Possible coexistence of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) and *Diaeretiella rapae* M'Intosh (Hymenoptera: Braconidae) in the biological control of *Lipaphis erysimi* (Homoptera: Aphididae)

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ABSTRACT

To study the interactions between the aphidophagous predator *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) and the specialist aphid parasitoid *Diaeretiella rapae* M'Intosh (Hymenoptera: Braconidae) in the biological control of mustard aphid, *Lipaphis erysimi* (Homoptera: Aphididae), the prey discrimination by *H. axyridis* among unparasitized, non-mummified parasitized and mummified aphids was examined under laboratory conditions. Prey/host selections were also tested by offering L. erysimi at various developmental stages to assess the possibility of coexistence between the two species, so the prey preference of *H. axyridis* when *D. rapae* parasitize aphids, and the host preference of *D. rapae* when *H. axyridis* interfered with the parasitization were detected. We found that *H. axyridis* could discriminate against mummies rather than non-mummified parasitized aphids. The ladybug showed a significantly positive preference for adult prey when *D. rapae* turned aphids into mummies, while *D. rapae* tended to parasitize younger nymphal aphids when *H. axyridis* was introduced. The present study suggests the prey discrimination against mummies by *H. axyridis*, and indicates that *H. axyridis* and *D. rapae* can avoid resource competition by attacking different and non-overlapping developmental stages of aphid. Thus, *H. axyridis* and *D. rapae* can potentially coexist and establish a stable ecosystem in the biological control of L. erysimi.

Introduction

Various natural enemies existing in a biological control system are common (Snyder and Ives, 2003), and the interactions among the agents are important to evaluate the effectiveness of pest suppression (Denoth et al., 2002). Aphid populations are frequently controlled by both generalist predators and specialist aphid parasitoids (Bilu and Coll, 2007; Costamagna et al., 2007), so the competitive interactions between the predators and parasitoids are inescapable (Gontijo et al., 2015). Some views are presented that predators may damage predator-parasitoid-aphid systems by consuming parasitized prey containing parasitoid (Chacón and Heimpel, 2010; Arim and Marquet, 2004; Rosenheim et al., 1993; Holt and Polis, 1997), resulting in significant losses of parasitoids (Colfer and Rosenheim, 2001; Taylor et al., 1998;

Brodeur and Rosenheim, 2000). However, others suggest parasitoids can coexist with predators in the biological control of aphids (Okuyama, 2009; Frago and Godfray, 2014). When both predator and parasitoid are introduced in an ecosystem, their interactions should be defined (neutral, positive or negative). Potential interactions in identical food webs may affect the practical results of intentional or accidental multi-species introduction, so the purpose of studying interactions between predator and parasitoid is to synergistically facilitate aphid suppression and maintain ecosystem stability.

The mustard aphid, *Lipaphis erysimi* (Homoptera: Aphididae) is one of the most harmful cruciferous crop pests, and is widespread across the world (Prasad and Phadke, 1988; Liu et al., 1997). The infestation rate in the field reaches occasionally up to 90% (Bakhetia, 1983; Malik and Anand, 1984; Rohilla et al., 1987). Since chemical pesticides would

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cause harm to both human and environment (Garratt and Kennedy, 2006; Youn et al., 2003), the release of biological control agents gains attention gradually (Leskey et al., 2012; Lee et al., 2013). *Diaeretiella rapae* M'Intosh (Hymenoptera: Braconidae) has a significant effect on controlling mustard aphid (Ohiman and Kunar, 1986; Desneux et al., 2005), and *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) is also widely used in the biological control of *L. erysimi* (Adachi-Hagimori et al., 2011). Both *D. rapae* and *H. axyridis* are regarded as biological control agents of mustard aphid, but *H. axyridis* always consume the parasitoid within aphids accidentally in predator-parasitoid-aphid systems (Pell et al., 2008). Therefore, the interactions between *H. axyridis* and *D. rapae* should be studied to properly use them in the biological control of *L. erysimi*.

Studies on the interactions between *H. axyridis* and *D. rapae* in stable ecosystems are meaningful from a IPM perspective as predator-parasitoid-aphid interactions may either disrupt existing ecological balance or create a more stable community. In this study, we addressed 3 main questions: 1) Whether *H. axyridis* can discriminate among unparasitized, non-mummified parasitized and mummified aphids. 2) Which developmental stages of aphids were preferred by *H. axyridis* when *D. rapae* turned them into mummies. 3) Which developmental stages of aphids were preferred by *D. rapae* when *H. axyridis* interfered with parasitization.

Materials and methods

Insects

The colonies of L. *erysimi* (about 3000) and *D. rapae* (500) were collected from the experimental farm of Florida A&M University, FL, in 2017. Aphids were reared on pepper plants, and parasitoids were provided with the fresh aphids twice a week. A *H. axyridis* colony (about 200) was collected in the same location and was reared using fresh aphids as prey. All colonies were maintained in greenhouse at LD 16: 8, 26 °C and 70% RH. Fresh aphids at various developmental stages used in experiments were < 12 h old. < 48 h old *H. axyridis* adults after pupation were selected, and starved for 24 h before the experiments. All *D. rapae* females in the experiments were 4-d-old and mated. The experiments were performed from 2017 to 2018 in the Center for Biological Control, Florida A&M University, under conditions at LD 16: 8, 26 °C and 70% RH.

Prey discrimination by H. axyridis

Our preliminary experiment showed that *H. axyridis* adults have a great ability to break the cuticle of mummies and consume the nutrients inside, and an adult could consume at most 40 4th-instar nymphal aphids in 3 h. Thus, to evaluate the prey discrimination by *H. axyridis* among unparasitized, non-mummified parasitized and mummified aphids, 40 fresh 4th-instar nymphal aphids on the leaves of pepper plant were exposed to randomly selected 10 *D. rapae* females in a Petri dish (9 cm diameter). Parasitization by *D. rapae* could be identified by the presence of a dark spot on the aphid. When all the nymphs were parasitized in 2 h, a *H. axyridis* adult was introduced into the Petri dish 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 or 11 days later. The number of consumed aphids was recorded after 3 h. Moreover, 40 fresh 4th-instar nymphs of *L. erysimi* were presented to a *H. axyridis* adult as control to assess consumption of fresh aphids. Each treatment was replicated 20 times (ladybug male:female = 1:1) simultaneously.

Effect of the parasitization by D. rapae on the prey preference of H. axyridis

Since *D. rapae* showed a negative preference for 1st-instar nymphal aphids with low parasitism rate, the 1st-instar nymphs were not used as treated subjects. Thus, to study whether the parasitization by *D. rapae* could affect the prey selection of *H. axyridis*, overall 40 fresh aphids (containing equal numbers of 2nd-, 3rd- and 4th-instar nymphs, and adults) were parasitized by *D. rapae* in a Petri dish (9 cm diameter). Based on the previous outcomes (trial "Prey discrimination by *H. axyridis*"), *H. axyridis* could discriminate against mummies rather than non-mummified parasitized aphids, so only mummies could potentially impact the prey selection of *H. axyridis*. Then the parasitizition events were monitored daily until all the 40 aphids became mummies, and a *H. axyridis* adult was introduced into the Petri dish. Besides, 40 fresh aphids containing equal numbers of aphids at the four developmental stages were offered to a *H. axyridis* adult as control. The number and stage of consumed prey were recorded after 3 h, then the preference and switching coefficients were calculated. Each treatment was replicated 10 times (ladybug male:female = 1:1) simultaneously.

Effect of introduced H. axyridis on the host preference of D. rapae

To analyze if the presence of *H. axyridis* could impact the host preference of *D. rapae*, overall 40 fresh aphids (containing equal numbers of 2nd-, 3rd- and 4th-instar nymphs, and adults) were exposed to a *D. rapae* female in a Petri dish (9 cm diameter). Instead of glass cover, the Petri dish was covered with medical gauze preventing *D. rapae* from escaping, and moved into a plastic container (22.0 × 15.0 × 8.0 cm) containing 20 *H. axyridis* adults free to wander around the Petri dish. Ladybugs could not enter the Petri dish (had no physical contact with the parasitoid and aphids), but the *D. rapae* female was potentially stimulated by chemical volatile released by *H. axyridis*. A similar protocol was followed as control, only the ladybugs were removed. Aphids were examined until the female parasitoid left them for > 30 min, the preference and switching coefficients were calculated by recording the number and stage of parasitized aphids. Each treatment was replicated 10 times simultaneously.

Statistical analyses

Preference coefficients of both predator (Zhou and Chen, 1987a) and parasitoid (Wu et al., 2017) can be analyzed through preference model (eq. 1), and the model is used to describe the preference of *H. axyridis* or *D. rapae* when aphids at various developmental stages co-exist:

$$Q_i = (1 + C_i)/(1 - C_i) \times F_i \tag{1}$$

where Q_i is the proportion of aphid i consumed by predator (or parasitized by parasitoid); F_i is the initial proportion of aphid i; C_i is the preference coefficient of predator/parasitoid for aphid i. $C_i = 0$ indicates no preference for aphid i; $0 < C_i < 1$ or $-1 < C_i < 0$ indicates positive or negative preference for aphid i.

The switching behavior equation (Eq. (2)) (Zhou and Chen, 1986, 1987b) is used to evaluate switching levels in preference when *H. axyridis* or *D. rapae* affects each other:

$$Q_i = \frac{1 + C_i'}{1 - C_i'} F_i^{1 - S_i} \tag{2}$$

where Q_i and F_i are described in eq. 1; C_i' is the preference coefficient in the control group; S_i is the switching coefficient in preference from the control to treatment group. $S_i = 0$ indicates no switching behavior for aphid i; $0 < S_i < 1$ or $-1 < S_i < 0$ indicates positive or negative switching behavior for aphid i.

Descriptive statistics were given as the mean values and standard errors of the mean. In the prey discrimination experiment, the proportions of consumed or parasitized aphids were analyzed with χ^2 tests, with values for each combination of factors calculated based on the resulting standardized residual (crosstab analysis), and compared to Bonferroni-corrected P values testing whether the each proportion of consumed or parasitized aphids significantly differed from a mean proportion of that outcome across the various time intervals or developmental stages of aphid. Overall proportions of consumed aphids
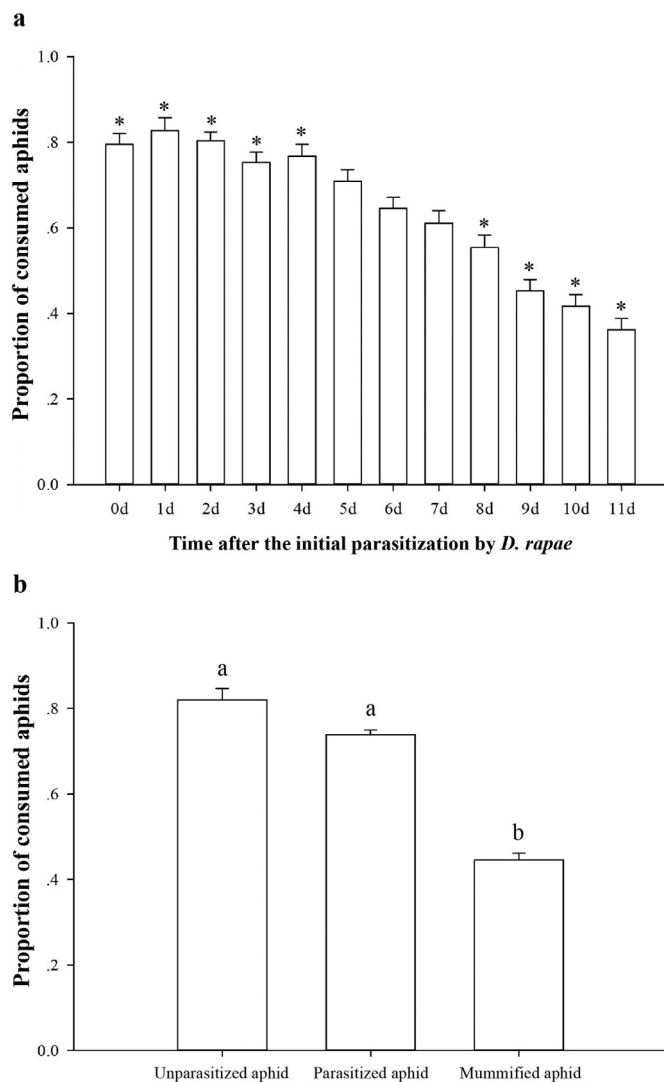
a

b

Fig. 1. (**a**) Proportion of previously parasitized 4th-instar nymphs of L. *erysimi* consumed by a *H. axyridis* (Mean ± SE). Bars with asterisks (*) indicate each proportion of consumed aphids that differed significantly from the mean expected proportion across the time after parasitization (χ^2 tests with Bonferroni corrections). (**b**) Overall proportion of unparasitized, parasitized and mummified aphids consumed by a *H. axyridis* adult (Mean ± SE). Different letters indicate significant differences among the treatments (mean separation by Tukey's HSD, $P < .05$).

among unparasitized, parasitized and mummified aphids were analyzed using one-way ANOVA with the Tukey HSD test of significance at the 5% level of statistical significance. The preference or switching coefficients were compared to $C_i = 0$ or $S_i = 0$ using one-sample t-test, P values $< .05$ were considered significant. All statistical analyses were conducted using the SPSS 20.0 software (IBM, Armonk, NY).

Results

Prey discrimination by H. axyridis

Non-mummified parasitized aphids were detected 0–7 days following exposure to *D. rapae*, then aphids were mummified and mummies were observed from the remaining time intervals (8–11 days). *H. axyridis* could discriminate among aphids of different ages previously parasitized by *D. rapae*. Although aphids were parasitized, *H. axyridis* still had high consumption of aphids recently parasitized by *D. rapae* (non-mummified parasitized aphids), whereas reluctantly consumed

older ones (mummies) ($\chi^2_{(11, \ N=9600)} = 1011.363$, $P < .0001$; 24 comparison tests, adjusted $\alpha = 0.002083$; Fig. 1a). Overall, compared to unparasitized aphids (82.0 ± 2.7%), mummies (44.6 ± 1.6%) rather than non-mummified parasitized aphids (73.9 ± 1.1%) were less acceptable ($F_{2,257} = 140.803$, $P < .001$; Fig. 1b).

Effect of the parasitization by D. rapae on the prey preference of H. axyridis

In control experiments, *H. axyridis* failed to discriminate among unparasitized aphids at different developmental stages ($\chi^2_{(3, \ N=400)} = 4.510$, $P = .211$; 8 comparison tests, adjusted $\alpha = 0.00625$, P of each test > adjusted α; Fig. 2a). When aphids were parasitized by *D. rapae* and become mummies, more adults were consumed by ladybugs, whereas the proportions of 2nd- and 3rd-instar nymphs decreased ($\chi^2_{(3, \ N=400)} = 130.122$, $P < .0001$; 8 comparison tests, adjusted $\alpha = 0.00625$; Fig. 2b). Based on Table 1, when unparasitized aphids at various stages coexisted, no preference was shown by ladybugs (P of each test > 0.05). After aphids were parasitized, *H. axyridis* significantly preferred adult mummies ($t_9 = 11.952$, $P < .001$) to 4th-instar nymphal mummies ($t_9 = 0.242$, $P = .814$), and totally ignored 2nd-instar ($t_9 = 5.611$, $P < .001$) and 3rd-instar ($t_9 = 3.799$, $P = .004$) nymphal mummies. Thus, after *D. rapae* turned aphids into mummies, *H. axyridis* changed the consumption strategy. It significantly switched from 2nd-instar ($t_9 = 7.34$, $P < .001$) and 3rd-instar ($t_9 = 3.488$, $P = .007$) nymphs to adults ($t_9 = 7.342$, $P < .001$) of L. *erysimi*, without showing a very strong switch to 4th-instar nymphs ($t_9 = 0.298$, $P = .773$).

Effect of introduced H. axyridis on the host preference of D. rapae

Diaeretiella rapae displayed a extremely aggressive behaviour towards 4th-instar nymphal aphids before *H. axyridis* was introduced, and a significantly smaller proportion of parasitization on 2nd-instar nymphs was detected ($\chi^2_{(3, \ N=400)} = 92.753$, $P < .0001$; 8 comparison tests, adjusted $\alpha = 0.00625$; Fig. 3a). With the presence of *H. axyridis*, 3rd-instar nymphal aphid suffered relatively frequent attacks from *D. rapae*, while significantly fewer adult aphids were parasitized ($\chi^2_{(3, \ N=400)} = 50.460$, $P < .0001$; 8 comparison tests, adjusted $\alpha = 0.00625$; Fig. 3b). Table 2 showed that 4th-instar nymphs of aphid ($t_9 = 6.871$, $P < .001$), were obviously preferred by *D. rapae*, whereas the 2nd-instar nymphs ($t_9 = 5.671$, $P < .001$) were dramatically less acceptable in control experiments. After *H. axyridis* was introduced, *D. rapae* showed significantly positive and negative preferences for the 3rd-instar nymphs ($t_9 = 4.813$, $P = .001$) and adults ($t_9 = 3.777$, $P = .004$), respectively. Therefore, when *H. axyridis* was present, *D. rapae* tended towards younger nymphal aphids (2nd-instar, $t_9 = 4.893$, $P = .001$; 3rd-instar, $t_9 = 2.424$, $P = .038$), while markedly neglected 4th-instar nymphs ($t_9 = 3.761$, $P = .004$) and adults ($t_9 = 2.72$, $P = .024$).

Discussion

Harmonia axyridis can discriminate against mummies of D. rapae

Interactions in predator-parasitoid-aphid systems can shape community structures and determine pest populations from a biological control perspective (Ferguson and Stiling, 1996; Symondson et al., 2002). Thus, understanding competitive interactions between predators and parasitoids, especially the degree of discrimination against parasitized prey by predators, contributes to establishing stable biological control systems (Rosenheim, 1998). Predators avoiding parasitized prey may work synergistically with the parasitoids in pest suppression (Heinz et al., 1994; Heinz and Nelson, 1996; Colfer and Rosenheim, 2001), while predators preferring parasitized prey may disrupt the biological control system (Snyder and Ives, 2001). Predators failing to discriminate between parasitized and unparasitized prey may have
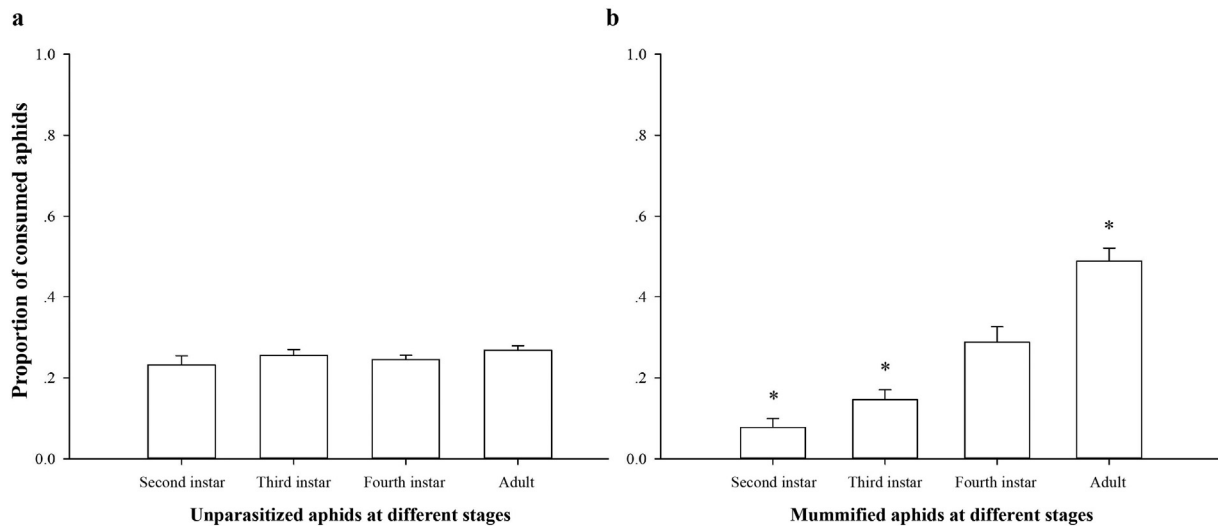
Fig. 2. Proportion of aphids (**a**) or mummies (**b**) at various stages consumed by a *H. axyridis* adult (Mean ± SE). Bars with asterisks (*) indicate each proportion of consumed aphids that differed significantly from the mean expected proportion across various stages of aphid (χ^2 tests with Bonferroni corrections).

Table 1
Preference and switching levels of *H. axyridis*.

Aphid i	C_i' (Control)	C_i (Treatment)	S_i
Second instar nymph	−0.0583 ± 0.0209	−0.5912 ± 0.1054**	−0.8093 ± 0.1103**
Third instar nymph	0.0025 ± 0.0310	−0.3102 ± 0.0817**	−0.5046 ± 0.1447**
Fourth instar nymph	−0.0155 ± 0.0233	0.0199 ± 0.0820	0.0431 ± 0.1447
Adult	0.0308 ± 0.0209	0.3138 ± 0.0263**	0.4276 ± 0.0583**

C_i' (C_i) is the preference coefficient of *H. axyridis* on fresh (mummified) aphid i; S_i is the switching coefficient in preference from the control to treatment group. Asterisks indicate significant differences in parameters compared to $C_i = 0$ or $S_i = 0$ (one sample *t*-test, **$P < .01$).

neutral effects on pest management (McGregor and Gillespie, 2005). Our study showed that *H. axyridis* could discriminate against mummies of *D. rapae*, suggesting that *H. axyridis* tended to reject mummies, even if this inferior prey still ensured healthy growth of the ladybug (Fu et al., 2017). Mummies are merely richer in proteins and lipids, while fresh aphids are more abundant in carbohydrates (Fu et al., 2017). Thus, accumulating insufficient energetic components can possibly result in developmental delay, triggering a series of negative effects on the growth (Takizawa et al., 2000). In order to avoid the adverse effect

on development, *H. axyridis* tends to select fresh aphids rather than mummies after evaluating the cost of consuming mummies, so *D. rapae* potentially benefits from the prey discrimination, and similar results are also reflected in other predator-parasitoid-pest systems (Snyder et al., 2004; Meyhöfer and Klug, 2002; Chong and Oetting, 2007). Interestingly, we found that *H. axyridis* failed to discriminate between unparasitized and non-mummified parasitized aphids, some studies even suggested *H. axyridis* preferred non-mummified parasitized aphids to unparasitized ones (Meisner et al., 2011). Even if *H. axyridis* can
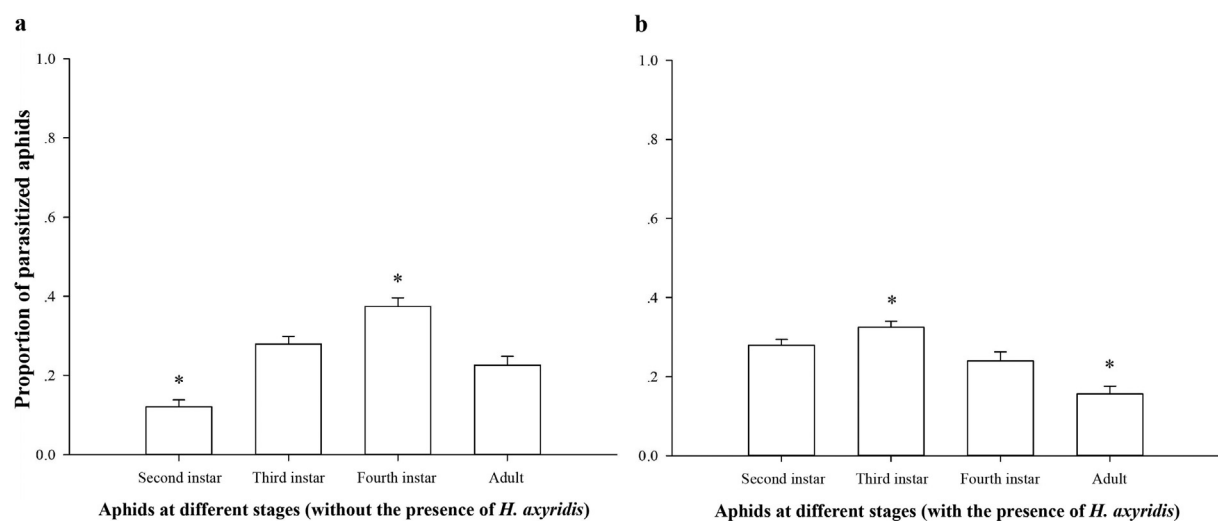

Fig. 3. Proportion of aphids at various stages parasitized by a *D. rapae* female without (**a**) or with (**b**) the presence of *H. axyridis* (Mean ± SE). Bars with asterisks (*) indicate each proportion of parasitized aphids that differed significantly from the mean expected proportion across various stages of aphid (χ^2 tests with Bonferroni corrections).

Table 2
Preference and switching levels of *D. rapae*.

Aphid *i*	C_i' (Control)	C_i (Treatment)	S_i
Second instar nymph	-0.3761 ± 0.0663**	0.0479 ± 0.0289	0.6770 ± 0.1384**
Third instar nymph	0.0438 ± 0.0348	0.1236 ± 0.0257**	0.1161 ± 0.0479*
Fourth instar nymph	0.1898 ± 0.0276**	-0.0396 ± 0.0463	-0.3377 ± 0.0898**
Adult	-0.0697 ± 0.0473	-0.2605 ± 0.069**	-0.3128 ± 0.115*

C_i' (C_i) is the preference coefficient of *D. rapae* on aphid *i* without (with) the presence of ladybug; S_i is the switching coefficient in preference from the control to treatment group. Asterisks indicate significant differences in parameters compared to $C_i = 0$ or $S_i = 0$ (one sample *t*-test, *P < .05; **P < .01).

discriminate against mummified aphids, the consumption rate of mummies still reaches 44.6%. The ladybug may only discriminate against aphids at specific developmental stages when they become mummies, so mummy preference of *H. axyridis* deserves further study.

Harmonia axyridis tends to the adults when aphids become mummies

Predators tend to search for the most beneficial prey (Crawley and Krebs, 1992), they benefit by recognizing chemical marks left by parasitoid females or morphological/physiological changes caused by larval parasitoids (Almohamad et al., 2008). Once testing the physical or chemical changes in parasitized prey, predators target the most suitable prey (Hoelmer et al., 1994). Therefore, *H. axyridis* positively switched to consuming the big-sized, more nutritional adults once aphids became mummies. The study suggests that, since *H. axyridis* spends a large amount of time handling a mummy (Bilu and Coll, 2009), it needs to maximize the energy collection every time it breaks the hardened cuticle. The choice of prey helps not only decrease loss of time, but also increase energy accumulation (Stephens and Krebs, 1986). Mummified aphids served as inferior prey have limited nutritional values (Bilu and Coll, 2009), but prey quality is extremely important for survival and development of coccinellids (Almohamad et al., 2007), so *H. axyridis* tended to search for relatively more nutritional adult mummies to keep energy return. Moreover, parasitized aphids still produce honeydew as a kairomone attracting predators (Carter and Dixon, 1984; Budenberg, 1990). Compared to nymphs, adult aphids may produce more carbohydrate-rich excretions before being mummified, potentially attracting more ladybugs. As the selection of prey/host can improve the survival and growth of offspring (Peckarsky et al., 2000), it is important not only to predators, but to parasitoids. Thus, the study on the host preference of parasitoids is also valuable.

Diaeretiella rapae switches to younger nymphal aphids when H. axyridis interferes with the parasitization

Parasitoids are prone to avoid competitive interactions with predators by visual recognition and chemical detection (Nakashima and Senoo, 2003; Nakashima et al., 2004). For instance, the aphid parasitoid *Aphidius ervi* significantly reduces the time spent searching for and handling the host when *C. septempunctata* presents (Taylor et al., 1998). In order to reduce the period of exposure to predatory competitors, the best strategy of parasitoids is to select to parasitize the less-resistant hosts within the shortest time frame. Thus we found that, when *H. axyridis* was introduced and interfered with the parasitization, *D. rapae* tended to attack younger nymphal aphids with low-resistance to reduce its handling time. Avoidance behavior can help parasitoids reduce direct confrontation with predatory opponents, benefiting the offspring fitness and population stability (Chong and Oetting, 2007). Both *H. axyridis* and *D. rapae* can avoid each other in competitive interactions, so they have the potential to coexist in the biological control of *L. erysimi*.

Potential coexistence of H. axyridis and D. rapae in the biological control of L. erysimi

Predators are likely to cause negative effects on parasitoids in predator-parasitoid-aphid systems by feeding on parasitoids within aphids, impacting the biological control of aphids (Snyder and Ives, 2003; Pell et al., 2008). Ideally, predators can coexist with parasitoids to improve aphid suppression (Moreno-Ripoll et al., 2013; Gontijo et al., 2015). The results from our laboratory experiments imply that *H. axyridis* can discriminate against mummies of *D. rapae*, and indicate that both *H. axyridis* and *D. rapae* can avoid direct resource competition by attacking different and non-overlapping developmental stages of *L. erysimi*. In fact, *H. axyridis* and *D. rapae* have the potential to coexist and establish a stable ecosystem in controlling *L. erysimi*. Nevertheless, this would have to be evaluated with subsequent field experiments as laboratory studies acting as simplified systems cannot be directly extrapolated to field results (Bogran et al., 2002).

In spite of possible coexistence, the compatibility between *H. axyridis* and *D. rapae* in the control of *L. erysimi* still depends on the interval between releases. Coccinellids fail to discriminate against non-mummified parasitized aphids, potentially resulting in massive losses of parasitoids, so *H. axyridis* should be released after mummies emerge to ensure the control effectiveness of parasitiods. Thus, eight days after the initial release of *D. rapae*, the release of *H. axyridis* is recommended based on the outcome of our study. Therefore, understanding the interactions between *H. axyridis* and *D. rapae* contributes greatly to practical applications of them in the biological control of *L. erysimi*.

Conflicts of interest

The authors declare that they have no conflicts of interest in this work.

Acknowledgments

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