


Oviposition in the onion fly *Delia antiqua* (Diptera: Anthomyiidae) is socially facilitated by visual cues

Sugihiko Hoshizaki* , Noriaki Koshikawa*, Takuya Toyoda* and Yukio Ishikawa

Laboratory of Applied Entomology, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan

Research Paper

*These authors contributed equally to this study.

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Author for correspondence:

Sugihiko Hoshizaki,

Email: ahossy@mail.ecc.u-tokyo.ac.jp

Abstract

Ovipositional decisions in herbivorous insects may be affected by social information from conspecifics. Social facilitation of oviposition has been suggested for the onion fly *Delia antiqua*. In the current study, we found that *D. antiqua* oviposition was unequal between paired oviposition stations of equal quality and that more eggs were laid on an oviposition station baited with decoy flies than on the control. The increased oviposition toward the decoys continued over time >8 h. When decoys were placed upside down, the number of eggs laid did not differ between the decoy and control sides of oviposition stations, suggesting that social facilitation of oviposition is mediated by visual cues. Based on these findings, mechanisms of social facilitation of oviposition in *D. antiqua* were discussed.

Introduction

When laying eggs, female herbivorous insects need to find their host plants, choose among potential host plants, and then decide how many eggs to lay there. Such decision may be affected by social information such as oviposition by conspecifics (Danchin *et al.*, 2004; Wagner and Danchin, 2010). Oviposition by early-arriving females may deter oviposition by late-arriving conspecifics (e.g., Roitberg and Prokopy, 1987; Li and Ishikawa, 2005; Tanaka and Sugahara, 2017) or may facilitate oviposition by late arrivers (social facilitation of oviposition; e.g., Browne *et al.*, 1969; Prokopy and Duan, 1998; Prokopy and Roitberg, 2001; Pasqualone and Davis, 2011; see also Otake and Dobata, 2018).

Maggots of the onion fly *Delia antiqua* (Diptera: Anthomyiidae) damage the bulb of onions and related plants in Europe, Asia, and North America (Ning *et al.*, 2017b); their life history is adapted to a wide range of climatic conditions (e.g., Ishikawa *et al.*, 1987; Nomura and Ishikawa, 2001). The onion fly is a model for studying host selection in herbivorous insects (Visser, 1986; Renwick, 1989; Romeis *et al.*, 2003; Gouinguené and Städler, 2005; Johnson *et al.*, 2006). Female flies of *D. antiqua* find hosts, such as onions, using visual and olfactory cues (Matsumoto and Thorsteinson, 1968; Ishikawa *et al.*, 1978, 1985; Harris and Miller, 1991; Degen and Städler, 1996; Gouinguené *et al.*, 2005; Ning *et al.*, 2017a). Several studies have suggested the social facilitation of oviposition in *D. antiqua* (Vernon, 1979; Harris and Miller, 1983); for example, a group of *D. antiqua* females often aggressively lay eggs on the cage floor when several hundreds of flies are confined without particular oviposition substrates (personal observation by the authors). Judd and Borden (1992) presented experimental evidence suggesting that oviposition of *D. antiqua* is facilitated to a weak degree by stimuli associated with ovipositing females and newly laid eggs. As the social facilitation of oviposition may confound laboratory bioassays of ovipositional stimuli in insects (Judd and Borden, 1992), a better understanding of the mechanisms of social facilitation of oviposition in *D. antiqua* is indispensable for the accurate assessment of oviposition stimulants.

The social information received by late-arriving females may induce different responses depending on the degree and timing of previous exploitation of oviposition sites (Lam *et al.*, 2007; Wasserberg *et al.*, 2014; Stephan *et al.*, 2015). For example, in the housefly, olfactory cues from eggs laid on the larval food change from induction to inhibition of oviposition over time in late-arriving females (Lam *et al.*, 2007). In *D. antiqua*, it remains unclear whether social information facilitating oviposition by late-arriving females continues over time or is independent of increases in the degree of oviposition site exploitation.

In *D. antiqua*, while the use of chemical cues in the social facilitation of oviposition has been suggested (Judd and Borden, 1992), involvement of visual cues has not been examined. Indeed, the use of visual information emitted by conspecifics was found in the damselfly (Byers and Eason, 2009).

The current study first aimed to verify the social facilitation of oviposition in *D. antiqua* by examining whether the number of eggs laid is unequal between paired oviposition stations of

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equal quality. Then, based on the finding that *D. antiqua* oviposition is biased to an oviposition station baited with decoy flies, we tested two specific hypotheses: (1) social information facilitating oviposition in *D. antiqua* continues over time and (2) socially facilitated oviposition in *D. antiqua* is mediated by visual information from conspecifics.

Materials and methods

Study insects

A laboratory population of *D. antiqua* originating from Hokkaido, Japan (Kayukawa *et al.*, 2007) has been maintained for >15 years according to the methods described by Ishikawa *et al.* (1983) and Kayukawa *et al.* (2007). Newly eclosed adults were reared in mesh cages (25 cm × 25 cm × 25 cm), and supplied with water, sugar cubes, and dried yeast at 23°C for 12–15 days until sexual maturation and mating (Ishikawa, 1979; Spencer and Miller, 2002).

Oviposition station

A plastic cup (9 cm in diameter; 4.5 cm in height) was filled with fine gravel, and 10 ml of water was poured into the cup. At the center of the top of the gravel field, a piece of green onion leaf ('Ban-nou-negi'; 10 cm in length) was vertically positioned with the core of a piece of steel wire (a standard oviposition station; Supplementary fig. S1). Eggs were laid in the gravel near the stand of the green onion in oviposition stations. A pair of standard oviposition stations was prepared using a single green onion plant, immediately before each trial.

Decoys

Gravid females of *D. antiqua* were chosen from 12 to 15 day-old flies based on the red color on the ventral side of abdomen (Ishikawa, 1979; Spencer and Miller, 2002). They were anesthetized by using CO₂ and then kept under –20°C for 1 h immediately before experiments using decoys. In each trial of experiments 2–4, five decoys were placed around the green onion stand in one of the paired standard oviposition stations (decoy side).

Experimental conditions

Two oviposition stations were placed on the floor of a mesh cage (25 cm × 25 cm × 25 cm) together with a water bottle, a sugar cube, and a small dish of dried yeast (Supplementary fig. S1). In each trial, 20 gravid female *D. antiqua* flies were released into the test cage immediately before the experiments started. The test cage was surrounded by a sheet (30 cm in height) of black paper. Experiments were conducted at 23°C and 15 L:9 D; the light phase in the room started at 8:00 and terminated at 23:00, and all experiments were started between 12:00 and 17:00. Thus, the test flies were allowed to start oviposition in the late afternoon during the photoperiod; *D. antiqua* females lay eggs most actively in the evening (Havukkala and Miller, 1987).

Experiment 1

Two standard oviposition stations, representing oviposition sites of equal quality, were presented for 24 h. Eggs were recovered

from each oviposition station and counted. Four test cages were used with ten trials per cage.

Experiment 2

Dead bodies of *D. antiqua* were placed on their legs, on one of the two standard oviposition stations. Eggs were recovered from each oviposition station and counted 24 h after the release of test flies. A total of 16 trials were conducted in four test cages. The decoy placement within cages was rotated among trials to avoid bias toward one side of the cage.

Experiment 3

Decoys were used as in experiment 2. Eggs were recovered from each oviposition station and counted 0.25, 1, 4, 8, or 24 h after the release of test flies. For 0.25-h oviposition, a total of 32 trials were conducted in five cages. In every cage, the decoy placement was rotated among trials. For 1-, 4-, 8-, or 24-h oviposition, the experiment was conducted in a total of 16 trials in the same manner as experiment 2.

Experiment 4

Decoys were placed on their back, on one of the two standard oviposition stations. Eggs were recovered from each oviposition station and counted 24 h after the release of test flies. The experiment was conducted in a total of 16 trials in the same manner as experiment 2.

Statistical analyses

For experiment 1, the probability of egg presence in one oviposition station in each trial was assessed against 0.5 by the binomial test. Trials with no significant differences from 0.5 were considered ties. Then, the potential oviposition preference toward either oviposition-station place over the other place in the cage was evaluated. The number of trials in favor of one place and that in favor of the other place were compared by the bilateral sign test, disregarding the tied trials, for each cage.

For experiments 2–4, the oviposition preference toward a particular side was examined in two approaches with different null hypotheses. The first approach adopted the null hypothesis that the number of trials in favor of the decoy side was equal to that in favor of control side. For each trial, the probability of egg presence on the decoy side was assessed against 0.5 by the binomial test. Trials with no significant differences from 0.5 were considered ties. Then, the numbers of trials in favor of the decoy and control sides were compared by the sign test, disregarding the tied trials.

The second approach adopted the null hypothesis that the numbers of eggs on the decoy and control sides were equal. Generalized linear mixed effect models (GLMM) were used to test this hypothesis. The dependent variables used were the numbers of eggs on the decoy and control sides. The treatment was used as the fixed factor, and the trial was used as the random factor for the slope and intercept. Poisson distributions were used as the error distribution.

In the statistical analyses, the two approaches were adopted to complement each other. In the first approach, the numbers of trials in favor of the decoy and control sides were compared. In this approach, the statistical power would not be significantly

Table 1. Experiment 1: the egg distribution between two oviposition stations of equal quality in four cages

Cage	Number of trials			Sign test
	More eggs on one side in the cage	Ties	More eggs on the other side in the cage	
I	3	2	5	$P = 0.73$
II	6	0	4	$P = 0.75$
III	4	2	4	$P = 1$
IV	6	0	4	$P = 0.75$

For each trial, the probability of egg presence at one oviposition station was assessed against 0.5 by the binomial test with the criterion of $P < 0.05$. Trials with $P > 0.05$ were considered ties. The number of trials with more eggs on one side of oviposition stations and that with more eggs on the other side were compared by the bilateral sign test.

affected by the degree of bias in oviposition toward a particular side of stations. On the other hand, the statistical power decreases as the number of tied trials increases, and hence may differ between experiments. The second approach does not disregard tied trials in the analysis; however, when trials in favor of the decoy and control sides occurred within an experiment, the distribution of egg number for a particular side of oviposition stations may not follow the assumed one.

R version 3.3.2 (R Core Team, 2016) was used for the statistical analyses. The `glmer()` function in the R package 'lme4' was employed for the GLMM analyses.

Results

Experiment 1

D. antiqua females were allowed to lay eggs at a pair of oviposition stations of equal quality for 24 h. In this and the other experiments, no or few eggs were laid outside the oviposition stations (personal observations by N. K., T. T., and S. H.). The even distribution of eggs between the oviposition stations tested in the pair was rejected in 36 of 40 trials (table 1). In every cage, the number of trials in favor of a particular side in the cage was not significantly larger than that in favor of the other side (table 1). The median ratio of egg number at the oviposition station with more eggs to the total eggs was 0.59 (fig. 1).

Thus, the egg distribution was mostly unequal between the paired oviposition stations of equal quality. Attention should be paid when interpreting the results of the following experiments, as the egg distribution between the paired oviposition stations may be unequal even if bait treatment is not effective.

Experiment 2

D. antiqua females were allowed to lay eggs at paired oviposition stations, one baited with decoys placed on their legs and the other not baited with decoys, for 24 h. The number of trials with more eggs on the decoy side was significantly larger than that with more eggs on the control side (table 2). In the GLMM analysis, the fixed effect of decoys was significant ($z = 2.87$, $P = 0.004$; fig. 2). Note that the data variance was large in experiment 2 and the others in the current study; we dealt with that using mixed models. The median ratio of egg number on the decoy side to the total number was 0.59. Thus, females laid more eggs in those oviposition stations where dead bodies were present.

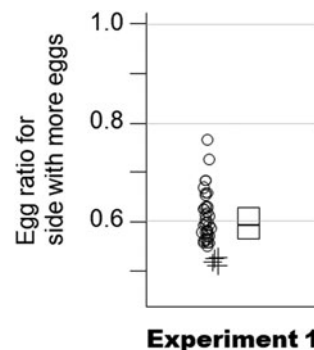


Figure 1. Distribution of eggs over two oviposition stations of equal quality (experiment 1). The egg ratio indicates the number of eggs on the side with more eggs divided by the total number of eggs. Circles and crosses represent trials rejecting (binomial test, $P < 0.01$) and supporting, respectively, the null hypothesis of the even distribution of eggs. The box plot indicates the median, and the first and third quartiles.

Table 2. Experiments 2 and 4: effects of decoys on oviposition facilitation

	Decoy posture	Number of trials			Sign test
		More eggs on the decoy side	Ties	More eggs on the control side	
Exp. 2	On the legs	11	3	2	$P = 0.02$
Exp. 4	On the back	6	2	8	$P = 0.79$

Decoys were placed on their legs or back. For each trial, the probability of egg presence on the decoy side was assessed against 0.5 by the binomial test with the criterion of $P < 0.05$. Trials with $P > 0.05$ were considered ties. The number of trials with more eggs on the decoy side and that with more eggs on the control side were compared by the bilateral sign test.

Experiment 3

D. antiqua females were allowed to lay eggs at paired oviposition stations as in experiment 2, but for different lengths of time. After 0.25-h oviposition, more eggs tended to be laid on the decoy side, but the numbers of trials with more eggs on the decoy and control sides were not significantly different (table 3). In the GLMM analysis, the fixed effect of decoys was not significant ($z = 1.21$, $P = 0.226$; fig. 3). The median ratio of eggs on the decoy side to total eggs after 0.25-h oviposition was 0.69, and was similar to the median egg probabilities observed in experiments 1 and 2.

After 1-, 4-, and 24-h oviposition, the number of trials with more eggs on the decoy side was significantly larger than that with more eggs on the control side; however, no significant difference was found for 8-h oviposition (table 3). In GLMM analyses, the fixed effect of decoys was significant after all of the oviposition periods examined (1-h oviposition: $z = 2.79$, $P = 0.005$; 4-h oviposition: $z = 2.05$, $P = 0.04$; 8-h oviposition: $z = 2.2$, $P = 0.028$; 24-h oviposition: $z = 3.66$, $P = 0.00025$; fig. 3). The median probability of egg presence on the decoy side after 1, 4, 8, or 24 h was approximately 0.6 (0.58–0.66).

The ratio of egg number on the decoy side to the total number of eggs was not correlated with the oviposition duration (Kendall's $\tau = -0.0545$, $z = -0.706$, $P = 0.48$). The total egg number continued to increase from 0.25 to 24 h (Kendall's $\tau = 0.833$, $z = 10.799$, $P < 0.001$; fig. 4), demonstrating that oviposition continued.

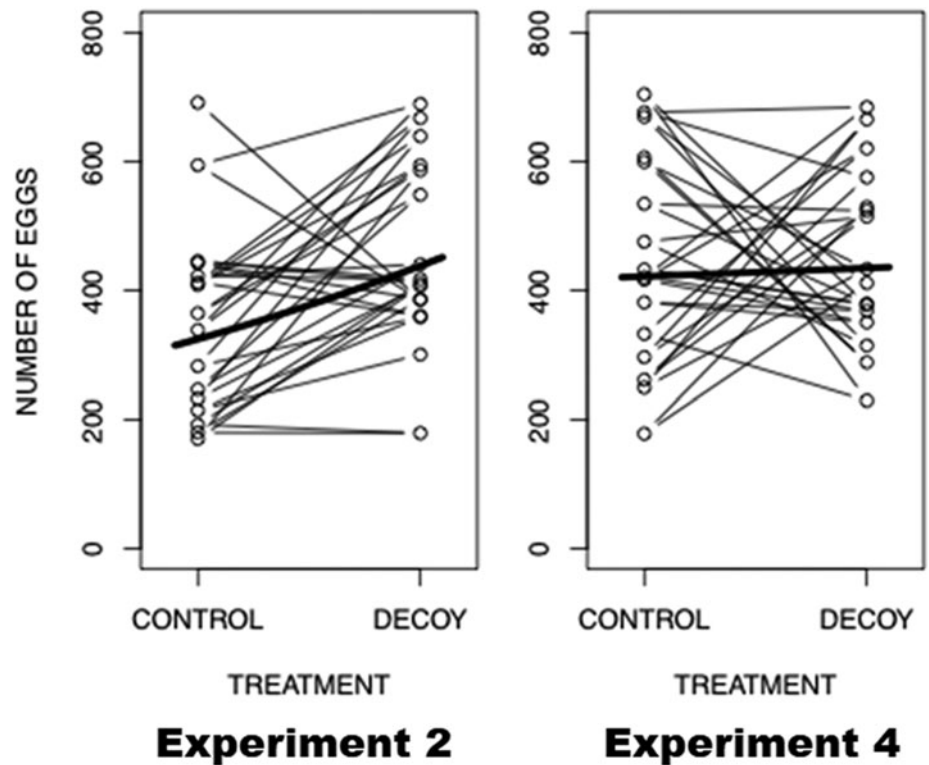


Figure 2. The GLMM analysis for experiments 2 (left) and 4 (right). Pairs of circles connected by lines represent single trials of the experiment. The thick line indicates the model prediction.

Table 3. Experiment 3: oviposition facilitation for varying durations of oviposition when decoys were placed on their legs

Oviposition duration (h)	Number of trials			Sign test
	More eggs on the decoy side	Ties	More eggs on the control side	
0.25	13	10	4	$P = 0.05$
1	10	5	1	$P = 0.01$
4	12	1	3	$P = 0.04$
8	10	3	3	$P = 0.09$
24	14	1	1	$P = 0.0009$

For each trial, the probability of egg presence on the decoy side was assessed against 0.5 by the binomial test with the criterion of $P < 0.05$. Trials with $P > 0.05$ were considered ties. The number of trials with more eggs on the decoy side and that with more eggs on the control side were compared by the bilateral sign test.

Experiment 4

Decoys were used as in experiment 2, but they were placed upside down. Oviposition was allowed for 24 h. There were no significant differences between the number of trials with excess of eggs on the decoy side and that on the control side (table 2). In the GLMM analysis, the fixed effect of decoys was not significant ($z = 0.20$, $P = 0.84$; fig. 2). The median ratio of egg on the decoy side to total eggs was 0.46.

Discussion

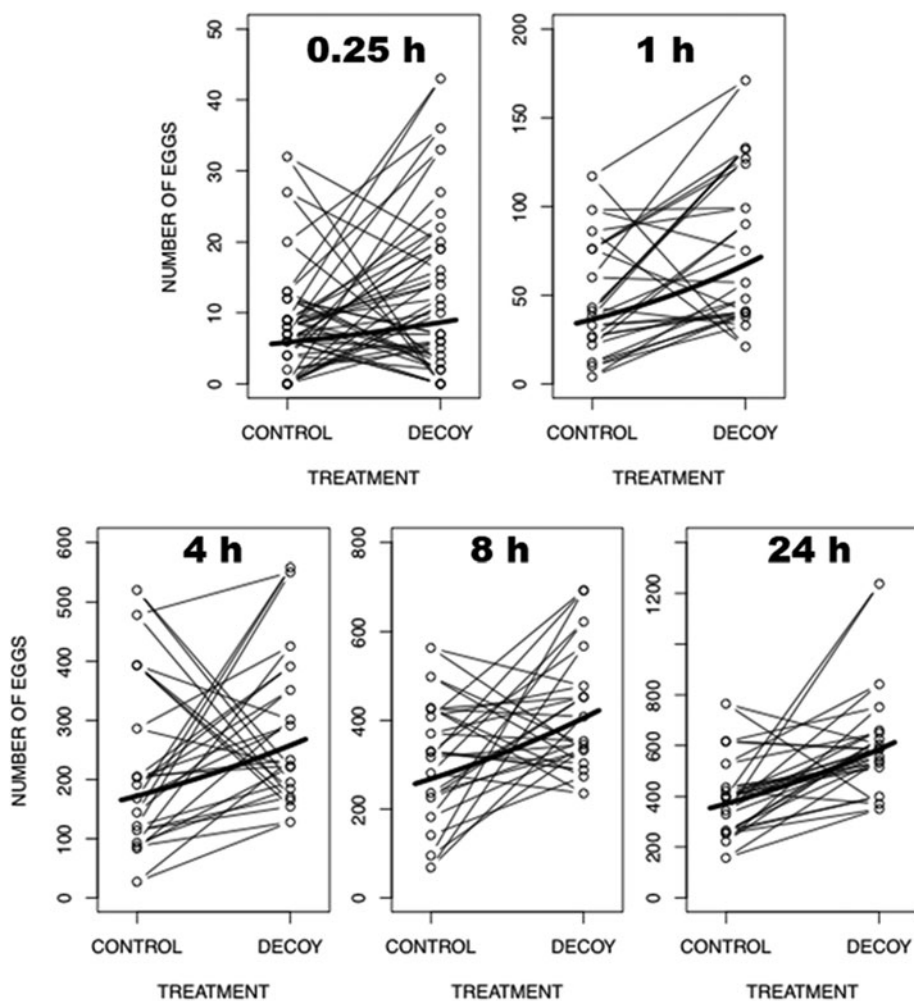
D. antiqua females laid eggs unequally between two oviposition stations of equal quality over 24 h (experiment 1). This indicates that the oviposition was socially facilitated by already laid eggs, some traces of oviposition, and/or egg-laying females themselves.

This finding is consistent with the previous study by Judd and Borden (1992).

When one of the two oviposition stations was baited with dead *D. antiqua* bodies placed on their legs, oviposition was mostly concentrated to the decoy side in almost all trials (experiment 2). This confirms the occurrence of social facilitation of oviposition in *D. antiqua* and indicates that the oviposition was facilitated by a cue(s) other than already laid eggs or some traces of oviposition. The degree of egg aggregation was weak (median probability of egg presence of 0.59 on the decoy side), as reported by Judd and Borden (1992).

The results of experiment 1 are particularly significant in that *D. antiqua* oviposition was socially facilitated without presenting extrinsic stimuli. Previous assays of social facilitation of *D. antiqua* oviposition (Judd and Borden, 1992) used extrinsic stimuli such as ten females, 300 eggs, or ovipositor extracts of *D. antiqua*. Such experimental designs represent a situation in which eggs are already concentrated at an oviposition site to a certain degree, and not an initial phase of the oviposition facilitation process.

In several insects, the degree of egg congestion at an oviposition site or the time since previous exploitation of an oviposition site affects the message of social cues; the message to late-arriving females changes from induction to inhibition of oviposition when an oviposition site becomes overcrowded or a prolonged period has passed since the previous oviposition (Lam *et al.*, 2007; Wasserberg *et al.*, 2014; Stephan *et al.*, 2015). In contrast, in *D. antiqua*, the degree of egg concentration to decoys did not significantly change with time (experiment 3 in the current study), suggesting that social facilitation continues even after the oviposition stations become crowded with eggs. This by itself may not be a notable finding; however, we did not find other reports of the continuous facilitation of oviposition via social information.



Experiment 3

Figure 3. The GLMM analysis for experiment 3. Pairs of circles connected by black lines represent single trials of the experiment. The thick line indicates the model prediction.

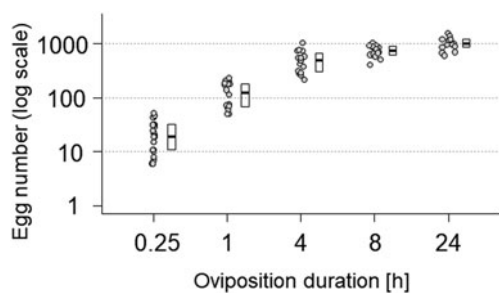


Figure 4. Total egg number at different times (experiment 3). One circle represents one trial. For both panels, the box plot indicates the median, and first and third quartiles.

The results of experiment 3 suggest that decoys placed on their legs continued to facilitate conspecific oviposition for >8 h. This raises a question about the possibility of social facilitation of oviposition during the scotophase; however, this is not likely because *D. antiqua* females are known to rarely lay eggs during the scotophase (Havukkala and Miller, 1987).

Decoys placed on their legs facilitated oviposition by conspecifics (experiment 2). However, such facilitation was not observed when the decoys were placed on their back (experiment 4). This

suggests that the social facilitation of oviposition in *D. antiqua* involves visual cues. We speculate that the decoys placed on their legs and back were recognized as living and dead flies, respectively, because flies died naturally tend to lie on their back on the ground.

The social facilitation of oviposition in *D. antiqua* was previously explained by olfactory cues, i.e., egg and female factors (Judd and Borden, 1992). As the egg factor, Judd and Borden (1992) reported that *D. antiqua* eggs in contact with onion tissues facilitate oviposition by late-arriving females; facilitation effects were not observed when eggs were laid away from the onion. In the current study, *D. antiqua* females were allowed to lay eggs not in onion tissues, but in gravel; therefore, the egg factor may not have been an influence. Regarding the female factor, Judd and Borden (1992) reported that the female ovipositor can attract conspecific females to oviposit. Ovipositors of decoy flies were not exposed in the current study (experiments 2, 3, and 4); therefore, the supposed female factor may not have influenced the decoy-using experiments. Given these findings, we interpret the results in experiments 2 and 3 as follows: visual cues from decoys likely facilitated oviposition by pioneer females, and then visual cues from the decoys, and visual and olfactory cues from late-arriving females may have further facilitated oviposition.

Social effects on oviposition have also been studied in species related to *D. antiqua*. The eggs of *D. radicum* stimulated oviposition by late-arriving conspecifics by means of chemical cues (de Jong and Städler, 2001; Gouinguéné et al., 2006). In another anthomyiid species, ovipositing females were suggested to deposit oviposition-detering pheromone (Zimmerman, 1979, 1980, 1982). Thus, there seems to be diversity among anthomyiid flies in the social effect on oviposition.

Several limitations in the current study should be noted. First, we used green onion leaves to prepare oviposition stations. There may be some difference in the quality of leaves used for a pair of oviposition stations. Since the leaf color, shape, and chemicals serve as ovipositional cues in the onion fly (reviewed by Gouinguéné and Städler, 2005; Johnson et al., 2006), differences in these factors may have affected the oviposition. Although we minimized this possibility by using leaves of the same plant for single trials, experiments by using artificial oviposition stimulants rather than onion leaves would further confirm the social facilitation of oviposition via visual cues in *D. antiqua*. Second, group oviposition behavior often occurs in mass-rearing cages of *D. antiqua* (Supplementary fig. 1; personal observation by the authors). This may have influenced the social facilitation of oviposition observed in the current study. Third, *D. antiqua* females may choose an oviposition site by social facilitation cues, or lay more eggs at a site with social facilitation cues than at that without them. Last, it is unknown why the degree of social facilitation of oviposition is weak in *D. antiqua* (the current study; Judd and Borden, 1992). It is possible that oviposition by each female fly is weakly facilitated by social cues or that oviposition by some females in the test cage is moderately/strongly facilitated. To examine these hypotheses, oviposition behavior in response to conspecific females and eggs should be directly observed for *D. antiqua*.

In conclusion, the current study revealed that the oviposition in *D. antiqua* is socially facilitated by visual cues, and that the facilitation continues over time. The social facilitation of oviposition in *D. antiqua* may play a role in improving the development of larvae in onion bulbs. Ovipositing *D. antiqua* females prefer damaged plants (Ikeshoji et al., 1980), and this preference is consistent with newly hatched *D. antiqua* larvae being able to better colonize onion bulbs damaged by conspecific larvae than healthy ones (Hausmann and Miller, 1989). Similarly, the aggregation of *D. antiqua* eggs due to social facilitation of oviposition may be adaptive for late-arriving females because their newly hatched larvae can more easily colonize onion bulbs that are pre-conditioned by larvae from pioneer females. Furthermore, larvae of *D. antiqua* usually aggregate on the larval diet in laboratory conditions (personal observation by Y.I. and S.H.), and larval aggregation may be promoted by the social facilitation of oviposition. It is possible that the success of larval colonization of onion bulbs increases with aggregation. These hypotheses follow the ‘mother knows best’ principle of the preference–performance relationships in host selection in herbivorous insects (Valladares and Lawton, 1991; Johnson et al., 2006; Garcia-Roberdo and Horvitz, 2012).

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0007485320000152>.

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Author contributions. S. H. and Y. I. conceived the study. S. H. and N. K. designed the experiments. N. K. conducted the preliminary

work. T. T. collected data. S. H. analyzed the data with the aid of N. K. and T. T. N. K., T. T., and S. H. wrote the first draft, and Y. I. edited it. Y. I. prepared the reagents and equipment.

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