

# Differential effects of experience on feeding and ovipositing preferences of a polyphagous leafminer

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Accepted: 4 August 2010

**Key words:** *Liriomyza huidobrensis*, host plant selection, natal habitat preference induction, learning, Diptera, Agromyzidae, *Vicia faba*, *Beta vulgaris*

## Abstract

Host preferences of phytophagous insects, although generally showing a strong hereditary component, can be modified by experience. Here we aim to elucidate the relative roles of larval and adult experience on host plant selection by *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae), a widely distributed pest on ornamentals and vegetables. Laboratory and field experiments evaluating feeding and oviposition preferences of *L. huidobrensis* females with larval, adult, or larva plus adult experience on either *Vicia faba* L. (Fabaceae) or *Beta vulgaris* var. *cicla* L. (Chenopodiaceae) were performed. Also, we measured offspring performance of *L. huidobrensis* on both host plant species. Our results show that *L. huidobrensis* females strongly preferred *V. faba* over *B. vulgaris* var. *cicla* for feeding and egg laying. Only larval and adult experience acting in concert modified feeding behaviour, whereas oviposition preferences remained unaltered regardless of female previous experience. Offspring performance was higher on the preferred host (*V. faba*), indicating a preference–performance linkage for this leafminer. Experience on *B. vulgaris* var. *cicla* could not overcome oviposition preferences, which appear driven by fitness benefits for offspring.

## Introduction

Polyphagous herbivore insects often prefer feeding and laying their eggs on particular plant species within their host range (Bernays & Chapman, 1994). These preferences show a strong heritable component, but can be modified by experience and other factors (Barron, 2001; Davis & Stamps, 2004; Dukas, 2008).

Some herbivorous insects show preferences for the host plant species on which they developed as larvae (Anderson et al., 1995; Rietdorf & Steidle, 2002; Akhtar & Isman, 2003; Moreau et al., 2008). Recently, natal habitat preference induction (NHPI) has been proposed as a broad concept to describe the effects of experience on preferences, encompassing specific terms of entomological (Hopkins host selection principle, chemical legacy hypothesis) and vertebrate (imprinting) literature (Davis & Stamps, 2004). This theory predicts that ‘experience with stimuli in an

individual’s natal habitat increases the probability that the individual will, following dispersal, select a habitat that contains comparable stimuli’.

On the other hand, successive encounters of adult insects with a host plant species can also lead to increased acceptance of that host, regardless of larval or early adult experience (AE) (e.g., Cooley et al., 1986; Cunningham et al., 1998; Wallin & Raffa, 2002). In general, this process is termed learning, although various mechanisms (habituation, sensitization, etc.) can be involved (Bernays & Weiss, 1996). Learning is not equally likely among species: generalist species (Papaj & Prokopy, 1989) or species capable of obtaining information about the probable impact that decisions would have on their fitness (Parmesan et al., 1995) appear to be more capable of learning. Resource predictability can also affect learning occurrence, which is most likely when host plant availability is constant within generations but varies unpredictably between generations (Stephens, 1993).

The relative importance of larval and adult experience on host plant selection by phytophagous insects has been

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studied in a number of species (e.g., Tabashnik et al., 1981; Solarz & Newman, 2001; Kerpel & Moreira, 2005). However, less attention has been paid to the possibility of synergistic interaction between larval and adult experience (Jaenike, 1983; Liu & Liu, 2006). In addition, although feeding and oviposition choices could have dissimilar ecological and evolutionary consequences and could be differentially affected by experience (McNeely & Singer, 2001), few studies have simultaneously analysed the effect of experience on both aspects of plant selection (McNeely & Singer, 2001).

The aim of this study was to elucidate the effects of experience at different life stages on feeding and oviposition preferences of the polyphagous leafminer *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae), a widely distributed pest of several ornamental and vegetable crops (Dempewolf, 2004). In this species, adult females can be highly selective during oviposition, ranking host plants according to suitability for offspring development (Videla et al., 2006). Moreover, their feeding preferences can be altered by larval experience (LE) (Facknath & Wright, 2007). Here we analyse the leafminer response to two plant species, *Vicia faba* L. (Fabaceae) and *Beta vulgaris* var. *cicla* L. (Chenopodiaceae), occupying the first and second positions, respectively, in the host-use ranking of *L. huidobrensis* in the study region (Valladares et al., 1996; Videla et al., 2006). Whether female preferences differ between these highly used hosts has not yet been tested.

Learning occurrence might be expected in *L. huidobrensis*, given its polyphagy and larger intra- than inter-generation host predictability (Cunningham et al., 1998). However, the effects of adult experience on feeding behaviour, as well as the influence of both larval and adult experience

on oviposition preferences remain unknown. Specifically, we asked whether feeding and oviposition choices of this leafminer are influenced by larval and/or by adult experience and whether additive effects of experience through both life stages can reinforce insect preference for the experienced host. We also explored possible underlying mechanisms for *L. huidobrensis* preferences, by examining host plant effects on leafminer performance.

## Materials and methods

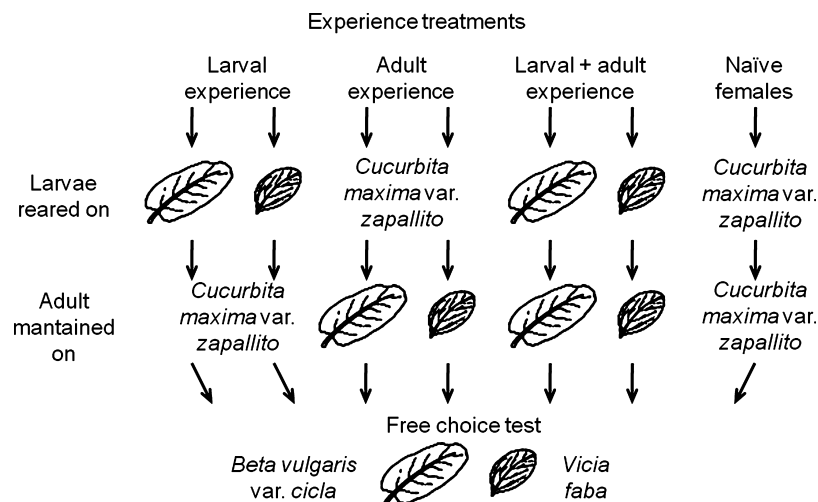
### Plants

*Vicia faba*, *B. vulgaris* var. *cicla*, and *Cucurbita maxima* var. *zapallito* (Carr.) Millan (Cucurbitaceae) plants were grown from commercial seeds in plastic pots (9 × 7 × 7 cm) containing sterilized soil. The plants were maintained under laboratory conditions (room temperature and L12:D12 photoperiod) and were used in the experiments when they had 4–6 expanded leaves.

### Experience treatments

Adults of *L. huidobrensis* were prepared in different ways for subsequent preference assays (see below). Females were obtained using the following four treatments (see Figure 1).

*Larval experience.* Mined leaves were collected from crops of *V. faba* and *B. vulgaris* var. *cicla* in the outskirts of Córdoba city, central Argentina (31°20'S, 64°10'W). Leaves were kept in plastic bags (5 × 30 cm), from which leafminer pupae were then transferred to glass vials until adults emerged. Prior to preference tests, adult females thus obtained were allowed to feed on *C. maxima* var.



**Figure 1** Schematic procedure followed to obtain *Liriomyza huidobrensis* females with different feeding experience.

*zapallito* plants within entomological cages (wooden frame, glass and voile walls, 30 × 30 × 30 cm), during their 3-day pre-oviposition period (Parrella & Bethke, 1984). This allowed us to obtain gravid females with larval experience on *V. faba* or *B. vulgaris* var. *cicla* and with adult experience on a host not closely phylogenetically related to either of the tested plants.

**Adult experience.** Newly emerged adult females obtained from a laboratory colony reared on *C. maxima* var. *zapallito* plants (initiated with larvae collected from mixed crops), were placed in groups of about 30 individuals within entomological cages with either *V. faba* or *B. vulgaris* var. *cicla* plants. After a 3-day exposure to the plants, females were randomly selected and their preferences tested.

**Larval plus adult experience.** Adult females reared from larvae on either *V. faba* or *B. vulgaris* var. *cicla* leaves collected from field crops, were placed in entomological cages containing the same host plant species on which they had developed. After the insects had been exposed to the plants for 3 days, preferences were tested.

**Naïve females.** Females without previous exposure to *V. faba* or *B. vulgaris* var. *cicla* were obtained by rearing larvae on *C. maxima* var. *zapallito* and maintaining the emerged adults on the same plant species for a 3-day period prior to preference tests.

#### Preference tests

**Laboratory tests.** Preferences of *L. huidobrensis* with larval, adult, or larva plus adult experience (LAE) on either *V. faba* or *B. vulgaris* var. *cicla* were assessed by means of free-choice tests. In each trial, one female was placed in a transparent plastic container formed by two closely fitting cups (25 cm total height, 18 cm in diameter). Two similar-sized leaves still attached to the plant (one from each host plant species) were simultaneously offered by inserting their petioles through the adjoining edges of the cups, which were cushioned with polystyrene foam. By thus avoiding leaf excision from their plants, we aimed to prevent water loss and other possible chemical changes in leaf tissues. After 24 h, the numbers of feeding punctures and eggs on the leaves of both plants were counted using a stereomicroscope (60×). Seven to nine replicates with individuals from each previous experience (LE, AE, and LAE) per host plant origin (*V. faba* or *B. vulgaris* var. *cicla*) treatment were performed. Replicates in which feeding punctures but no eggs were observed were excluded from the analysis of oviposition preferences.

In order to determine host preferences independently of learning, a naïve female was placed with one plant of each host species (similar size) in an entomological cage, and the number of feeding punctures and eggs per leaf were counted after 24 h. Sixteen replicates were made.

**Field test.** Four wooden containers (50 × 20 × 30 cm) with 10 plants of each species, similar in size and alternately positioned, were placed within a *V. faba* horticultural field in the outskirts of Córdoba city. An identical experiment was set at the same time in another field cultivated with *B. vulgaris* var. *cicla*. We assumed that leafminer populations on those fields had both larval and adult previous experience on the corresponding host crop. The experimental plants remained 15 days in the field, after which they were transported back to the laboratory and the number of mines on each plant was recorded; larval instead of egg counting is frequently used as an indicator of oviposition preference in leafminers (Parrella et al., 1983; Marino & Cornell, 1993; Mayhew, 1998). Although egg mortality might obscure the relationship between larval and egg distribution of *L. huidobrensis* on some hosts (Videla & Valladares, 2007), no differences in egg survival among the host plants considered here were observed (M Videla, G Valladares & A Salvo, unpubl.).

#### Performance tests

Individuals for performance assessment were reared from leaves collected in field surveys on *V. faba* and *B. vulgaris* var. *cicla* crops, in the outskirts of Córdoba City, in central Argentina. Four and three small fields (1–3 ha) of each host plant species, at least 1 000 m away from each other, were sampled in 2002 and 2003, respectively. Wing length of nearly 100 randomly selected adults (similar number of males and females) reared from each host, was measured. Wing length was taken as an indicator of insect performance (e.g., Mayhew, 1998; Scheirs et al., 2000), as it has been shown to be correlated to other fitness parameters in this species (Videla et al., 2006).

#### Data analysis

For the laboratory experiments, a t- or Wilcoxon test for paired samples was used to compare the number of feeding punctures or eggs on each plant species, in the free-choice tests performed for each treatment. In order to allow cross-comparisons between leafminer life stage (LE, AE, or LAE) and host plant species used (*V. faba* or *B. vulgaris* var. *cicla*), we calculated indices of feeding and ovipositing preferences (IFP and IOP, respectively) as the proportion of feeding punctures or eggs on *V. faba* out of total punctures or eggs recorded in each replicate for each treatment. In this way, we obtained one datum point per replicate,

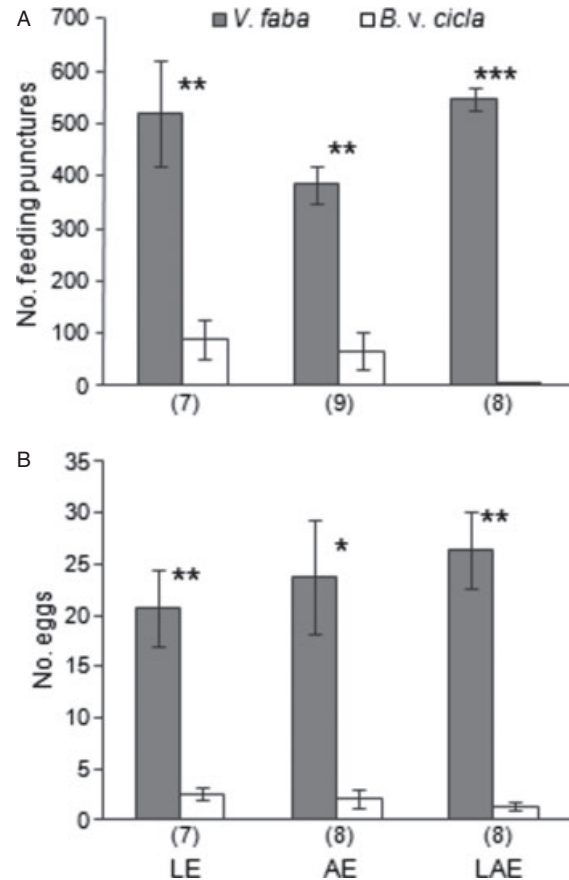
ranging between 1 (total preference for *V. faba*) and 0 (total preference for *B. vulgaris* var. *cicla*). Generalized linear models (GLM) were then used to analyse the effects of experience treatment (LE, AE, or LAE), host plant in which the individuals had experience (*V. faba* or *B. vulgaris* var. *cicla*), and the interaction between these two factors, on feeding and oviposition preferences. As data were overdispersed, a quasi-binomial distribution and the link function logit were used (Crawley, 2005).

Data from the field experiment were analysed in a similar way to those from laboratory experiments: the number of mines on *V. faba* and *B. vulgaris* var. *cicla* plants that had been placed within either *V. faba* or *B. vulgaris* var. *cicla* crops were compared through paired t-test, and the IOP was calculated and compared using GLM as above. As males are smaller than females (Videla et al., 2006), forewing length of individuals emerged from *V. faba* and *B. vulgaris* var. *cicla* was compared separately for each sex, by means of t-tests. All data analyses were carried out using the R freeware, version 2.0.1 (R Development Core Team, 2009).

## Results

In laboratory choice tests, *L. huidobrensis* females that had experience on *V. faba* either as larva ( $t = 3.75$ ,  $P = 0.009$ ), adult ( $W = 2.54$ ,  $P = 0.01$ ), or both stages ( $t = 25.5$ ,  $P < 0.001$ ), preferred feeding on this host plant over *B. vulgaris* var. *cicla* (Figure 2A). In all cases, the number of feeding punctures on *V. faba* was at least four times higher than on *B. vulgaris* var. *cicla*, the difference being most evident when females had accumulated both larval and adult experience (LAE treatment) on the former plant. Females that had experience on *B. vulgaris* var. *cicla* as larvae ( $t = 3.7$ ,  $P = 0.01$ ) or adults ( $t = 7.16$ ,  $P = 0.0002$ ) also preferred *V. faba* (Figure 3A). However, such preference was only marginally significant ( $t = 1.99$ ,  $P = 0.081$ ) when females accumulated larval and adult experience on *B. vulgaris* var. *cicla*. Females without exposure to either host made significantly more feeding punctures ( $t = 2.64$ ,  $P = 0.018$ ) on *V. faba* (mean  $\pm$  SD =  $158 \pm 26.46$ ) than on *B. vulgaris* var. *cicla* ( $53.5 \pm 23.3$ ).

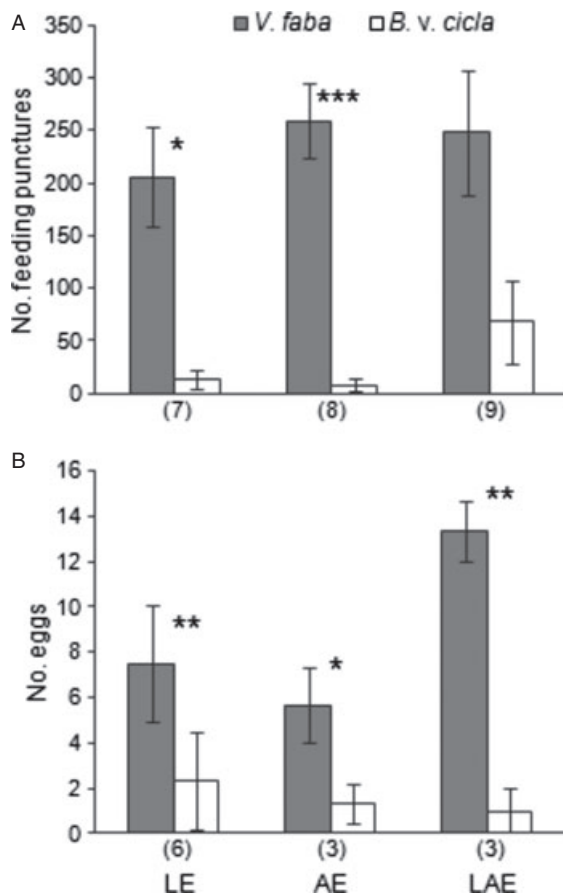
The mean IFP values were all above 0.5 and close to 1 (ranging from 0.74 to 0.99), as could be expected from the strong female preference for feeding on *V. faba* (Figure 4A). The magnitude of the preference for feeding on the favourite plant was independent of the stage at which previous contact with the plant was experienced ( $F_{2,43} = 0.15$ ,  $P = 0.86$ ), or even whether the favourite plant species had at all been involved in previous experience (i.e., female origin) ( $F_{1,43} = 0.18$ ,  $P = 0.67$ ). However, individuals that had both larval and adult experience



**Figure 2** Mean ( $\pm$  SD) (A) feeding and (B) oviposition preferences, as indicated by the no. feeding punctures and eggs, respectively, performed by *Liriomyza huidobrensis* females with larval (LE), adult (AE), or larval and adult (LAE) experience on *Vicia faba*, in laboratory choice tests on *V. faba* and *Beta vulgaris* var. *cicla*. No. replicates within parentheses; t- or Wilcoxon tests for paired samples: \* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$ .

on either *V. faba* or *B. vulgaris* var. *cicla* showed the highest and lowest IFP values, respectively (Figure 4A), resulting in a significant interaction ( $F_{2,43} = 5.13$ ,  $P = 0.01$ ) between previous experience treatment and female origin (*V. faba* or *B. vulgaris* var. *cicla*). Interestingly, within-treatment data variability was dramatically reduced for individuals with larval and adult experience on *V. faba*, whereas it noticeably increased for those with larval and adult experience on *B. vulgaris* var. *cicla* (Figure 4A; see also Figure 2A and 3A). IFP values of naïve females (mean  $\pm$  SD =  $0.78 \pm 0.08$ ) fell within the range observed for experienced females mentioned before.

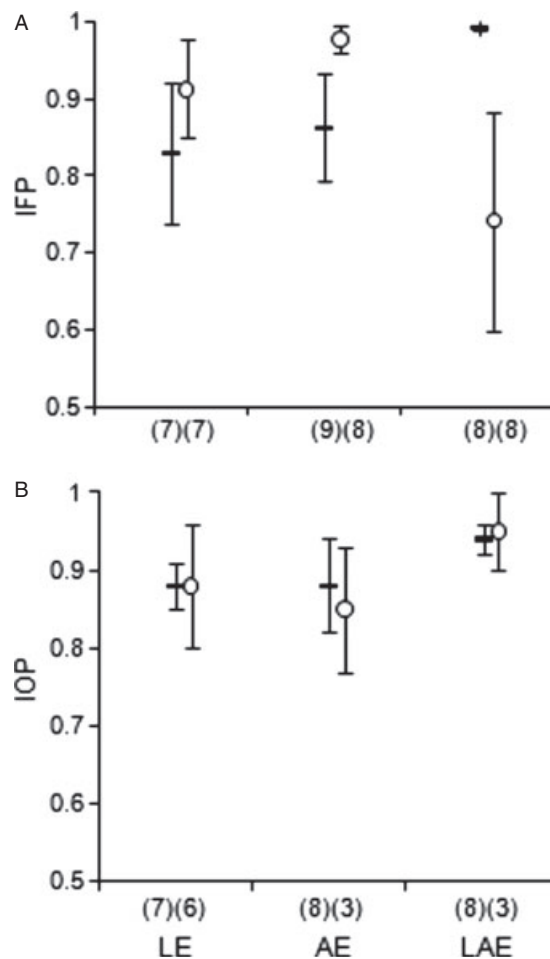
*Liriomyza huidobrensis* females with experience on either *V. faba* or *B. vulgaris* var. *cicla* also preferred the former host plant for egg laying. From eight to almost 20 times more eggs were recorded on *V. faba* than on



**Figure 3** Mean ( $\pm$  SD) (A) feeding and (B) oviposition preferences, as indicated by the no. feeding punctures and eggs, respectively, performed by *Liriomyza huidobrensis* females with larval (LE), adult (AE), or larval and adult (LAE) previous experience on *Beta vulgaris* var. *cicla*, in laboratory choice tests on *Vicia faba* and *Beta vulgaris* var. *cicla*. No. replicates within parentheses; t- or Wilcoxon tests for paired samples: \* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$ .

*B. vulgaris* var. *cicla* for females having LE ( $t = 4.72$ ,  $P = 0.003$ ), AE ( $t = 3.48$ ,  $P = 0.010$ ), and LAE ( $t = 6.36$ ,  $P < 0.001$ ) on *V. faba* (Figure 2B). Females from *B. vulgaris* var. *cicla* origin laid their eggs mainly on *V. faba* as well (Figure 3B), despite having experienced the former host as larvae ( $W = 2.22$ ,  $P = 0.026$ ), adult ( $t = 4.91$ ,  $P = 0.039$ ), or both stages ( $t = 37$ ,  $P < 0.001$ ). Naïve *L. huidobrensis* females also laid significantly more eggs ( $t = 3.63$ ,  $P = 0.011$ ) on *V. faba* (mean  $\pm$  SD =  $2.86 \pm 0.7$ ) than on *B. vulgaris* var. *cicla* ( $0.14 \pm 0.14$ ).

The mean IOP values ranged from 0.85 to 0.95 (Figure 4B). These values were independent of the stage in which experience took place ( $F_{2,30} = 1.77$ ,  $P = 0.19$ ) and of the host plant to which females were previously exposed ( $F_{1,30} = 2.09$ ,  $P = 0.16$ ). Also, no significant interaction



**Figure 4** Indices of (A) feeding and (B) ovipositing preferences (IFP and IOP), for *Liriomyza huidobrensis* females with larval (LE), adult (AE), or larval and adult (LAE) experience on *Beta vulgaris* var. *cicla* (○) or *Vicia faba* (●) in choice tests. Index values near to one express total preference for *V. faba*, whereas values close to zero indicate total preference for *B. vulgaris* var. *cicla*. No. replicates within parentheses.

( $F_{2,30} = 0.09$ ,  $P = 0.91$ ) between female origin and experience treatment was observed (Figure 4B). Mean IOP values of naïve females (mean  $\pm$  SD =  $0.95 \pm 0.05$ ) also fell within the range observed for experienced females.

Results from the field experiment supported those obtained in the laboratory with regard to oviposition preference (Table 1). The mean number of *L. huidobrensis* mines was significantly higher on *V. faba* than on *B. vulgaris* var. *cicla* when plants were placed in *V. faba* crops, and the same tendency was observed for plants placed within *B. vulgaris* var. *cicla* crops although differences were then marginally significant (Table 1). The IOP values recorded on *V. faba* and *B. vulgaris* var. *cicla* were similar

**Table 1** Oviposition preferences, as indicated by the number of mines (mean  $\pm$  SD;  $n = 4$ ) performed by *Liriomyza huidobrensis* in field choice tests, in which *Vicia faba* and *Beta vulgaris* var. *cicla* plants were simultaneously offered, analyzed by a paired t-test

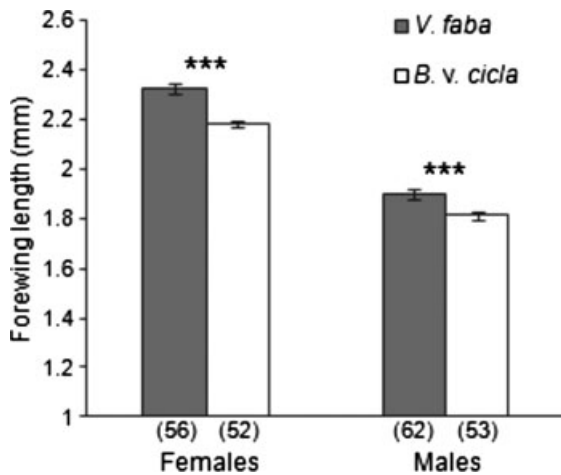
Crop field	No. initial mines		t	P
	<i>Vicia faba</i>	<i>Beta vulgaris</i> var. <i>cicla</i>		
<i>Vicia faba</i>	28.5 $\pm$ 6.61	4.75 $\pm$ 1.18	3.28	0.046
<i>Beta vulgaris</i> var. <i>cicla</i>	16.25 $\pm$ 5.78	1.0 $\pm$ 0.41	2.69	0.074

( $F_{1,7} = 2.22$ ,  $P = 0.18$ ) regardless of whether females belonged to populations associated to *V. faba* (mean  $\pm$  SD = 0.83  $\pm$  0.05) or *B. vulgaris* var. *cicla* (0.91  $\pm$  0.04) crops.

The leafminer performed better on *V. faba* than on *B. vulgaris* var. *cicla*, as indicated by longer forewings of males ( $t = 3.97$ ,  $P < 0.0001$ ) and females ( $t = 5.63$ ,  $P < 0.0001$ ) emerged from the former host plant in comparison with individuals reared on *B. vulgaris* var. *cicla* (Figure 5).

## Discussion

Our results show that *L. huidobrensis* females strongly preferred *V. faba* over *B. vulgaris* var. *cicla*, producing more feeding punctures and laying more eggs on the former plant species, whether or not they had previous experience on this host. The magnitude of feeding and oviposition preferences for the favourite host was similar in most of



**Figure 5** Mean ( $\pm$  SD) forewing length (mm) of *Liriomyza huidobrensis* females and males reared on *Vicia faba* and *Beta vulgaris* var. *cicla*. Number of replicates within parentheses; t-test: \*\*\* $P < 0.001$ .

the experiments, the only exception being provided by larval and adult experience acting in concert to modify feeding behaviour, as indicated by a significant interaction between the stages and the plant species at which previous experience took place. In particular, oviposition preferences remained unaltered regardless of female previous experience on either *V. faba* or *B. vulgaris* var. *cicla* plants, in both laboratory and field experiments.

Lack of larval experience effects on host plant selection, as here observed, has been reported for other phytophagous insects (e.g., Tabashnik et al., 1981; Rojas & Wyatt, 1999; Kerpel & Moreira, 2005; Liu & Liu, 2006; Janz et al., 2009). However, Facknath & Wright (2007) observed that *L. huidobrensis* preferred feeding on either tomato or potato, depending on which of these host plants they experienced as larvae. Empirical evidence has shown that the effects of adult experience on host plant preference by herbivorous insects can vary intra-specifically among individuals belonging to different populations (Chiu & Messina, 1994) and host races (Boller et al., 1998). The difference between our results and those reported by Facknath & Wright (2007) from a widely separated population, suggest that intra-specific variation can also occur in relation to the influence of larval experience on host plant choice, at least for feeding preferences (as oviposition choices were not assessed in that study).

Several features of *L. huidobrensis* are supposed to promote learning. First, resource or habitat generalists are expected to learn better than specialists (Papaj & Prokopy, 1989), and *L. huidobrensis* is a polyphagous pest with hosts in 14 plant families worldwide (Spencer, 1990; Weintraub & Horowitz, 1995; Dempewolf, 2004), feeding on over 50 plant species (Valladares, 2004) in the study region. Second, learning would be advantageous and more likely to occur when individuals are able to obtain information about the impact of their decisions on their fitness (Parmesan et al., 1995). Agromyzid females have been shown to evaluate host quality when feeding, often preferring the most suitable hosts (Scheirs et al., 2000, 2004; Scheirs & De Bruyn 2002). Finally, learning should be favoured when host plant availability is relatively constant within the life span of individual insects but varies unpredictably between generations (Stephens, 1993), conditions usually found in polyphagous agricultural pests such as *L. huidobrensis* (Cunningham et al., 1998). Although ecological features of the system should thus favour learning, adult experience per se did not influence either feeding or oviposition preference of *L. huidobrensis*. However, the strongest and weakest feeding preference for *V. faba* were recorded when individuals accumulated larval and adult previous experience on *V. faba* or *B. vulgaris* var. *cicla*, respectively. This suggests NHPI and learning operating at some level on

feeding behaviour, through synergistic effects of larval and adult experience. On the contrary, egg laying preferences for *V. faba* of *L. huidobrensis* females were unaltered by previous experience.

Differential effects of adult experience on feeding and oviposition behaviour may arise from differences in the frequency and impact on fitness of feeding and oviposition decisions (McNeely & Singer, 2001). Learning could be more likely to occur if decisions are repeated several times and each one has a low impact on individual fitness, whereas decisions performed few times with a large impact on fitness would favour an innate rule for decisions (Roitberg et al., 1993). This could explain the differential plasticity of feeding and oviposition behaviour observed here, as the number of feeding punctures performed by *L. huidobrensis* usually exceeded the number of eggs by approximately one order of magnitude (Parrella & Bethke, 1984) and the costs of feeding mistakes will obviously be lower than those of ovipositing in the wrong place.

According to the optimal oviposition theory (Jaenike, 1978), female insects will preferably lay eggs on plants where their progeny perform best, as this will optimize both offspring and their own fitness. This could be particularly expected for sessile insects such as leafminers, gallers, etc., but the evidence is contradictory (Scheirs et al., 2000; see review by Gripemberg et al., 2010). Here, *L. huidobrensis* preference was related to offspring performance, as indicated by larger males and females emerging from the preferred host *V. faba*, in comparison with those from *B. vulgaris* var. *cicla*. Larger individuals could have higher fecundity (reviewed by Honek, 1993), chances of mating (Rhainds et al., 1999; Honek, 2003; Sisodia & Singh, 2004), egg fertility (Yenisetti & Hegde, 2003; Jiménez-Pérez & Wang, 2004), dispersion capacity, and longevity (Nylín & Gotthard, 1998; Colinet et al., 2007). Altogether, our results suggest that previous experience could not overcome oviposition preferences that appear driven by fitness benefits for offspring.

The effects of insect experience on host plant preferences have been studied in various contexts, such as host plant fidelity, host range expansion (Solarz & Newman, 2001), and host race formation and speciation (Dukas, 2008). The results we obtained suggest that the possible interplay between larval and adult experiences should be considered in order to improve our understanding of these crucial aspects of plant\*insect interactions. Moreover, our results emphasize that both feeding and oviposition choices should be regarded in preference studies, as decisions in either case can drive the evolution of host plant selection (Jaenike, 1978; Scheirs et al., 2000) and, as shown here, can be differentially affected by previous experience.

## Acknowledgements

We are very grateful to L. Cagnolo and three anonymous referees for helpful comments on the manuscript and to land owners who gave permission for field experiments. This study was supported by Secretaría de Ciencia y Técnica – Universidad Nacional de Córdoba, and by a grant from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) to MV. AS and GV are members of CONICET.

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