

The influence of aphids (*Myzus persicae*) and pink lady beetle larvae (*Coleomegilla maculata*) on host plant preference of imported cabbageworm (*Pieris rapae*)

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Abstract Oviposition decisions by herbivorous insects hinge on multiple factors, with some of the most important being enemy-free space and competition for resources. It is important to understand whether and how herbivores and predators can influence the maternal egg-laying preference when they are alone and in combination with host plants. Here, we evaluate whether the presence of aphids (a competitor) or a lady beetle larvae (a predator) influence host plant selection by an ovipositing butterfly. Canola (*Brassica napus* L.) was the highest quality of three putative Brassicaceae host plants for aphids *Myzus persicae* (Sulzer) (Hemiptera: Aphididae), while the butterfly *Pieris rapae* (L.) (Lepidoptera: Pieridae) showed similar survival on all. Canola was used to determine that the presence of a competitor herbivore (aphids) had no effect on butterfly oviposition behavior. However, predators significantly influenced the number of eggs laid on the plants, especially on those plants that had both aphids and a lady beetle larva present in combination. We expect that adult female *P. rapae* did not lay their eggs on the treatment that involved both herbivorous competition and predation risk, due to the combined risk factors along with the volatile chemicals and aphid alarm pheromones emitted on those plants that contained both the aphids and lady beetle larva.

Keywords Canola · Maternal preference · Multi-trophic interactions · Oviposition · Predator

Introduction

Oviposition decisions for herbivorous insects are often a compromise between two opposing needs: A female must select a site that maximizes the survival of her offspring (Jaenike 1978; Craig et al. 1989; Stein and Price 1995), but must also capitalize their lifetime reproductive potential by considering the accessibility and concentration of host plants within a habitat (Wiklund 1975, 1984; Thompson 1988; Thompson and Pellmyr 1991; Nishida 1995; Heisswolf et al. 2005; Wiklund and Friberg 2008). Allelochemicals, nutritional chemistry, morphology, and feeding style influence host plant preference in ovipositing insects (Miller and Strickler 1984; Thompson and Pellmyr 1991; Awmack and Leather 2002; Seagraves 2009; Lundgren et al. 2011). Host plant preference is also often affected by the resident insect community on a particular plant, resulting in potential multi-trophic interactions (Price et al. 1980; Bernays and Graham 1988; Wiklund and Friberg 2008). The resident community on a potential host plant can alter the oviposition decision in several ways; for example, the mother may decide to change where she lays her egg on the host plant to avoid predation or competition (Thompson and Pellmyr 1991; Renwick and Chew 1994; Pumarinno et al. 2012), readjust her plant preferences within a habitat (Mousseau and Fox 1998; Seagraves and Yeargan 2006), or decide to oviposit in a different habitat altogether (Craig et al. 1989). When other herbivores are present on particular host plants, butterflies can be warned by chemical deterrents to avoid that plant, allowing for reducing offspring competition for the food source (Dicke

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2000; Ngu et al. 2008). Also, undamaged plants can emit combinations of volatile chemicals that may affect their attractiveness to herbivores (Visser 1986), making the damaged plant more obvious to them in comparison with its undamaged neighbors (Dicke 2000). Threat of predation strongly influences maternal decisions, and natural selection can favor the ability to detect predators in order to choose enemy-free plants (Schmitz et al. 2004; De-Silva et al. 2011). For example, insects will sometimes preferentially choose to oviposit on plants with thorns, spines, or prickles, or that produce secretions which impede the movements of smaller predators and parasitoids in search of prey (Price et al. 1980; Raven et al. 2013). Sendoya et al. (2009) found that *Eunucia bechina* (Hewitson) (Lepidoptera: Nymphalidae) butterflies shift their egg-laying preferences to less risky foliage by using visual cues to determine whether predacious ants are present on particular plants, and this adaptive behavior improves offspring survival.

Plants in the Brassicaceae host a broad insect community of both specialist and generalist herbivores (Hopkins et al. 2009; Layman and Lundgren 2015). Many of these herbivores use *Brassica*-produced glucosinolates to help them identify potential host plants (Hopkins and van Loon 2001; Richards 1940). A specialized herbivore that occurs on *Brassica* spp. (including canola) is the imported cabbageworm (*Pieris rapae* L.; Lepidoptera: Pieridae), which oviposits and feeds only on plant species that produce glucosinolates (Hopkins and van Loon 2001). Adult females use gustatory receptors to detect glucosinolates on the leaf surface (Ma and Schoonhoven 1973; Renwick et al. 1992), and ovipositing females are capable of differentiating among different species of brassicas and even among different leaf stages within the plants (Ives 1978). Larvae of *P. rapae* are well-known pest insects on brassica crops (Hopkins and van Loon 2001; Lundgren et al. 2002). One generalist herbivore in particular that occurs on some *Brassica* spp. is the green peach aphid (*Myzus persicae* Sulz; Hemiptera: Aphididae). This species is found on a variety of crops, including the oilseed crop canola (*Brassica napus* L; Brassicales: Brassicaceae) (Desneux and Ramirez-Romero 2009).

Predators of these specialist and generalist herbivores also reside on *Brassica* spp. Predators and parasitoids of *M. persicae* include adult and immature Coccinellidae, Syrphidae, Nabidae, Miridae, many parasitoids including *Aphidius matricariae* (Hymenoptera: Aphidiidae), and *Aphidius sonchi* (Hymenoptera: Aphidiidae), to name only a few (van Emden et al. 1969). The predator community of *P. rapae* eggs ranges from ants to lady beetle adults and larvae, to ground-dwelling predators such as *Phalangium opilio* (Arachnida: Phalangidae) (Dempster 1967; Evans 2009; Ashby and Pottinger 2012). The caterpillar stage is

commonly killed by four main parasitoids: *Cotesia rubecula* (Hymenoptera: Braconidae), *Cotesia glomeratus* (Hymenoptera: Braconidae), *Phryze vulgaris* (Diptera: Tachinidae), and *Epicamponera succinata* (Diptera: Tachinidae) (Dempster 1967; Ashby and Pottinger 2012), while the pupae of *P. rapae* are frequently parasitized by *Pteromalus puparum* (Hymenoptera: Pteromalidae) (Ashby and Pottinger 2012).

Predacious ants have been found to readily consume eggs as an alternative food source to aphids in laboratory studies, and likely in the field (Layman and Lundgren 2015). However, under choice conditions would an ovipositing female butterfly choose to lay her eggs on plants that had predacious or herbaceous forms of competition present? In order to assess how these potential competitors and predators on host plants influence maternal egg-laying preference of female *P. rapae*, we instigated oviposition decisions by egg-laying females within an enclosed canola system, and provided experimental justification for selecting this study system. We hypothesized that adult female *P. rapae* will not lay their eggs on treatments that involve both herbivorous competition from aphids and risk of predation in the form of the lady beetle larva, and also that consumption of *P. rapae* eggs by the lady beetle larva increases with the presence of aphids. In order to test these hypotheses, female *P. rapae* were put under choice conditions with host plants infested with differing degrees of competition.

Materials and methods

Plants

Canola, cabbage (var. Copenhagen Markey Early, *Brassica oleracea* L., Brassicales: Brassicaceae), and black rapeseed (*Brassica carinata*, A. Braun) plants were sprouted in peat pellets (Jiffy Products, Shippagen NB, Canada) and then transferred to soil mix (4:2:1 parts vermiculite/peat moss/field soil) at the first growth stage. Plants were grown in a greenhouse with an average temperature of 27 °C and a photoperiod of 16:8 h L/D (light/dark), and they were watered daily. To test for aphid preferences, plants were grown in the greenhouse until the black rapeseed and canola reached the second growth stage (≈ 12.7 cm tall), and the cabbage reached stage 2 (Andaloro et al. 1983) with up to five true leaves (≈ 15.24 cm tall).

Insects

A population of imported cabbageworm, *P. rapae*, was developed from locally collected adults and reared on canola plants. Enclosed adults were housed in a 61 × 61 cm mesh-

covered cage and were fed a sports drink (Cool Blue, Gatorade, Chicago, IL), and a salt-mineral water solution (Champion's Choice Trace Mineral Small Animal Spool Salt Lick, Cargill Inc., Minneapolis, MN) in separate dishes. A colony of *M. persicae* were reared on russet potato plants (≈ 35 – 50 cm tall) in the laboratory for 24–68 days prior to the treatment, in a $42 \times 33 \times 31$ cm plastic enclosure (Sterlite Corporation, Townsend, MA). *Coleomegilla maculata* De Geer (Coleoptera: Coccinellidae) were obtained from a colony of locally collected beetles that had been in culture for at least 6 mo. Individuals were sexed, and females were separated into individual 30-mL plastic cups (Dixie Consumer Products LLC, Atlanta GA) and fed Lundgren Super C mac Diet (Lundgren et al. 2011). Larvae were raised on this diet until they reached the second stadium, when they were used for the experiment.

Aphid performance on different host plants

Aphid population growth on three *Brassica* species was quantified using 20 plants each of canola, cabbage, and black rapeseed. Each plant was infested with 50 aphids, and the populations of aphids were weighed prior to infestation. The plants were enclosed within clear, plastic columnar cages (13 cm diameter, 41 cm tall) with the top covered in fine mesh for ventilation. Cages were housed with a 16:8 L/D photoperiod, an average temperature of 27 °C, and an average relative humidity of 29 %. After 7 days, the aphids were removed from the plants, counted, and weighed again.

Pieris rapae performance on different plants

Maternal preference and survival potential for the three *Brassica* species were tested under no choice conditions using 15 groups of butterflies with means (SEM) of 6.53 ± 2.12 , 7.33 ± 1.94 , and 7.13 ± 1.49 butterflies for black rapeseed, canola, and cabbage, respectively. The groups of butterflies were tested in 61×61 cm mesh-covered cages, each which housed one of the three plant types. Eggs and pupae produced from each egg cohort after 3 weeks were counted daily to determine oviposition preferences, and egg-to-pupae ratios were calculated for each group on each host plant.

Pieris rapae oviposition preferences

The influence of an herbivore competitor (aphids) and a predator (*C. maculata* larvae) on oviposition preferences of *P. rapae* females was examined under choice conditions on canola. Canola plants ($n = 104$) were randomly assigned to one of four treatments ($n = 26$ for each treatment) infested with one of the following: (1) no other

insects/clean, (2) 20 aphids, (3) a lady beetle larva in the second stadium, or (4) both aphids and a lady beetle larva. Plants were placed into screen-ventilated, clear plastic cages ($42 \times 33 \times 63$ cm). Each of the trials contained a plant from each treatment which was randomly placed in one of the four corners of the arena. To restrict movement among plants, a 1-cm band of Tanglefoot® (Contech Enterprises, Victoria, BC) was applied to the lower stem of each plant, and care was taken to ensure that neither the pot nor the plant touched either the wall of the enclosure or neighboring plants.

Each arena received two female and one male butterflies to reduce sperm limitation for the length of the trial. The tests were conducted in the greenhouse with a photoperiod of 16:8 and an average temperature of 29° C. Adult butterflies were fed sports drink during the experiment. Egg placement per plant was monitored daily for 5 days. Leaves on each plant (except for the first day of counting) were labeled sequentially from bottom to top. Counts were separated based on plant structure in an attempt to better understand spatial patterns in relationship to the egg-laying butterflies.

The number of eggs laid on the leaves was recorded along with the location of the eggs on either the top or the bottom of the leaf. Predation by lady beetle larvae often leaves the egg chorion as evidence of the predation event; these chorions were searched daily to determine lady beetle predation. Once the eggs were counted, they were removed with a dampened paint brush. Any missing insects from a plant were replaced daily.

Data analysis

Statistical analyses and significance tests ($\alpha < 0.05$) were performed by using Systat 13 (Systat Software Inc., San Jose, CA.). We compared the mean aphid weights and number of aphids remaining on each plant species using ANOVA, and means were separated using Fisher's LSD test and presented with their SEM.

The number (square root transformed to accommodate the assumptions of ANOVA) of eggs laid on each of the four treatments was compared among treatments using a two-way, repeated-measures ANOVA; the presence of aphids or lady beetles was the main factor in the analysis, and each plant leaf and side of each plant leaf (top or rim) were considered within-subject effects. ANOVAs were used to determine which of the four treatments differed significantly from one another in total number of eggs, and whether different treatments received significantly different egg numbers within particular plant structures. In these univariate ANOVAs, significantly different means were separated using Fisher's LSD test.

Results

Herbivore performance on brassica hosts

Aphids survived and reproduced differently on the three plant species, and the number of aphids that remained at the end of the experiment differed among the three host plants significantly ($F_{2,57} = 23.064$, $P < 0.001$) (Table 1). This reinforces the significant difference found among the treatments in the weight of the remaining aphids ($F_{2,57} = 40.75$, $P < 0.001$). *Pieris rapae* survived similarly on the three host plants. The mean (SEM) pupae-to-egg ratio was 0.08 ± 0.05 , 0.02 ± 0.01 , and 0.02 ± 0.01 for canola, cabbage, and black rapeseed, respectively. Since the caterpillar performance data showed no differences on any of the three plants, the information gathered from the aphid preference experiment was used to focus the subsequent assay on canola.

Pieris rapae oviposition preferences

Oviposition by cabbageworm butterflies was affected by the presence of lady beetle larvae (between-subjects ANOVA: Aphid: $F_{1,100} = 2.71$, $P = 0.10$; lady beetle: $F_{1,100} = 8.21$, $P = 0.005$; aphid \times lady beetle interaction: $F_{1,100} = 0.72$, $P = 0.40$). Univariate comparisons among the four treatments revealed that plants that had both aphids and a lady beetle larva had significantly fewer eggs in comparison with the treatments with no other insects ($F_{1,50} = 10.12$, $P = 0.03$) and with aphids only ($F_{1,50} = 8.81$, $P = 0.05$) (the two treatments that had lady beetles were statistically similar in oviposition) (Fig. 1). There were significantly different numbers of eggs laid on the different plant structures (within-subjects ANOVA: plant structure: $F_{9,900} = 32.78$, $P < 0.001$; plant structure \times aphid interaction: $F_{9,900} = 1.13$, $P = 0.34$; plant structure \times lady beetle interaction: $F_{9,900} = 2.46$, $P = 0.009$; plant structure \times aphid lady \times beetle interaction: $F_{9,900} = 1.21$, $P = 0.29$) (Table 2). Specifically, there were significantly fewer eggs laid in the treatment with both aphids and lady beetles compared to the treatment with aphids alone or with other insects removed from the system; this was particularly true for the third leaf (Table 2). The significant plant

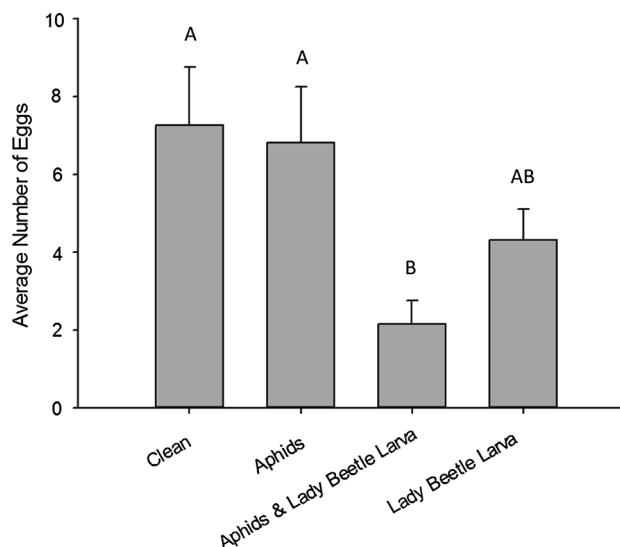


Fig. 1 Role of competitors and predators on oviposition preferences of a butterfly. Prior to the introduction of *Pieris rapae*, canola host plants were inoculated with one of four treatments: either aphids *Myzus persicae* (50 per plant), the predacious lady beetle larva *Coleomegilla maculata* (one per plant), both aphids and lady beetle larva, or un-inoculated/clean with no insects added ($n = 26$ plants per treatment). Two *P. rapae* females and one male were added into the system, and the number of eggs laid per treatment was monitored daily for 5 days. Bars represent treatment mean \pm SEM for each treatment. Bars topped with different letters are significantly different from one another ($\alpha = 0.05$)

structure \times lady beetle interaction was related to differences in the number of eggs laid on the leaf tops; more eggs were laid on tops of leaves 1 and 2 when lady beetles were present on the plants, and the opposite pattern was observed on leaves 3–5.

Discussion

Predators and herbivore competitors altered the ovipositional behavior of female butterflies, but only when the predator and herbivore co-occurred. Aphids performed better on canola in comparison with two other *Brassica* host plants, increasing both their population numbers and overall weight, while *P. rapae* performed equally well on

Table 1 *Myzus persicae* performance on three different brassica host plants

Plant	Number of aphids surviving	Average weight change (g)
Canola	261.6 ± 30.9	0.02 ± 0.002
Black rapeseed	217.5 ± 30.9	0.02 ± 0.003
Cabbage	23.6 ± 6.8	0.004 ± 0.0008
Statistics	$F_{2,57} = 23.064$, $P < 0.001$	$F_{2,57} = 40.75$, $P < 0.001$

Aphids (initially $n = 25$ per plant; $n = 20$ plants per species) were counted and weighed after 7 days

Table 2 Mean and SEM of the numbers of butterfly (*Pieris rapae*) eggs laid per canola plant on each of the four treatments

Treatment	First Leaf		Second Leaf		Third Leaf		Fourth Leaf		Fifth Leaf	
	Rim	Top	Rim	Top	Rim	Top	Rim	Top	Rim	Top
Clean	1.85 ± 0.56	0.08 ± 0.05	1.85 ± 0.66	0.23 ± 0.12	2.08 ± 0.43a	0.04 ± 0.04b	0.73 ± 0.27	0.27 ± 0.16	0.15 ± 0.12	0
Aphids	0.92 ± 0.29	0.08 ± 0.08	2.50 ± 0.83	0	2.08 ± 0.55a	0.46 ± 0.21a	0.35 ± 0.17	0.35 ± 0.18	0.04 ± 0.04	0.04 ± 0.04
Aphids and lady beetle larva	0.58 ± 0.19	0	0.73 ± 0.30	0.08 ± 0.05	0.54 ± 0.21b	0b	0.12 ± 0.06	0.08 ± 0.08	0	0.04 ± 0.04
Lady beetle larva	0.62 ± 0.17	0.15 ± 0.09	1.19 ± 0.32	0.23 ± 0.12	1.38 ± 0.42ab	0.23 ± 0.16ab	0.31 ± 0.13	0.08 ± 0.08	0.12 ± 0.12	0
Statistics	$F_{3,100} = 2.07,$ $P = 0.11$	$F_{3,100} = 1.05,$ $P = 0.37$	$F_{3,100} = 1.51,$ $P = 0.22$	$F_{3,100} = 1.77,$ $P = 0.16$	$F_{3,100} = 3.29,$ $P = 0.02$	$F_{3,100} = 2.68,$ $P = 0.05$	$F_{3,100} = 1.66,$ $P = 0.18$	$F_{3,100} = 1.19,$ $P = 0.32$	$F_{3,100} = 0.68,$ $P = 0.57$	$F_{3,100} = 0.67,$ $P = 0.57$

Aphids were *Myzus persicae*, and lady beetle larvae were *Coleomegilla maculata*. Different letters within a column indicate significant difference from one another ($\alpha = 0.05$)

all three plants, justifying our focus on canola as the plant for testing maternal preference. Female butterflies preferred laying a majority of their eggs on those plants with no other insects present, and laid the fewest eggs on the plants with both forms of competition. Aphids alone did not significantly affect egg-laying behavior of female butterflies despite being a potential competition source for butterfly offspring. However, the presence of a predacious lady beetle larva reduced oviposition when in combination with aphids. Reasons for these patterns are discussed below.

The three brassica host plant species supported aphid population growth differently, but *P. rapae* had equal survival on all three plants. Canola, cabbage, and black rapeseed are accepted hosts for both green peach aphids (Desneux and Ramirez-Romero 2009) and the imported cabbageworm (Hopkins and van Loon 2001). Aphid performance on the three plants showed that those aphids introduced on canola performed better than on the other two plants, as reflected both in aphid number and weight gain on the different plant species (Table 1). It is possible that black rapeseed and cabbage provided less nutrition or increased defenses relative to canola (VanEtten et al. 1976; Carlson et al. 1987; Kushad et al. 1999; Ciska et al. 2000; Cippollini 2002). For example, *M. persicae* populations are poorly supported if phloem is composed of less than 2 % amino acid (van Emden et al. 1969). This same pattern in relative performance was not seen in *P. rapae* larval development. We were unable to find information on relative larval performance on these three crops, but other studies observed a 16 % survival rate at pupation when this species was raised on black rapeseed (Traw and Dawson 2002; Van Dam et al. 2005). The egg-to-pupa ratio was fairly low (<10 % of eggs survived to pupation), which likely indicates that the butterflies were laying unfertilized eggs (we did not observe substantial larval mortality). Using the obtained information (that canola supported the highest aphid growth, and that the female butterflies survived equally well on the three test plants), canola was selected as the focal plant type for the maternal preference tests.

Aphids alone did not deter oviposition by the butterflies. Aphids consume phloem from the plant (Baker 1982; Johnson and Lyon 1988) (whereas imported cabbageworm larvae are defoliators), and direct competition for leaf tissue was likely minimal for these two herbivores. Still, aphid feeding changes the plant physiologically, which can affect herbivore competitors (Wool 2004; Qureshi and Michaud 2005; van Veen et al. 2006; Herbert et al. 2007). Damage by aphid feeding was not visually apparent in the 5-day trials, and therefore, the physiological changes in the host plant from aphid feeding (Palaniswamy and Lamb 1993; Siemens and Mitchell-Olds 1996) may have been

minimal in our experiment. When aphids were present on the leaves, they were found on the central vein on the bottom leaf surface. Nearly 80 % of the *P. rapae* eggs were laid on the outer edge of the leaf surface (Harcourt 1963), so direct interactions of the ovipositing females and aphids were likely minimal. Recent data (M.L.L. unpublished data) also demonstrate that these two species do not have adverse effects on survival of either herbivore in the absence of predators.

The presence of the predacious lady beetle larva deterred oviposition by *P. rapae* females, but only significantly so when aphids were present in combination with the lady beetle larva (Fig. 1). It was found that the third leaf was the only significantly different plant structure in both the number and proportion of eggs laid. This is most likely due to the fact that the third leaf is a bridge between the older leaves which *P. rapae* usually prefer to lay their eggs on, and the newer leaves which is where *M. persicae* prefer to feed. Due to its age, both *M. persicae* and *P. rapae* can often occur in combination with one another on this plant structure. Our experimental design supports the notion that this egg recovery pattern was driven by the oviposition behavior of the butterfly such that butterflies avoided aphid and beetle-occupied plants, but we cannot rule out the idea that predation may have contributed to the reduced egg numbers in the treatments with predators. Complete egg removal did not occur in any of the treatments over 5 days, most likely because aphids were also consumed by the developing larvae. Although we did not quantify aphid removal formally, replacement of aphids on those plants with a lady beetle larva was approximately twice as high in comparison with the plants with aphids only, likely due to the beetle larvae eating this preferred food source. If egg predation was occurring, this should have drastically reduced egg numbers in both predator treatments relative to the no-predator treatments; but we saw this reduction only when aphids were in the system. Moreover, if predation was responsible for the egg reductions, we would expect that the absence of aphids as an additional source of food would have lowered egg numbers relative to the treatment with aphids, but just the opposite pattern emerged. Given these patterns in the data, it seems likely that *P. rapae* adjusted its oviposition preferences in response to the treatments. Female butterflies use visual cues to determine whether predators are present on a plant (Sendoya et al. 2009). Information about risks of predation is critical for ovipositing females, and natural selection allows for the ability to detect and avoid predators in favor of enemy-free foliage (Schmitz et al. 2004). These visual cues are also known from flower-visiting bees and the ability to detect predator risk through the use of visual cues (Goncalves-Souza et al. 2008). However, it seems unlikely that visual cues entirely explain why females avoided aphids and the larva together but not when these other species were

present alone. Predation on aphids within a colony elicits a pheromone-based alarm signal (Pickett et al. 1992; Dixon 1998). These plant volatiles were most likely induced in these trials, along with the alarm signal when the aphids and the larva were present together, but not when the species in the system are alone. If the butterflies can detect this alarm, it might explain the pattern in oviposition we saw in our study.

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