dudley KE, Whiskin EE (2008) Social learning of food preferences in ‘dissatisfied’ and ‘uncertain’ Norway rats. Anim Behav **75**:631–637. https://doi.org/10.1016/j.anbehav.2007.06.024

Giraldeau LA, Valone TJ, Templeton JJ (2002) Potential disadvantages of using socially acquired information. Philos Trans R Soc B **357**:1559–1566. https://doi.org/10.1098/rstb.2002.1065

Grüter C, Leadbeater E (2014) Insights from insects about adaptive social information use. Trends Ecol Evol **29**:177–184. https://doi.org/10.1016/j.tree.2014.01.004

Grüter C, Segers FHID, Ratnieks FLW (2013) Social learning strategies in honeybee foragers: do the costs of using private information affect the use of social information? Anim Behav 85:1443–1449. https://doi.org/10.1016/j.anbehav.2013.03.041

Gokhale VG, Honda H, Yamamoto I. (1990) Role of Physical and Chemical Stimuli of Legume Host Seeds in Comparative Ovipositional Behaviour of *Callosobruchus maculatus* (Fab.) and *C. chinensis* (Linn.) (Coleoptera: Bruchidae). In Fujii K, Gatehouse AMR, Johnson CD, Mitchel R, Yoshida T (eds.) *Bruchids and Legumes: Economics, Ecology and Coevolution.* Dordrecht: Springer Netherlands. Kluwer Academic Publishers. https://doi.org/10.1007/978-94-009-2005-7_4

Golden S, Dukas R (2014) The value of patch-choice copying in fruit flies. PLoS ONE **9**:e112381. https://doi.org/10.1371/journal.pone.0112381

Heard SB (1994) Imperfect oviposition decisions by the pitcher plant mosquito *Wyeomyia smithii*. Evol Ecol 8:493–502. https://doi.org/10.1007/BF01238254

Ishii S (1951) Studies on the host preference of the cowpea weevil (*Callosobruchus chinensis* L.). Bull Nat Inst Agric Science Ser C**1**:185–256.

Kawaguchi LG, Ohashi K, Toquenaga Y (2007) Contrasting responses of bumble bees to feeding conspecifics on their familiar and unfamiliar flowers. Proc R Soc B **274**:2661–2667. https://doi.org/10.1098/rspb.2007.0860

Laland KN (2004) Social learning strategies. Anim Learn Behav **32**:4–14. https://doi.org/10.3758/BF03196002

Messina FJ, Karren ME (2003) Adaptation to a novel host modifies host discrimination by the seed beetle *Callosobruchus maculatus*. Anim Behav 65:501–507. https://doi.org/10.1006/anbe.2003.2107

Messina FJ, Jones JC (2009) Does rapid adaptation to a poor-quality host by *Callosobruchus maculatus* (F.) cause cross-adaptation to other legume hosts? J Stored Prod Res 45:215–219. https://doi.org/10.1016/j.jspr.2009.02.004

Mbata GN (1994) Sensory organs involved in egg distribution in Callosobruchus subinnotatus Pic. (Coleoptera: Bruchidae). J Stored Prod Res **30**:339–346. https://doi.org/10.1016/S0022-474X(94)90325-5

Nordell SE, Valone TJ (1998) Mate choice copying as public information. Ecol Lett **1**:74–76. https://10.1046/j.1461-0248.1998.00025.x

Oshima K, Honda H, Yamamoto I (1973) Isolation of an oviposition marker from Azuki bean weevil, *Callosobruchus chinensis* (L.). Agric Biol Chem **37**:2679–2680. https://doi.org/10.1080/00021369.1973.10861061

Papaj DR, Messing RH (1996) Functional shifts in the use of parasitized hosts by a tephritid fly: the role of host quality. Behav Ecol **7**:235–242. https://doi.org/10.1093/beheco/7.3.235

Parr MJ, Tran BMD, Simmonds MSJ, Kite C, Credland PF (1998) Influence of Some Fatty Acids on Oviposition by the Bruchid Beetle, *Callosobruchus maculatus*. J Chem Ecol 24:1577–1593. https://doi.org/10.1023/A:1020894410107

Prokopy RJ, Roitberg BD (2001) Joining and avoidance behavior in nonsocial insect. Annu Rev Entomol **46**:631–665. https://doi.org/10.1146/annurev.ento.46.1.631

Raitanen J, Forsman JT, Kivelä SM, Mäenpää MI, Välimäki P (2013) Attraction to conspecific eggs may guide oviposition site selection in a solitary insect. Behav Ecol **25**:110–116. https://doi.org/10.1093/beheco/art092

R Core Team (2017) R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. (See https://www.R-project.org/)

Rieucau G, Giraldeau LA (2011) Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. Philos Trans R Soc B **366**:949–957. https://doi.org/10.1098/rstb.2010.0325

Saleh N, Ohashi K, Thomson JD, Chittka L (2006) Facultative use of the repellent scent mark in foraging bumblebees: complex versus simple flowers. Anim Behav **71**:847–854. https://doi.org/10.1016/j.anbehav.2005.06.014

Schmidt KA, Dall SRX, van Gils JA (2010) The ecology of information: an overview on the ecological significance of making informed decisions. Oikos **119**:304–316. https://doi.org/10.1111/j.1600-0706.2009.17573.x

Shinoda K (1989) Studies on life cycle of azuki bean beetle in the field. Okayama University Ph. D. thesis. (in Japanese)

Stamps JA (1987) Conspecifics as Cues to Territory Quality: A Preference of Juvenile Lizards (*Anolis aeneus*) for Previously Used Territories. Am Nat **129**:629–642. https://doi.org/10.1086/284663

Ueno T, Kuwahara Y, Fujii K, Taper ML, Toquenaga Y, Suzuki T (1990) D-Catechin: An oviposition stimulant of azuki bean weevil *Callosobruchus chinensis* in the host azuki bean. J Pestic Sci **15**:573−578. https://doi.org/10.1584/jpestics.15.573

Utida S (1941) Studies on experimental population of the azuki bean weevil, *Callosobruchus chinensis* L. Kyoto: Memoirs of the College of Agriculture, Kyoto Imperial University.

Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. Philos Trans R Soc B 357:1549–1557. https://doi.org/10.1098/rstb.2002.1064

Ward P, Zahavi A (1973) The Importance of certain assemblages of birds as “information-centres” for food-finding. Ibis, 115, 517–534.

Webster MM, Laland KN (2008) Social learning strategies and predation risk: minnows copy only when using private information would be costly. Proc Biol Sci **275**:2869–2876. https://doi.org/10.1098/rspb.2008.0817

Westneat DF, Walters A, McCarthy TM, et al (2000) Alternative mechanisms of nonindependent mate choice. Anim Behav **59**:467–476. https://doi.org/10.1006/anbe.1999.1341

Wray MK, Klein BA, Seeley TD (2011) Honey bees use social information in waggle dances more fully when foraging errors are more costly. Behav Ecol **23**:125–131. https://doi.org/10.1093/beheco/arr165

Yamamoto I (1990) Chemical ecology of bruchids. In Fujii K, Gatehouse AMR, Johnson CD, Mitchel R, Yoshida T (eds.) *Bruchids and Legumes: Economics, Ecology and Coevolution.* Dordrecht: Springer Netherlands. Kluwer Academic Publishers. https://doi.org/10.1007/978-94-009-2005-7_1

Yoshida T (1990) Historical review of Bruchid studies in Japan In Fujii K, Gatehouse AMR, Johnson CD, Mitchel R, Yoshida T (eds.) *Bruchids and Legumes: Economics, Ecology and Coevolution.* Dordrecht: Springer Netherlands. Kluwer Academic Publishers. https://doi.org/10.1007/978-94-009-2005-7_1

Figure legends

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

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

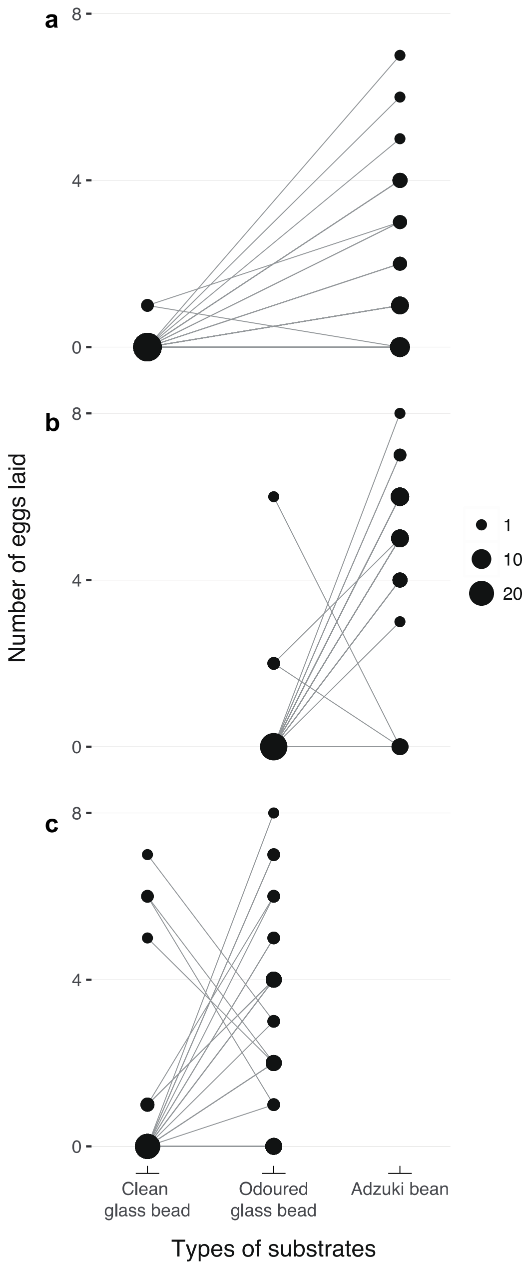

Figure 3. (a−c) Total numbers of eggs laid by females within 1 hour on each pair of egg-laying substrates in the first experiment. Each line connecting two data points represents one female and overlapping of the data points was indicated by the size of the circle.

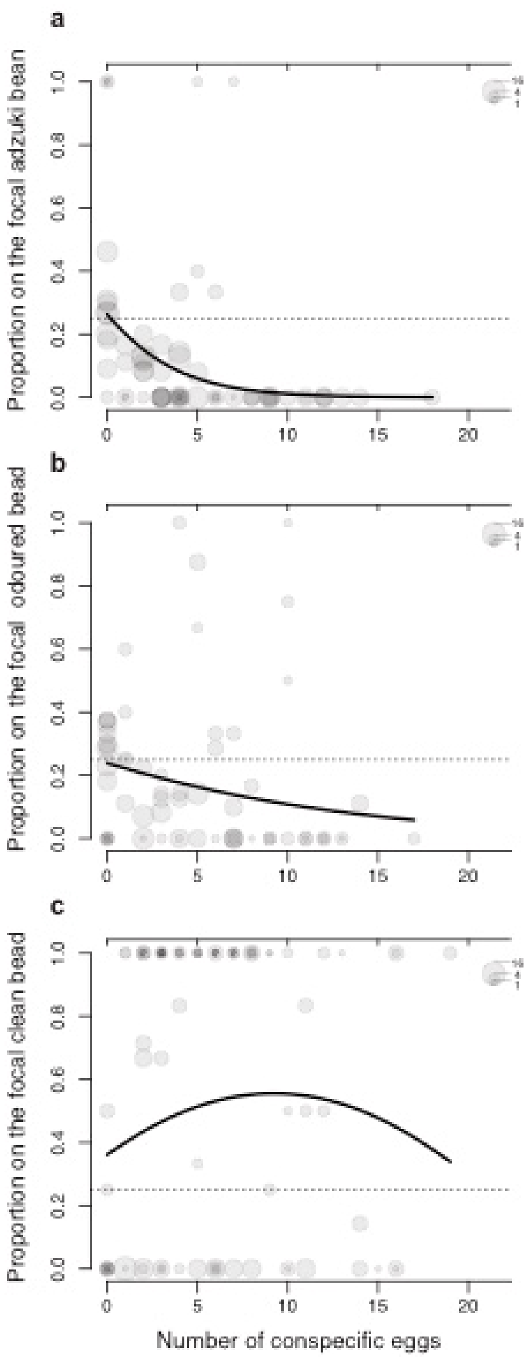

Figure 4. Proportions of eggs laid on the focal (a) adzuki bean, (b) odoured glass bead, and (c) clean glass bead in the second experiment. Each datapoint (depicted by a circle) corresponds to a result obtained from one female. The size of the circle reflects the total number of eggs laid by that female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