A tritrophic analysis of host preference and performance in a polyphagous leafminer

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Abstract

The optimal oviposition theory predicts that oviposition preferences of phytophagous insects should correlate with host suitability for their offspring. As plant host suitability depends not only on its quality as food, but also on its provision of enemy-free space, we examined the relationship between adult host preference and offspring performance for the leafminer *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae) on various host plants, considering also the interaction with natural enemies. Preference and offspring performance were assessed through observational field data and laboratory experiments in central Argentina. Field data suggested a positive host preference – performance linkage, as the leafminer attained larger body size on the crops where it was more abundant. Laboratory trials supported these results: *Vicia faba* L. (Fabaceae) was the preferred host in the laboratory as well as in the field, performance of *L. huidobrensis* being also best on this host, with highest survival rates and shortest development time. The actively feeding larval stage showed the largest plant-related effects. Higher overall parasitism rates were found on plants from which smaller leafminers were reared, reinforcing the preference–performance linkage. On the other hand, the main parasitoid *Phaedrotoma scabriventris* Nixon (Hymenoptera: Braconidae) reached larger body size, and caused higher mortality rates on crops where the leafminer was larger. Changes in abundance of particular parasitoid species could thus modify overall parasitism trends.

Introduction

The optimal oviposition theory is central to understanding the evolution of interactions between herbivorous insects and their host plants (Thompson & Pellmyr, 1991). This theory predicts that oviposition preferences of phytophagous insects should correlate with host suitability for their offspring, as they would maximize their fitness by laying eggs on high quality plants (Thompson, 1988). However, such correlation was only partial or even nonexistent in nearly half of 133 studies (Mayhew, 1997).

Studies on preference–performance relationships have generally limited their focus to ditrophic interactions between herbivore insects and their host plants (Singer et al., 2004). Nevertheless, the value of a plant to an herbivore depends not only on its quality as food, but also on its provision of enemy-free space (Stamp, 2001). A trade-off between food suitability and enemy avoidance may lead a herbivore to prefer nutritionally inferior plants on which chances of encountering parasitoids are predictably low, over more nutritive plants that are frequently visited by natural enemies (Dicke, 2000; Singer et al., 2004). Also, from the perspective of the parasitoid, host suitability may be enhanced or reduced on different plants (Salvo & Valladares, 2002). Although natural enemies frequently play an important role in determining host plant selection (e.g., Valladares & Lawton, 1991; McMillin & Wagner, 1998; Stamp, 2001; Singer et al., 2004; Heisswolf et al., 2005), they have rarely been considered in herbivore preference–performance studies.

A strong linkage between preference and performance seems to be more commonly associated with latent species of insect herbivores, i.e., species that do not reach outbreak densities and cause minimal damage to the host plants (Leyva et al., 2000, 2003). Conversely, herbivore insect species showing outbreak population dynamics frequently lack a preference–performance linkage (Price, 1997; Leyva et al., 2003), maybe because increasing population densities impose progressively less selection on the herbivores to

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discriminate among hosts (Bigger & Fox, 1997; Wallin & Raffa, 2004). A tight preference–performance linkage and latent population dynamics would be expected for leafminers, whose larvae feed and dwell within a leaf selected by the ovipositing females, yet many of them are serious pests and are highly outbreaking (Price, 1997). Approximately a quarter of leafmining species with published density estimates either occur at chronically high densities or present occasional outbreaks (Auerbach et al., 1995).

We look here at the relationship between preference and performance for a widely distributed leafminer pest (Dempewolf, 2004), *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae). This extremely polyphagous species has been recorded on 39 different crops in central Argentina (Valladares et al., 1999), reaching high levels of infestation on many of them (Valladares et al., 1996; Valladares & Salvo, 1999). When several host species are simultaneously available in the field, *L. huidobrensis* consistently occurs at higher densities on particular crops (Salvo & Valladares, 1995; Valladares et al., 1996, 1999), suggesting host preferences as observed for other *Liriomyza* species (Murphy & LaSalle, 1999). Preference and performance appeared uncorrelated for a laboratory colony of this species in Canada, according to a recent study (Martin et al., 2005), in which natural enemies were not included. However, North and South American populations of this leafminer represent two different clades or even cryptic species (Scheffer & Lewis, 2001), and widely distributed species like *L. huidobrensis* may experience different selection pressures along their geographical range (Potting et al., 1997). In central Argentina, parasitoids are an extremely important source of mortality on agromyzid leafminers, causing on average 30–40% parasitism (Valladares et al., 2001). Therefore, we have included the parasitoids of the leafminer in our analysis of preference and performance.

Here, we asked first whether variations in *L. huidobrensis* abundance on different crops reflect female preference. To answer this question, we assessed patterns of host use in the field and compared them with preference tests in the laboratory, using plants from the extremes in the host range.

We then analysed whether *L. huidobrensis* females prefer the hosts in which their offspring perform best, by looking at correlations between leafminer abundance and wing length for field data, and by comparing leafminer survival, development time, and wing length when reared on selected plants in laboratory tests.

Finally, we asked how parasitoids relate to this plant-host interaction, by comparing parasitoid species richness and parasitism rates from field data, as well as body size of the main parasitic species (in order to contemplate reciprocal effects), for hosts reared from the different plants.

Materials and methods

Natural history

Liriomyza huidobrensis, first described in Argentina, is currently known as a pest on various crops throughout the New and Old World (Dempewolf, 2004). Adult females pierce the leaves with their ovipositor, both to feed on plant sap and to lay eggs. All punctures can be considered feeding punctures, but only some of them contain eggs (Parrella, 1987). The damage caused by feeding punctures and by the serpentine mines resulting from larval activity, can induce considerable yield losses (Spencer, 1973; Dempewolf, 2004). *Liriomyza huidobrensis* is a multivoltine species, completing a life cycle in 14–57 days depending on temperature (Head et al., 2002), and active larvae are found in the study area throughout the year (Valladares et al., 1996). A number of life-history traits (Murphy & LaSalle, 1999) may be related to the high population levels reached by *L. huidobrensis*, although its outbreaks in agricultural systems are probably also driven by insecticide resistance and crop management practices (Weintraub & Horowitz, 1995). Local outbreaks of this leafminer have also been observed in native habitats in central Argentina (G Valladares and A Salvo, unpubl.).

Parasitoids of *L. huidobrensis* and other agromyzids in central Argentina include species in the hymenopteran families Eulophidae, Pteromalidae, Eucoilidae, and Braconidae (Salvo & Valladares, 1995, 1999), which represent the main natural enemies of these leafminers, predation being negligible in our system. *Phaedrotoma scabriventris* Nixon (Hymenoptera: Braconidae: Opiinae), a koinobiont parasitoid attacking leafmining larvae and emerging from puparia, has been mentioned as the most important parasitoid of the leafminer in the study area, and as a potential agent for its population regulation (Valladares & Salvo, 1999; Valladares et al., 1999).

Patterns of host use and leafminer performance in the field

All crops in four fields with horticultural and ornamental policultures (1–3 ha) in the outskirts of Córdoba City, in central Argentina (31°20′S; 64°10′W), were surveyed at approximately 14-day intervals over 2 years (1993–94). Additional information about the study system can be found in Valladares et al. (1996). In each of seven crops (Table 1), the number of mined leaves in 100 leaves haphazardly selected was counted in order to assess larval density. In addition, all mined leaves found in a searching period of 30 min were cut, placed in plastic bags, transported to the laboratory, and kept until flies and parasitoids emerged (Salvo & Valladares, 1998).

Patterns of host use, which might reflect leafminer host preferences (Auerbach & Alberts, 1992), were assessed by estimating, for each crop: (i) the total number of adults

Table 1 Variables indicating host use by *Liriomyza huidobrensis* on crops in central Argentina, based on abundance estimates from periodical 2-year sampling in four agricultural fields

Plant species	Total adults reared	Maximum percentage mined leaves	Maximum adult abundance
Vicia faba	6311	100	1334
Beta vulgaris cicla	2419	84	604
B. vulgaris rapacea	216	79	77
Callistephus chinensis	129	60	89
Solanum tuberosum	91	52	52
Phaseolus vulgaris	506	42	164
Cucurbita maxima var. *zapallito*	154	40	49

(flies + parasitoids) reared along the study period, (ii) the highest number of adults reared on any particular sample date, and (iii) the maximum value of larval density. Only those plant species producing 100 or more adults in the sampling period were included in the present analysis.

Wing length of *L. huidobrensis* specimens reared from each plant species was measured as a correlate of reproductive potential (Honek, 1993; Harris et al., 2001). Males (n = 189) and females (n = 268) were measured separately as males are generally smaller than females.

Plant and leafminer cultures in the laboratory

Three plant species, representing the extremes in the full range of host plant use and in performance (as indicated by wing length) observed in the field surveys, were selected for experimental assessment of preference and performance in the laboratory: *Vicia faba* L. (Fabaceae, 'broad bean'), *Phaseolus vulgaris* L. (Fabaceae, 'bean'), and *Cucurbita maxima* var. *zapallito* (Carr.) Millan (Cucurbitaceae, 'courgette'). The plants were grown from seeds in the laboratory, using plastic pots and standard commercial compost. Plants used in the experiments were as similar as possible in size.

Adults of *L. huidobrensis* obtained from broad bean plants growing in horticultural fields were used for the establishment of a laboratory colony of leafminers, on the same host plant. To check for learned or laboratory selected responses to the experimental plant species, preference tests were also carried out with adults reared on field plants of *Beta vulgaris* var. *cycla* L. (Chenopodiaceae, 'common beet'). Four- to 6-day-old females were used in experiments.

Preference laboratory tests

Three plants, one of each of the species above mentioned, were placed in a cage (wood, glass, and voile, 30 × 30 × 30 cm) and exposed to 20 males and 20 females of *L. huidobrensis* for 3 h. A piece of cotton wool imbibed with sugar water was always added as a feeding supplement. All experiments were done at room temperature and L12:D12 photoperiod. Ten replicates were made. Number of leaves per plant was recorded and foliar area of each plant species was measured from leaf tracings.

The following variables were estimated for each plant: (i) density of feeding punctures (number punctures cm^2 leaf area), indicating feeding preferences; (ii) density of viable eggs (number of mines/cm^2 leaf area); oviposition patterns were estimated from the number of newly initiated mines (3–4 days after plants were exposed to flies) assuming, in common with most studies on leafminers, that larval distribution accurately reflects egg distribution (Parrella et al., 1983; Marino & Cornell, 1993; Mayhew, 1998); and (iii) egg/feeding puncture ratio, estimated also from first-instar mine or 'viable egg' counts (Parrella et al., 1983). This ratio has been used to assess host plant suitability (Parrella, 1987) and as an index of host preference (Hussey & Gurney, 1962; Martin et al., 2005).

Performance assessment in laboratory

Five female and five male *L. huidobrensis* were placed in a cage, as above, but with only one of the selected host plants (five replications for each species). Additional replicates were made with courgettes, as very few mines were obtained on these hosts. Data from the preference experiments were also included, the final number of replications being 14, 10, and seven plants (with 144, 50, and 20 initial larvae) for *V. faba*, *P. vulgaris*, and *C. maxima*, respectively. The following variables were measured: (i) larval survival: proportion of larvae reaching pupation, (ii) pupal survival: proportion of pupae from which adults emerged, (iii) total (from the start of the experiment to adult emergence) and stage-specific (egg, larval, and pupal) development time, and (iv) male and female wing length.

The third trophic level

The number and identity of parasitoid species associated with the leafminer on each crop was assessed over all samples. The overall impact of parasitoids on *L. huidobrensis* developing on different host plants was estimated as total apparent parasitism, i.e., the total number of reared parasitoids in relation to the total number of available hosts (Mills & Kenis, 1991), for samples providing at least 50 individuals from a particular sample date/locality (14 samples). Maximum parasitism rates, representing an estimation of how much mortality a parasitoid is capable of inflicting on its hosts (Hawkins, 1994), were also analysed for the dominant parasitoid *P. scabriventris* using the same samples. Moreover, wing length of *P. scabriventris* adults (n = 255) reared from hosts developing on different crops was measured, as a correlate of parasitoid reproductive potential (Honek, 1993), in order to compare parasitoid fitness trends among plants.

Statistical analysis

Relationships among the different variables selected as indicators of *L. huidobrensis* host use in the field (mine density, total and highest adult abundance per crop), as well as between those measurements and leafminer wing length, were analysed through Pearson's correlation analysis. Body size of male and female leafminers reared from different host plants, and parasitoid wing length on plants providing big and small hosts were compared by two-way and one-way ANOVA, respectively. Kruskal–Wallis test was used to compare fitness variables measured in the laboratory trials, as data did not comply with normality and/or homoscedasticity requirements. Results from laboratory preference tests were analysed using a mixed generalized linear model with Poisson error distribution and log link function; egg/feeding puncture ratios were compared using a mixed general linear model with normal error distribution and identity link function, as variables were normally distributed. In both cases, PROC GENMOD (SAS Institute, 2000) was used, and a compound symmetry covariance structure was incorporated instead of the traditional random effect in order to contemplate data dependence (Littel et al., 1996). Wing length and preference measurements were log transformed and all percentage data were arcsine square-root transformed prior to statistical analyses.

Results

Host use and performance of *Liriomyza huidobrensis* in the field

From a hundred up to over 6000 adults of *L. huidobrensis* and its parasitoids were reared from seven different crops (Table 1). The three variables used as indicators of host use in the field were highly correlated (total adults vs. highest adult abundance per sampling date: r = 0.98, P<0.001; total adults vs. maximum larval density: r = 0.81, P<0.05; highest adult abundance per sampling date vs. maximum larval density: r = 0.81, P<0.05). From these patterns of host use, *V. faba* appeared as the favourite host for *L. huidobrensis* in the study area (Table 1).

Average wing length of *L. huidobrensis* females varied between 1.85 mm (on *C. maxima*) and 2.19 mm (on *V. faba*); males were always smaller than females (from 1.53 mm to

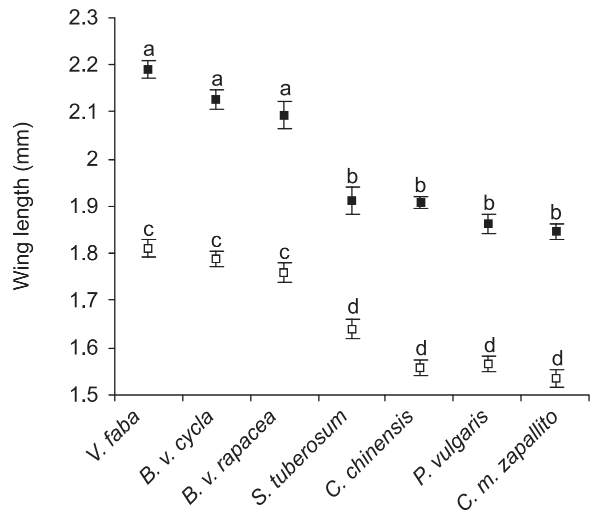

Figure 1 Mean (± SE) female (■) and male (□) wing length of *Liriomyza huidobrensis* adults as a function of plant host, from seven crops in central Argentina. Means with the same letter does not differ significantly (two-way ANOVA followed by Bonferroni test, P>0.05).

1.81 mm on *C. maxima* and *V. faba,* respectively). Significant differences between sexes ($F_{1,442}$ = 769.65, P<0.001) and among host plants ($F_{6,442}$ = 76.29, P<0.001) were revealed by two-way ANOVA, without significant interaction between both factors ($F_{6,442}$ = 1.36, P = 0.229). Two groups were clearly defined: larger flies were reared from *V. faba*, *B. vulgaris* var. *cycla*, and *B. vulgaris* var. *rapacea* (Koch) Aellen than from *Callistephus chinensis* (L.) Nees (Asteraceae), *Solanum tuberosum* L. (Solanaceae), *P. vulgaris,* or *C. m. zapallito* (Figure 1).

Differences in adult size were related to all indicators of leafminer host use in the field, suggesting that females selected the most nutritionally adequate host species for their progeny. The strongest relationship was found between *L. huidobrensis* wing length and the highest density of mined leaves (Figure 2) recorded on each crop (females: r = 0.94, P = 0.001; males: r = 0.88, P = 0.008). Wing length was also correlated with the total number of reared insects (females: r = 0.76, P = 0.047; males: r = 0.71, P = 0.072) and with the highest number of insects reared on any sampling date (females: r = 0.76, P = 0.046; males: r = 0.71, P = 0.075) from each plant species, although the relationships were only marginally significant for males.

Preference and performance in the laboratory

Liriomyza huidobrensis females given a choice among *V. faba*, *C. maxima*, and *P. vulgaris* consistently preferred *V. faba* for oviposition, as indicated by the number of mines starting development. Ranking of hosts for oviposition

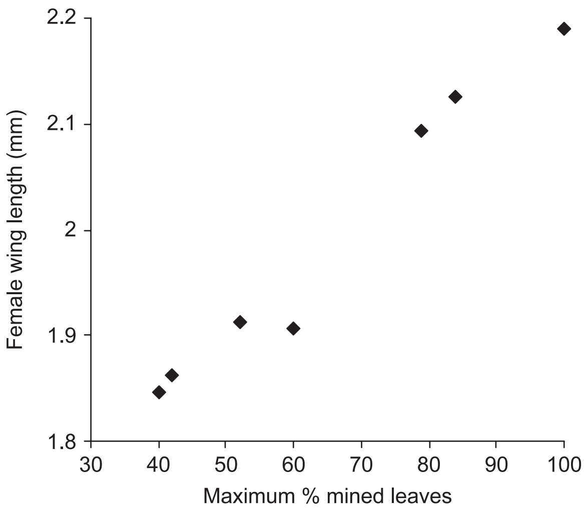

Figure 2 Relationship between mean wing length of *Liriomyza huidobrensis* females reared on different plant hosts and maximum larval density (% mined leaves) on the same plants.

was consistent, independent of whether females had been reared on *V. faba* or on *B. vulgaris* var. *cycla*, the number of viable eggs on *V. faba* plants being at least four times higher than on *P. vulgaris*, and two orders of magnitude higher than on *C. maxima* (Table 2).

Feeding punctures made by females were also most abundant on *V. faba*, with *C. maxima* receiving the lowest number of punctures (Table 2). Egg/puncture ratios were lowest on *C. maxima* and highest on *V. faba* independently of female origin, although differences among plants reached significant values only for females reared on *V. faba* (Table 2). In the latter case, females laid an egg every 5.5 feeding punctures on their native host, but made 125 punctures on *C. maxima* before laying an egg on this host. Flies reared on *B. vulgaris* var. *cycla* behaved very similarly on *C. maxima*, but made 40 punctures for each egg they laid on *V. faba*.

Leafminers reared in the laboratory showed plant-related differences in their development time (Table 3). The most pronounced variations were observed at the larval stage: the time required for larvae to pupate was 15 and 25% shorter when reared on *V. faba* than on *P. vulgaris* or *C. maxima*, respectively. Larval survival (Table 3) was also significantly different among host plants, being highest for larvae reared on *V. faba* and lowest on *C. maxima*. Pupal survival, although following the pattern observed for larvae, did not show significant differences for insects reared on different plants. For the whole development cycle (Table 3), survival rates were 2.5 times higher for insects developing in *V. faba*, than for those in any of the other hosts. Wing length of laboratory-reared adults followed the pattern observed in the field (Table 3), with the largest adults being reared from *V. faba* and *C. maxima* providing the smallest specimens.

The third trophic level

Species richness of parasitoid assemblages (Figure 3) associated with *L. huidobrensis* varied between five (on beetroot) and 13 species (on *V. faba*), but no significant differences were found between the two groups of plants providing large or small hosts reported above ($F_{1,5} = 1.59$, $P = 0.263$).

Comparisons of parasitism rates did not include data from *S. tuberosum*, as the required minimum sample size (50 adults reared from a particular date and locality) was not reached on this crop. Total mortality inflicted by parasitoids on *L. huidobrensis* varied among crops from 33 to 71%, and was significantly higher ($F_{1,12} = 5.05$, $P = 0.044$) on those plants where the leafminer was smaller (Figure 4).

Parasitoid assemblages of *L. huidobrensis* on the studied crops were generally dominated by the braconid *P. scabriventris;* this species accounted for 26–80% of total parasitism (Figure 3). Maximum parasitism rates due to *P. scabriventris* varied between 13 and 35%, increasing by about a third on plants where the leafminer reached a larger size ($F_{1,4} = 16.23$, $P = 0.016$; Figure 4). Furthermore, adults of *P. scabriventris* were larger (2.1 mm ± 0.014) when they developed on plants providing large hosts than

Table 2 Feeding and ovipositing preferences of *Liriomyza huidobrensis* in laboratory choice-tests among three plant hosts: mean (± SE) number of feeding punctures and eggs cm^{-2} leaf area

Females reared on	Variable	*V. faba*	*P. vulgaris*	*C. maxima* var. *zapallito*	Statistics[1]	P-value
V. faba	Punctures	1.05 ± 0.14	0.47 ± 0.16	0.11 ± 0.04	$\chi^2 = 8.11$	0.017
	Eggs	0.17 ± 0.03	0.02 ± 0.001	0.003 ± 0.003	$\chi^2 = 8.41$	0.014
	Egg/puncture ratio	0.18 ± 0.03	0.06 ± 0.03	0.008 ± 0.008	F = 18.155	<0.001
B. vulgaris var. *cycla*	Punctures	4.78 ± 0.88	2.93 ± 1.09	0.2 ± 0.05	$\chi^2 = 7.57$	0.022
	Eggs	0.18 ± 0.05	0.04 ± 0.02	0.002 ± 0.002	$\chi^2 = 6.02$	0.049
	Egg/puncture ratio	0.025 ± 0.007	0.019 ± 0.011	0.007 ± 0.007	F = 1.219	0.33

[1]χ^2 from mixed generalized linear model, F from mixed general linear model, d.f. = 2 in all cases.

Table 3 Mean (± SE) development time (days), survival rates (%), and wing length (mm) of *Liriomyza huidobrensis* reared on three different host plants in the laboratory

Parameter	*V. faba*	*P. vulgaris*	*C. maxima* var. *zapallito*	H[1]	P-value
Egg development time	3.58 ± 0.04	3.46 ± 0.1	3.5 ± 0.17	6.27	0.043
Larval development time	4.14 ± 0.04	4.8 ± 0.18	5.62 ± 0.32	34.32	<0.001
Pupal development time	8.24 ± 0.05	8.25 ± 0.16	8.0 ± 0.0	1.11	0.56
Total development time	15.81 ± 0.065	15.9 ± 0.17	19.0 ± 1.22	15.32	<0.001
Larval survival	0.93 ± 0.04	0.55 ± 0.11	0.33 ± 0.17	10.49	0.005
Pupal survival	0.73 ± 0.03	0.61 ± 0.12	0.53 ± 0.29	0.816	0.665
Total survival	0.67 ± 0.05	0.28 ± 0.28	0.27 ± 0.14	10.69	0.005
Female forewing length	1.97 ± 0.01	1.87 ± 0.04	1.85 ± 0.13	5.61	0.059
Male forewing length	1.64 ± 0.02	1.57 ± 0.06	1.39 ± 0.09	7.19	0.026

[1]degrees of freedom = 2 in all cases, Kruskal–Wallis test.

on plants where the leafminer was small (2.01 mm ± 0.012) ($F_{1,253} = 18.49$, P<0.001).

Discussion

Does variation in leafminer abundance on different crops reflect female preference?

Field assessment of host use showed higher abundance of *L. huidobrensis* on *V. faba* plants, despite it being one of the least abundant crops in the study area. Although many factors influence insect abundance on a particular host, the observed differences in attack intensity in the field seem to involve a strong preference component, as indicated by laboratory tests for three of the host plant species: *V. faba* plants received more eggs as well as more feeding punctures than *P. vulgaris*, whereas *C. maxima* was rather ignored. It must be noted that the crops surveyed were grown in highly diversified polycultures, thus providing a situation rather similar to that represented by choice tests, in contrast to the no-choice situation offered by monocultures.

Induction of preference, i.e., an increased fidelity to the plants the herbivores have fed on or been reared on, seems to occur in some polyphagous *Liriomyza* species (Parrella, 1987; Scheirs et al., 2004). However, the consistent host ranking, both for feeding and for oviposition, shown by *L. huidobrensis* females reared from different hosts, appeared to be unrelated to their previous experience as larvae.

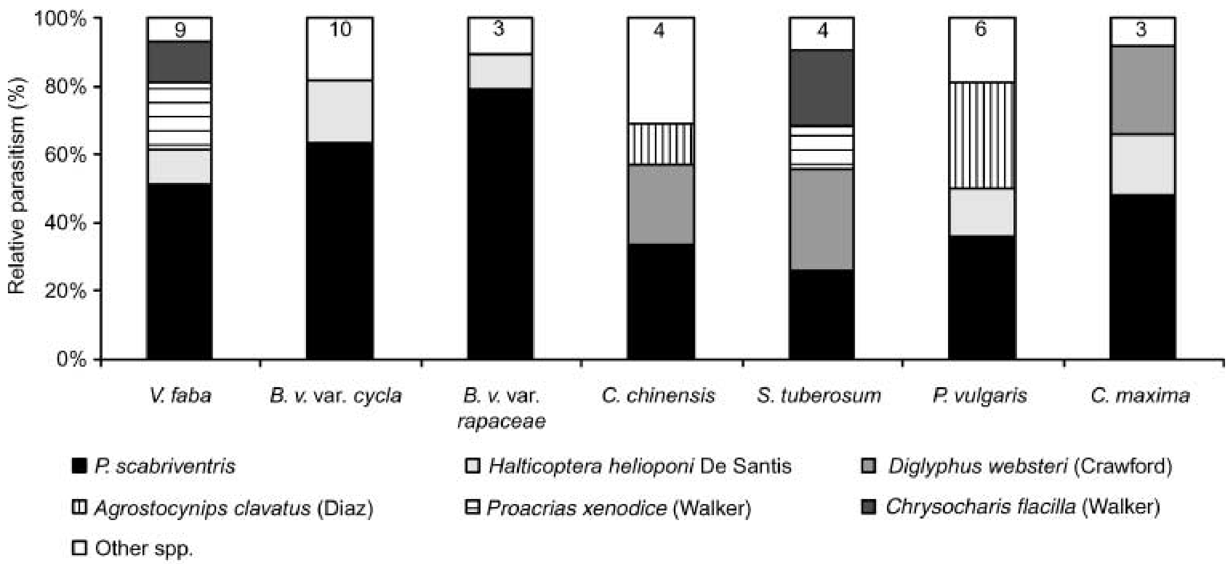

Figure 3 Contribution (%) of the main parasitoid species to overall parasitism of *Liriomyza huidobrensis* on crops in central Argentina. Values at the top of each column indicate the number of other parasitic species (each producing less than 10% of total parasitism) recorded on each host plant.

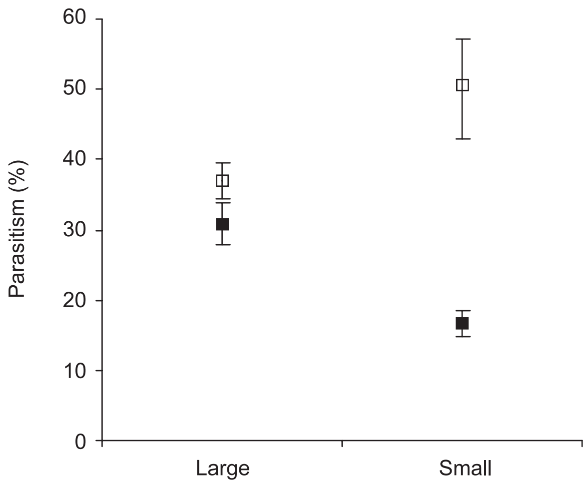

Figure 4 Mean (± SE) overall parasitism rates (□) and maximum parasitism rates (■) by *Phaedrotoma scabriventris* on *Liriomyza huidobrensis*, when reared from plants providing large or small leafminer individuals.

Besides serving a major role in host plant assessment, leaf puncturing and feeding can provide the adult females with proteins for ovary maturation and carbohydrates for their own nutrition (Spencer, 1973). Patterns of female feeding punctures and oviposition can differ (Marino & Cornell, 1993; Martin et al., 2005), which might be explained by optimal foraging (adult performance) driving host preference, as seen for some phytophagous insects (Scheirs et al., 2000, 2004). Our results show no difference in host selection for feeding or for oviposition, as *V. faba* received the highest number of feeding punctures as well as the highest number of eggs, whereas *C. maxima* was the least preferred for both activities.

Changes in egg/feeding puncture ratio among host plants could also suggest a differential host utilization by the leafminer. In our experiments, *V. faba* consistently showed the highest ratio of eggs to feeding punctures. This could be interpreted as the sap of *V. faba* offering more nutrients for oviposition from fewer punctures, in comparison with the other plant hosts (Hussey & Gurney, 1962).

Do *Liriomyza huidobrensis* females prefer the best hosts for their offspring?

Adult *L. huidobrensis* females and males varied in size depending on the plant host on which they had developed, and such variation was highly correlated with the apparent preferences of the leafminer in the field. Because female size is frequently associated with reproductive potential (Valladares & Lawton, 1991; Honek, 1993; Harris et al., 2001), this result suggests a link between preference and performance.

Analyses of other performance indicators in the laboratory also supported a positive relationship between female host preference and offspring performance. Plant species affected development time, particularly for larvae, which are actively feeding and thus are more exposed to the nutritional quality and defensive compounds of plant tissues than other life stages. *Liriomyza huidobrensis* larvae developed fastest on *V. faba* and slowest on *C. maxima*. Shorter development times may increase herbivore fitness by decreasing susceptibility to parasitoids (Williams, 1999). Vulnerability of leafminers to parasitoids is highest during the larval stage (Hendrickson & Plummer, 1983), particularly for serpentine mines, where larvae are easily detected by the visual cues offered by the mine (Salvo & Valladares, 2004). Thus, *L. huidobrensis* larvae on *V. faba* should benefit from reduced exposure to parasitoids, which is also suggested by our field data on parasitism rates, as discussed below. Besides, if generations overlap as is the case with *L. huidobrensis*, faster generation times may lead to greater rates of population increase (Mayhew, 1998).

As observed for development time, the larval stage also showed the most dramatic differences in plant-related mortality, probably due as well to their active consumption of plant tissues. Again, development on *V. faba* proved to be advantageous for the leafminer, resulting in the greatest survival rates. According to these results, *L. huidobrensis* females seem to be able to choose the hosts where their offspring will have higher survival, faster development, and larger size. Because we used specimens originating from *V. faba* for these tests, a tight preference–performance linkage might be attributed to a host-race specialized on this plant. However, this notion is not supported by our oviposition preference results with females of different origin, by the rarity of *V. faba* as a resource in the study area, nor by separate tests with other plant species, in which leafminers originating in *C. maxima* also had higher fitness on *V. faba* (M Videla, unpubl.).

In the closely related *Liriomyza trifolii* (Burgess), adult rather than offspring performance appeared to determine oviposition decisions (Scheirs et al., 2004). Instead, the concordance between oviposition or feeding preference and offspring performance seems to support the optimal oviposition theory in the case of *L. huidobrensis*. The contrast between our results and those reported by Martin et al. (2005) could be attributed to differential responses from two cryptic species (Scheffer & Lewis, 2001) or to geographical variations in resource utilization (Potting et al., 1997). However, the lack of a preference–performance relationship in the above-mentioned work (Martin et al., 2005) may as well result from other factors, e.g., loss of responsiveness after 8–12 laboratory generations (the inconsistent preference rankings of their different subpopulations should not be overlooked), or reduced efficiency in decision-making when facing a highly complex system (Bernays, 1999).

How do parasitoids relate to this plant–host interaction?

Vulnerability of herbivores to parasitoids can be strongly influenced by the herbivore's host plants (Barbosa et al., 2001), whereas the parasitoid response to particular plant traits can in turn provide a selection pressure on herbivores (Stamp, 2001; Mulatu et al., 2004; Singer et al., 2004). *Liriomyza huidobrensis* larvae developing on plants where the leafminer was smaller experienced higher parasitism rates than larvae on plants that allowed them to reach larger sizes. This could be explained by the slow-growth, high-mortality hypothesis (Clancy & Price, 1987), which predicts that herbivores feeding on plants with low nutritional quality or digestibility are more susceptible to natural enemy attack. Such a trend would be mainly due to early attacking koinobionts, which are precisely the most abundant parasitoids of *L. huidobrensis* (Salvo & Valladares, 1995). Our laboratory data suggest that smaller size can be accompanied by slower developmental rates. On such low-quality plant hosts, prolonged exposure of the vulnerable larval stage may have led to a larger impact of parasitoids. Alternative explanations such as enhanced physiological resistance of larger herbivores to parasitoids (Zvereva & Rank, 2003), however, cannot be ruled out.

Susceptibility of herbivore populations to parasitoid attack is frequently linked to parasitoid species richness (Hawkins, 1994). However, the observed patterns of parasitism rates were not related to differences in species number among host plants. The parasitic assemblages of *L. huidobrensis* in central Argentina comprised up to 13 species, depending on the host plant, and much information can be lost when considering just the number of species in parasitic assemblages or total parasitism rates (e.g., Gross & Price, 1988; Salvo & Valladares, 2004). Independent consideration of parasitism by the dominant *P. scabriventris* showed a pattern opposite to that observed for total parasitism: higher mortality rates by *P. scabriventris* were found on those crops where the leafminer was larger. Moreover, the parasitoid itself had a larger body size on the latter plant hosts. Plant-related variations in leafminer size have been shown to affect body size of *P. scabriventris* and other species, with possible effects on their performance (Salvo & Valladares, 2002). This particular species seems to support the proposition that if large, fast-growing herbivores represent high quality hosts, parasitoids should have increased fitness when developing on them and thus should preferentially attack hosts on the plants where the latter have higher intrinsic fitness (Williams, 1999; Zvereva & Rank, 2003). Host location by leafminer parasitoids, including closely related species (Sugimoto et al., 1988), seems to be based on visual, vibrational, and chemical cues (Casas, 1989; Meyhofer & Casas, 1999; Salvo & Valladares, 2004). The mechanisms involved in host location by *P. scabriventris*, apparently allowing intraspecific host size selection while having a host range of over 20 species, deserve further study.

Plants acting as intrinsically high quality hosts for the leafminer, allowing them to develop quickly and to reach larger body size, were the ones providing also larger enemy-free space from the local parasitic assemblage. Therefore, in this system there would be no need of a trade-off between food selection and avoidance of natural enemies (Dicke, 2000). However, these are dynamic interactions, and changes in abundance of particular parasitoid species could result in a different picture. There is evidence that enemy-free space can be affected by frequency of attack (Singer et al., 2004). As field mortality is likely to be highly variable in time and space, and particularly considering that all the parasitoid species recorded here are generalists (Salvo & Valladares, 1999), long-term spatially replicated fieldwork would be necessary to obtain more accurate data in this regard (Mayhew, 1998). However, experimental evidence supports the tendency observed here, with lower overall parasitism rates of *L. huidobrensis* on *V. faba* than on *C. maxima* even for different habitat types (Salvo et al., 2005).

From the present results, *L. huidobrensis* females appear to be able to select those plants that provide a higher performance for their offspring, as expected from their leafmining habits, but contrary to expectations for insects belonging to outbreaking, high-density populations (Bigger & Fox, 1997; Leyva et al., 2000, 2003). These results underscore the importance of simultaneously considering the relative effects of insect population dynamics, host range, offspring mobility, and natural enemies in order to understand the mechanisms determining the strength of preference–performance relationships.

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