

# Oviposition Preference and Larval Performance of *Liriomyza helianthi* (Diptera: Agromyzidae) on Normal and Novel Host Plants

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**ABSTRACT** The relationship between oviposition preference and larval performance has often been regarded as central to the evolution of insect-plant interactions. Studies examining correlations between oviposition preference and larval performance have yielded results ranging from good to poor suggesting that features other than a positive correlation between the preference and performance may influence the evolution of host plant use. In this study, we examined oviposition behavior and larval performance of the specialist leafminer *Liriomyza helianthi* Spencer on normal host plants—sunflower, *Helianthus annuus* L., and cocklebur, *Xanthium strumarium* L. (Asteraceae, tribe Heliantheae), and a number of novel, but related, plants in the Asteraceae. Using choice and no-choice oviposition experiments, *L. helianthi* was observed to oviposit preferentially in its normal host plants and in some novel hosts in the same tribe (Heliantheae). Plants outside the normal tribe in both subfamilies of the Asteraceae were rarely used for oviposition. Larval performance, as assayed by development time, developmental rate, larval survivorship and pupal weight, was assessed by transfers of larvae between normal and novel hosts as well as by direct oviposition into those hosts. The transfer of leafminer larvae allows the decoupling of oviposition and larval performance components of host use, a traditionally difficult task when studying herbivores living inside plant tissues. Our results found no significant relationship between oviposition preference and larval performance in normal and novel hosts. Leafminer larvae have greater latitude than adults in successful use of novel hosts, including use of plants in the alternate subfamily, Cichorioideae. There are some novel plants that are not used for oviposition but are as suitable for development as the normal host. Thus, there is an asymmetry between oviposition preference and larval performance in novel hosts.

**KEY WORDS** *Liriomyza helianthi*, host specialization, diet breadth, larval transfers, host shift

THE STUDY OF diet breadth in phytophagous insects is, in essence, the study of factors that promote or retard the acquisition of novel host plants by herbivores. Although oviposition behavior is the initial determinant of potential host use, host suitability also is a known source of natural selection on host preference (Futuyma and Keese 1992). It is argued that understanding the evolution of oviposition preference and larval performance across a range of host plants is central to the study of diet breadth (Thompson 1988b, Thompson and Pellmyr 1991). If plant characteristics, including plant chemistry, are dominant, then insects should maximize their fitness by ovipositing on plants on which larvae perform best. Evidence for this positive correlation ranges from excellent to poor (Wiklund 1975, Thompson 1988b, Roininen and Tahvanainen 1989, Courtney and Kibota 1990, Jaenike 1990, Nylin and Janz 1993, Hanks et al. 1995, Barker and Maczka 1996). Some herbivores feed on plants in which larval performance (i.e., larval survivorship and developmental time) is suboptimal, raising the possibility that other extrinsic factors, such as competition or enemy-free space, may contribute to insect fitness and influence the evolution of diet breadth (Gilbert and Singer 1975, Gilbert 1979, Jeffries and Lawton

1984, Bernays and Graham 1988, Courtney and Kibota 1990, Jaenike 1990). In fact, Courtney and Kibota (1990) argue forcefully that there are no a priori reasons to expect positive correlations between oviposition preference and larval performance and that plant chemistry is but one of many factors that influence host use patterns (Bernays and Graham 1988, Thompson 1988a).

In this study, we examined the oviposition preference and larval performance of a specialist agromyzid leafminer, *Liriomyza helianthi* Spencer, in normal and novel host plants. We first determined oviposition preference (total eggs per female per day) for normal and novel plants in a series of choice and no-choice oviposition experiments. Second, we measured larval performance in different novel and normal plant species (survivorship, development time, developmental rate, pupal weight, and adult emergence). Finally, we examined the relationship between oviposition preference and larval performance across these hosts.

Normal hosts of *L. helianthi* are restricted to wild sunflower, *Helianthus annuus* L., and cocklebur, *Xanthium strumarium* L., both in the tribe Heliantheae of the Asteraceae (Spencer 1981). Oviposition and larval performance also were assayed in a series of plants in

the Asteraceae not normally used by the flies in nature. Novel hosts were selected arbitrarily to represent a diverse array of plants in the Asteraceae that would present a variety of chemical and morphological challenges to leafminers. Because female flies rarely oviposit in novel plants, larval performance in novel hosts was examined using the technique of larval transfers (Sehgal 1971). Larvae were manually removed from normal hosts and inserted into novel hosts and performance measured. This method allows the decoupling of oviposition and larval performance components of host use, normally a difficult task when studying herbivores living inside plant tissues.

Using normal host utilization patterns as the null hypothesis, we expected oviposition to be restricted to normal hosts (*H. annuus* and *X. strumarium*) with little or no oviposition occurring in novel hosts. Expectations of larval performance on novel hosts relative to normal hosts are less obvious, although as a null hypothesis we also predict that performance would be greatest in normal plants. This assumes that larvae may not be physiologically capable of successful development in novel hosts, having never before encountered or developed in them. That is, we assumed that plant chemistry has the most direct and measurable impacts on larval performance. As a corollary, we expected that as novel plants were more distantly related from the normal hosts, and presumably more different in their chemical, nutritional, and morphological composition, performance in those hosts would decrease relative to the normal host. Consequently, we predict a positive relationship between oviposition preference and larval performance; that is, plant species in which many eggs are laid also have high larval performance, whereas plants in which larval performance is poor would not be used for oviposition.

### Materials and Methods

**Natural History and Colony Rearing.** *Liriomyza helianthi* has a life cycle typical of many leafmining agromyzids: females lay eggs in leaves of their host plant, eggs hatch, and larvae feed in the upper mesophyll layer of the leaves. Larvae progress through 3 instars in  $\approx 5$ –6 d under field conditions before cutting a characteristic crescent-shaped exit hole in the bottom surface of the leaf. Larvae exit the mine and fall to the soil for pupation. Adults emerge after 10–14 d and rendezvous on host plants to mate and oviposit. *L. helianthi* is multivoltine during the summer months with an egg-to-adult cycle of  $\approx 21$ –28 d (C.G., unpublished data). *L. helianthi* has been found only in the Pacific coast states of the United States on *H. annuus* and *X. strumarium* (Spencer 1981), native plants normally found in waste places, low-lying areas, and roadside ditches (Whitson 1992, Hickman 1993).

In our experiments, flies from a laboratory colony were used. A colony was started in 1993 from *L. helianthi* pupae reared from sympatric stands of wild *H. annuus* and *X. strumarium* collected near the towns of Rio Vista, Isleton, and Hood in the Sacramento River Delta (Sacramento County). Adult flies were housed

in sleeve cages where they oviposited into a cultivated sunflower variety (variety small black, Turner Seeds, Breckenridge, TX), hereafter referred to as *H. annuus* (cultivated). Plants were changed on a twice-weekly basis. Cages were maintained at a photoperiod of 16:8 (L:D) h at room temperature ( $\approx 21^\circ\text{C}$ ). Tabletop fans were used to allow better air circulation in the cages. Leaves of colony plants were cut and placed in trays just before larval development terminated. Many larvae only partially exited these leaves to pupate despite the fact that larvae completely emerge from leaves in the field. Leaves and pupae were placed in an emergence box and eclosing adults were aspirated every 2–3 d and reintroduced into colony cages. Honey was streaked on the interior glass of cages every other day to provide a carbohydrate source. Colony output ranged between 500 and 2,000 adult flies per week. Additional wild-collected flies (100–200) were added to the colony during the summer months when available to minimize the loss of genetic variation.

**Oviposition Preference.** To test oviposition preference across different hosts, we performed 2 types of oviposition trials as follows: (1) no-choice experiments, in which flies were placed in cages with only 1 test plant, and (2) choice experiments, in which flies were presented with a control plant and a test plant. No-choice oviposition experiments examined if flies could accept novel plants when no alternatives were present. Strict preference of normal hosts in a choice situation does not preclude the possibility of accepting a novel host when no alternative is present. Plants used for oviposition experiments included the control plant, *H. annuus* (cultivated), on which flies were normally reared in the laboratory; the normal hosts in nature *H. annuus* (wild), and *X. strumarium*; and novel hosts *Ambrosia trifida* L., *Centaurea solstitialis* L., and *Lactuca serriola* L.

Eight replicate cages (60 by 60 by 30 cm) constructed of Plexiglas with large openings covered with fine mesh netting on 4 sides were used for all choice and no-choice experiments. The bottom of the cage had 4 holes (10 cm diameter) equally spaced from the sides of the cage. The openings were closed with a foam disk with a small slit through which plants were introduced. The cage was suspended on stilts ( $\approx 50$  cm). This procedure allowed adjustment of plants to keep them at the same height in the cage relative to each other. To improve adult survivorship, the inside top of the cage was streaked with honey at the beginning of the experiment to provide an additional carbohydrate source. Plants were watered and cages were lightly misted with water on a daily basis to increase humidity.

Colony-reared *L. helianthi* of known age (2–3 d old) were used to achieve optimal oviposition rates. Research on other *Liriomyza* spp. found that maximal oviposition occurred between 4 and 10 d (Parrella 1987). Ten male and 10 female flies were introduced into the center of the oviposition cages and were allowed to oviposit for either 4 or 7 d. There was no difference in the number of eggs laid daily by females on control plants for the experiments of 4-d compared

Table 1. Larval performance of *L. helianthi* transferred into plants in the Asteraceae

Species	Tribe <sup>a</sup>	% larval survival <sup>b</sup>	<i>n</i>	Mean development time, h ± SEM	<i>n</i>	Developmental rate ± SEM <sup>c</sup>	<i>n</i>	Adult emergence <sup>d</sup>
Subfamily Asteroideae								
<i>Helianthus annuus</i> L. (cultivated) <sup>e</sup>	Heliantheae	91.3	28	108.9 ± 2.8a	39	0.00753 ± 0.00024a	21	+
<i>Helianthus annuus</i> L. (wild)	Heliantheae	87.5	9	78.9 ± 6.0a	14	0.00803 ± 0.00026a	19	+
<i>Ambrosia artemisiifolia</i> L. <sup>f</sup>	Heliantheae	90	17	89.7 ± 9.2a	8	0.00791 ± 0.00041a	9	+
<i>Rudbeckia hirta</i> L. <sup>g</sup>	Heliantheae	50	15	101.3 ± 7.5a	5	0.00597 ± 0.00134a	6	+
<i>Zinnia elegans</i> Jacquin <sup>g</sup>	Heliantheae	100	12	102.9 ± 9.0a	9	NA	—	+
<i>Tagetes erecta</i> L. <sup>h</sup>	Tageteae	100	15	102.8 ± 3.5a	13	0.00787 ± 0.00034a	13	NA
<i>Achillea ptarmica</i> L. <sup>g</sup>	Anthemideae	100	14	95.3 ± 5.8a	4	0.00863 ± 0.00057a	5	+
<i>Artemisia douglasiana</i> Besser	Anthemideae	0	6	—	—	—	—	—
<i>Chrysanthemum coccineum</i> Willd. <sup>g</sup>	Anthemideae	50	15	146.9 ± 3.1b	4	0.00439 ± 0.00044b	6	+
<i>Aster alpinus</i> L. <sup>h</sup>	Astereae	18.7	16	111.9	1	0.00741	1	NA
<i>Calendula officinalis</i> L. <sup>h</sup>	Calenduleae	0	14	—	—	—	—	—
<i>Senecio vulgaris</i> L.	Senecioneae	62.5	13	NA	—	NA	—	+
Subfamily Cichorioideae								
<i>Lactuca sativa</i> L. (cultivated) <sup>g</sup>	Lactuceae	75	16	85.2 ± 6.9a	9	0.00642 ± 0.00104a	8	+
<i>Lactuca serriola</i> L.	Lactuceae	0	10	—	—	—	—	—
<i>Sonchus oleraceus</i> L.	Lactuceae	60	11	NA	—	NA	—	—
<i>Cichorium intybus</i> L. <sup>h</sup>	Lactuceae	70	13	137.4 ± 4.3b	6	0.00345 ± 0.00064b	8	+
<i>Taraxacum officinale</i> Wigg.	Lactuceae	73.3	20	97.9 ± 3.6a	11	0.00726 ± 0.00038a	16	+
<i>Centaurea solstitialis</i> L.	Cardueae	66.7	32	135.5 ± 4.0b	29	0.00505 ± 0.00039b	27	+
<i>Cirsium brevistylum</i> Cronq.	Cardueae	0	11	—	—	—	—	—
<i>Gazania Gaertner</i> (x hybrid) <sup>g</sup>	Arctoteae	75	4	92.0 ± 0.7a	3	NA	—	+

Plants were grown from wild-collected seed unless otherwise indicated. Same letters in columns indicate no significant difference from control (Dunnnett test,  $P > 0.05$ ).

<sup>a</sup> Heliantheae sensu stricto (Bremer et al. 1992).

<sup>b</sup> Based on number of larvae that survived the transfer procedure.

<sup>c</sup> Increase in length per unit time, log(mm)/h.

<sup>d</sup> +, successful adult emergence.

<sup>e</sup> Control plant, Turner Seeds, Breckenridge, TX.

<sup>f</sup> Valley Seed County, Fresno, CA.

<sup>g</sup> Burpee Seed County, Warminster, PA.

<sup>h</sup> Advance Seed County, Fulton, KY.

with 7-d duration ( $t = 0.318$ ,  $df = 20$ ,  $P = 0.75$ ). Plants and flies were removed from the cages and all eggs and developing larvae were counted for each plant. Plants and cages were kept on greenhouse benches for the duration of the experiments (conducted January–April 1997).

**No-Choice Oviposition Experiments.** In the no-choice experiments, 2 or 4 plants of a species were placed within each cage. In trials comparing oviposition between the normal (*H. annuus* (cultivated)) and novel plants (*A. trifida*, *C. solstitialis*, or *L. serriola*), half of the cages ( $n = 4$ ) contained *H. annuus* (cultivated) serving as the control host, whereas the remaining half ( $n = 4$ ) contained plants of 1 novel test species. Each no-choice experiment with host plants normally used in the field (*H. annuus* (wild) and *X. strumarium*) simultaneously tested *H. annuus* (cultivated) ( $n = 2$ ) and 3 cages each of *H. annuus* (wild) ( $n = 3$ ) and *X. strumarium* ( $n = 3$ ). All no-choice experiments were repeated twice for each plant species tested. For each repetition of the experiment, a fresh set of control and test plants were used. The total number of eggs (and any developing larvae that emerged) on each plant species was divided by 10 (number of initial females in each cage) and expressed on a per diem basis with each cage serving as a replicate (total eggs on species X per cage per female per day). Differences in oviposition rates (total eggs per cage per female per day) between plant species were tested either using a 1-way analysis of variance

(ANOVA) (for normal plant no-choice tests) and the Dunnnett test with the control (Zar 1984) or *t*-tests with data log ( $x + 1$ ) transformed to normalize variances between plant species.

**Choice Oviposition Experiments.** In the choice experiments, 2 *H. annuus* (cultivated) plants were placed diagonally to each other in the cage with positions assigned at random; 2 experimental plants were placed in the remaining positions (except in the choice experiment with *L. serriola* when only 1 plant was paired with 1 *H. annuus* (cultivated)). Eight replicate cages of each comparison were used at any one time. Leaf area of each plant was measured to the nearest square centimeter using a leaf area meter with automated conveyor belt assembly (Model 3000A, LICOR, Lincoln, NE) to account for size differences that may influence the total number of eggs laid in each plant. Analyses were performed on the total number of eggs on species X per cage per female per day per centimeter squared. Differences between plants were tested using *t*-tests with data log ( $x + 1$ ) transformed.

**Larval Performance Measurements Via Oviposition and Larval Transfers.** Larval performance on different plants was measured by allowing larvae to develop in normal and novel plants. A wide array of plants grown from seed was used to examine larval performance in novel plants (Table 1). Plants were chosen from different tribes and subfamilies in the Asteraceae to see if larvae could survive and develop in novel plants, irrespective of the ability of adults to

Table 2. Pupal weight, development time, and adult emergence of larvae from oviposition and larval transfers

Species	Tribe <sup>a</sup>	% adult emergence	Mean development time, h $\pm$ SEM	n	Mean pupal wt, $\mu$ g $\pm$ SEM	n
Oviposition						
<i>H. annuus</i> L. (cultivated) <sup>b,c</sup>	Heliantheae	72.7	104.7 $\pm$ 2.8a	53	396.0 $\pm$ 9.8a	142
<i>H. annuus</i> L. (wild)	Heliantheae	71.4	NA		380.2 $\pm$ 13.1a	64
<i>H. maximiliani</i> Schrader <sup>c</sup>	Heliantheae	52.4	113.5 $\pm$ 2.1a	64	272.1 $\pm$ 9.5b	169
<i>X. strumarium</i> L.	Heliantheae	86.1	118.6 $\pm$ 4.3b	32	418.5 $\pm$ 10.1a	126
<i>A. artemisiifolia</i> L. <sup>d</sup>	Heliantheae	78.3	NA		337.6 $\pm$ 11.6b	60
<i>A. trifida</i> L. <sup>d</sup>	Heliantheae	71.2	129.7 $\pm$ 4.2b	23	345.1 $\pm$ 13.1b	66
Larval transfers						
<i>H. annuus</i> L. (cult.) <sup>b,c</sup>	Heliantheae	61.9	108.9 $\pm$ 2.8a <sup>e</sup>	39	417.7 $\pm$ 17.8a	45
<i>C. solstitialis</i> L.	Cardueae	57.1	135.5 $\pm$ 4.0b <sup>e</sup>	29	454.9 $\pm$ 24.5a	26

Plants were grown from wild-collected seed unless otherwise indicated. Oviposition and transfer data were analyzed separately. Same letters in column indicate no significant difference from control (Dunnett test,  $P > 0.05$ ).

<sup>a</sup> Heliantheae sensu stricto (Bremer et al. 1992).

<sup>b</sup> Control plant.

<sup>c</sup> Turner Seeds, Breckenridge, TX.

<sup>d</sup> Valley Seed County, Fresno, CA.

<sup>e</sup> Data from Table 1 for comparisons.

oviposit into nonhosts. Larval development time (i.e., time to pupation), survivorship, pupal weight, and adult emergence were measured. When possible, flies were allowed to oviposit in test plants placed in colony cages for 24 h (Table 2). Densities of larvae were kept low ( $<1/\text{cm}^2$ ) to minimize effects of crowding on larval size, pupal weights, and development time (Parella 1983). Because of the low densities of leafminers used in each plant, each developing larva within a plant was considered independent of others and used as a replicate.

When flies would not lay sufficient eggs in novel hosts, larval performance in novel plants was examined by manually moving larvae from normal to novel hosts via a larval transfer procedure (Sehgal 1971). *L. helianthi* larvae were removed from a donor leaf (colony *H. annuus*) and were inserted into a recipient leaf. Larvae were transferred 12–24 h after egg hatch when they were  $\approx 0.6$  mm in length. Using sharp forceps or a minuten pin mounted on an applicator stick, the upper epidermis of the donor leaf was carefully torn and peeled back, exposing the larva feeding just beneath it. Using a lightly moistened, fine sable-hair brush, the larva was lifted out of the mine. In the recipient plant, the upper epidermis of the leaf was punctured with a minuten pin probe and a small pocket formed just under the cuticle. The previously removed larva was carefully inserted head-first into the pocket with the aid of the brush. Transfers were checked at a later time (1–6 h) for mining activity. Movement of mouth hooks and midgut indicated an initially successful transfer.

For all larvae, pupal weights were measured using a Mettler MT5 and Cahn C33 microbalance 3–5 d after pupation. For larval transfers, pupal weights were measured only in *H. annuus* (cultivated) and *Centaurea solstitialis*. Adult emergence was monitored and scored qualitatively and percentage emergence was calculated. To estimate larval development time, plants exposed to ovipositing females were examined daily for initiation of mining activity. For larval transfers, mining was assumed to start when larvae were

transferred. Mines were individually labeled with a small square of laboratory tape and checked once or twice daily until emergence. Pupation was estimated to occur at the midpoint between the last 2 examination periods. Time to pupation was calculated between 1st mining activity and pupation/exiting of mine. In addition, percentage larval survivorship was calculated. For larval transfers, only those larvae that survived the initial transfer were used in survivorship calculations. Developmental rates were calculated by measuring the length of each developing larva with an ocular micrometer on a daily basis. Length data were log-transformed and regressed against time and the slope of the regression,  $\log(\text{length mm})/h$ , was used as a measure of developmental rate. Only larvae for which at least 3 consecutive measurements could be made were used. All larval performance experiments were performed on laboratory benchtops at room temperature (average daily temperature  $21.3 \pm 0.1^\circ\text{C}$ ; average daily deviation of  $3.3 \pm 0.3^\circ\text{C} \pm \text{SEM}$ ,  $n = 28$ ).

Differences in larval performance measures (pupal weight and development time) were tested separately by ANOVA for hosts which received larvae via transfer and those which received larvae by oviposition. To examine differences between plant species, a priori comparisons with *H. annuus* (cultivated) as the control were performed using the Dunnett test (Zar 1984). Although there was a significant sexual dimorphism in pupal weights (mean female pupal weight =  $453.6 \pm 5.1 \mu\text{g}$ , male =  $369.4 \pm 5.1 \mu\text{g}$ ,  $F = 179.3$ ;  $df = 1, 391$ ;  $P < 0.0001$ ), there was no significant plant species  $\times$  sex interaction ( $F = 1.26$ ;  $df = 3, 391$ ;  $P = 0.28$ ). Therefore, data were combined across sexes. Conclusions were identical when sex was taken into account. The differences in larval survivorship across plant taxonomic groups (plants within normal tribe, normal subfamily and novel subfamily) was examined using a Wilcoxon nonparametric test (Zar 1984). Data are reported as means  $\pm$  standard errors. Analyses were performed using JMP 3.1 (SAS Institute 1995).

**Relationship Between Oviposition Preference and Larval Performance.** To relate larval performance to

oviposition preference on normal and novel host plants, an additional set of no-choice oviposition experiments was performed to examine the oviposition preference on a greater number of novel plant species. Individual test plants were placed into Plexiglas cages (30 by 30 by 60 cm) with mosquito netting over large openings on the sides. Three pairs of virgin females and males were introduced into the cages and allowed to oviposit for 3–7 d. The total number of eggs per cage per female per day was calculated for each cage. The following plants were used for these additional oviposition experiments: *Helianthus maximilianii* Schrader, *Ambrosia artemisiifolia* L., *Chrysanthemum coccineum* Jacquin, *Aster alpinus* L., *Achillea ptarmica* L., *Tagetes erecta* L., *Taraxacum officinale* Wigg., *Lactuca sativa* L. (cultivated), and *Cichorium intybus* L. in addition to *H. annuus* (cultivated) as the control. The relationship between larval performance (percentage survivorship) and oviposition preference (total eggs per cage per female per day) for all no-choice experiments combined was measured using both parametric and nonparametric measures of association (Spearman  $r$  and  $\rho$ , respectively).

## Results

**Oviposition Preference.** Oviposition experiments showed that normal host plants were preferred over novel plants. A 2-way ANOVA using repetition over time and plant species as factors showed no significant effect of repetition on oviposition rate for any of the experiments (*H. annuus* (wild), *X. strumarium*,  $F = 0.038$ ;  $df = 2, 12$ ;  $P = 0.849$ ; *A. trifida*,  $F = 2.43$ ;  $df = 1, 10$ ;  $P = 0.15$ ; *C. solstitialis*,  $F = 4.36$ ;  $df = 1, 13$ ;  $P = 0.52$ ; *L. serriola*,  $F = 0$ ;  $df = 1, 8$ ;  $P = 1.0$ ), thus data was pooled across the 2 repetitions. In the no-choice tests, there were no differences in oviposition between *H. annuus* (cultivated) and either *H. annuus* (wild) or *X. strumarium*, the normal host plants of *L. helianthi* in the field (Fig. 1a, normal,  $F = 0.043$ ;  $df = 2, 10$ ;  $P = 0.958$ ) with a grand mean of  $4.60 \pm 0.60$  eggs per female per day laid in each cage. The no-choice oviposition tests however demonstrated significantly lower oviposition in the novel hosts *A. trifida* ( $t = 6.45$ ,  $df = 11$ ,  $P < 0.0001$ ), *C. solstitialis* ( $t = 6.87$ ,  $df = 14$ ,  $P < 0.0001$ ), and *L. serriola* ( $t = 13.04$ ,  $df = 6$ ,  $P < 0.0001$ ; Fig. 1a, novel). No eggs were deposited into *L. serriola* although feeding punctures in leaves were visible. When damaged, *L. serriola* leaves produced a milky exudate that probably prevented oviposition. In addition, the majority of eggs laid into *C. solstitialis* (76 of 126 total eggs) were deposited in only 2 leaves of 1 plant suggesting egg dumping by 1 or 2 females.

The choice experiments followed a trend similar to that of the no-choice experiments, with normal host plants being more preferred than novel plants. Control *H. annuus* (cultivated) plants always received more eggs than other plants. This was also true when comparing *H. annuus* (cultivated) to either *H. annuus* (wild) ( $t = 3.05$ ,  $df = 14$ ,  $P = 0.009$ ) or *X. strumarium* ( $t = 3.69$ ,  $df = 14$ ,  $P = 0.0024$ , Fig. 1b, normal). Novel plants had significantly fewer eggs than the normal

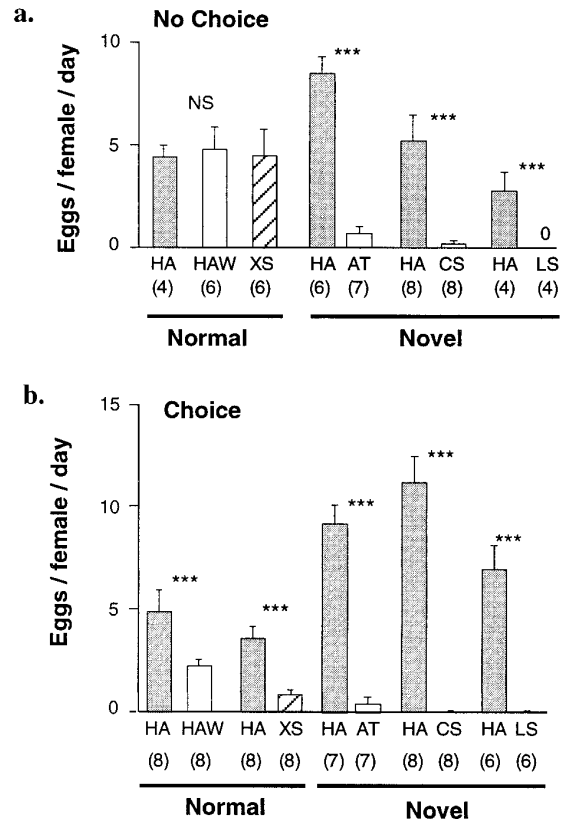


Fig. 1. Mean number of eggs per female per day deposited per cage ( $\pm$ SEM) in (a) no-choice and (b) choice oviposition experiments for normal and novel hosts. HA, *Helianthus annuus* (cultivated); HAW, *H. annuus* (wild); XS, *Xanthium strumarium*; AT, *Ambrosia trifida*; CS, *Centaurea solstitialis*; LS, *Lactuca serriola*. Numbers in parentheses represent sample size. \*\*\*,  $P < 0.001$ ; NS, not significant.

host, although *A. trifida* received more eggs ( $0.439 \pm 0.133$  eggs per female per day) than either *C. solstitialis* or *L. serriola* ( $0.0062 \pm 0.0041$  and  $0.0125 \pm 0.0125$  eggs per female per day respectively; Fig. 1b, novel). Oviposition by *L. helianthi* was greatest in plants most closely related to the normal hosts (i.e., within the same tribe) and significantly lower in more distantly related plants (i.e., outside the normal tribe but within the same subfamily or in the different subfamily (Wilcoxon  $\chi^2 = 9.27$ ,  $df = 2$ ,  $P = 0.01$ )).

**Larval Performance.** Larval transfer experiments demonstrated that *L. helianthi* can utilize a wide range of novel plants and that performance in these novel plants was variable yet roughly equivalent to performance in the normal host. Larvae were able to develop successfully in a variety of plants in both subfamilies of the Asteraceae (Table 1). In the Heliantheae, the normal host tribe, survivorship was consistently high (range, 50–100%; median, 90%). The median survivorship in the subfamily Asteroideae, the subfamily containing normally used hosts, was 75% (range, 0–100%), although some plants were unsuitable for

larval development. All larvae died in *Artemisia douglasiana* Besser and *Calendula officinalis* L.; larvae in *Chrysanthemum coccineum* Willdenow and *Rudbeckia hirta* L. experienced high mortality (50%). In the other subfamily of the Asteraceae, Cichorioideae, larvae experienced comparable survivorship (0–75%; median, 68.4%) compared with survivorship in the Heliantheae or the remaining tribes in the Asteroideae (Wilcoxon  $\chi^2 = 3.40$ ,  $df = 2$ ,  $P = 0.18$ ). All larvae died in *Cirsium brevistylum* Cronq. and development was impossible in *Lactuca serriola* because of the production of a sticky milky exudate when leaves were punctured for transferring larvae.

In most instances, for larval transfer experiments, there was no difference in larval performance measures between normal and novel hosts (Table 1). Development times and developmental rates were comparable between plants in the normal host tribe, Heliantheae, plants in the remaining tribes in the same subfamily, Asteroideae, and plants in the subfamily Cichorioideae (Wilcoxon  $\chi^2 = 0.62$ ,  $df = 2$ ,  $P = 0.73$  and  $\chi^2 = 1.04$ ,  $df = 2$ ,  $P = 0.59$  for developmental time and rate, respectively). Average duration of larval development was 108.2 h (4.5 d) after transfer. Development time and rate in *Centaurea solstitialis*, *Chrysanthemum coccineum*, and *Cichorium intybus*, however, were significantly worsened compared with the normal host (Table 1); larvae in *Centaurea* took 25% longer to reach pupation than those developing in *H. annuus*. Development time of larvae transferred into *H. annuus* (cultivated) compared with those in which eggs were oviposited by females were not significantly different (Table 2;  $t = 1.01$ ,  $df = 90$ ,  $P = 0.27$ ), suggesting that the larval transfer procedure does not significantly influence larval development. Furthermore, development times of larvae oviposited into plants by females were longer in *Ambrosia trifida* and *X. strumarium* than for larvae in control plants (Table 2).

Another measure of larval performance, pupal weight, showed that some novel plants were as suitable for development as the normal host, whereas some were not (Table 2 oviposition, Species effect,  $F = 33.6$ ;  $df = 3, 391$ ;  $P < 0.0001$ ). Pupal weights of larvae feeding in *Ambrosia trifida*, *A. artemisiifolia*, and *Helianthus maximilianii* were lower than larvae in *H. annuus* (cultivated) (Table 2). In contrast, despite lower survivorship and longer development times, transferred larvae feeding in *C. solstitialis* had pupal weights comparable to those in *H. annuus* (cultivated). Pupal weights between *H. annuus* (cultivated) and wild *H. annuus* were not statistically different, suggesting that both plants were similar in resource quality (nutrients, secondary chemistry) and indicating that using *H. annuus* (cultivated) as a control plant for comparison with other hosts is valid. Distribution of pupal weights showed that pupae falling below  $\approx 250 \mu\text{g}$  were less likely to emerge as adults (mean weight of failed pupae,  $214.7 \pm 7.5 \mu\text{g}$ ,  $n = 155$ , successful pupae,  $407.5 \pm 5.2 \mu\text{g}$ ,  $n = 322$ ,  $t = 21.0$ ,  $df = 475$ ,  $P < 0.0001$ ). Therefore, for successful pupation, it was important that larvae achieved a minimum critical size. Some host plants (e.g., *H. maximilianii*) may not

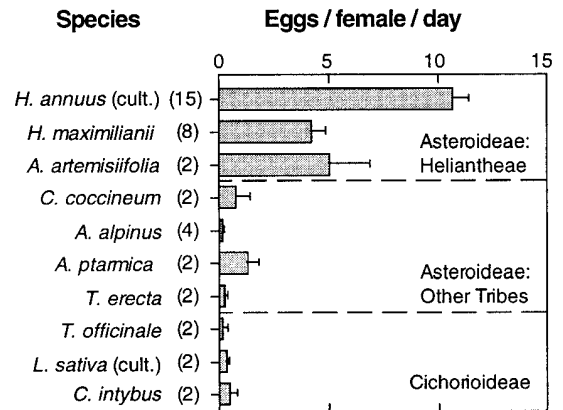


Fig. 2. Mean number of eggs per female per day deposited per cage (+SEM) in additional no-choice oviposition trails. Numbers in parentheses represent sample sizes. Dashed lines indicate subfamilial or tribal affiliations.

have provided sufficient resources to achieve the minimum size (or were toxic) and, as a consequence, adults had lower rates of successful emergence (Table 2).

**Relationship Between Oviposition Preference and Larval Performance.** Oviposition trials in novel plants again showed that females laid more eggs in plants in the normal host tribe, Heliantheae, compared with other plants in the same subfamily, Asteroideae, or the alternate subfamily, Cichorioideae (Wilcoxon  $\chi^2 = 6.75$ ,  $df = 2$ ,  $P = 0.03$ ; Fig. 2). For plant species that had both oviposition and larval performance measurements available ( $n = 13$  for development time and growth rates,  $n = 14$  for survivorship), we estimated correlations among preference and performance measures across all species. There was no significant relationship between mean oviposition preference, eggs per female per day, and larval performance, as measured by development time and growth rate, ( $r = -0.35$ ,  $P = 0.24$ ,  $\rho = -0.20$ ,  $P = 0.52$ , and  $r = 0.36$ ,  $P = 0.30$ ,  $\rho = 0.35$ ,  $P = 0.33$ ,  $n = 13$ , respectively). When mean oviposition preference was compared with larval survivorship, there was no significant parametric correlation ( $r = 0.46$ ,  $P = 0.09$ ), but there was a significant nonparametric association ( $\rho = 0.54$ ,  $P = 0.05$ ,  $n = 14$ ), caused by the inclusion of *Aster alpinus*. The relationship between oviposition preference and larval performance, nevertheless, breaks down into the following 3 groups: (1) plants that receive many eggs and larval performance is high (Fig. 3, most Heliantheae); (2) plants that receive few eggs (<1 eggs per female per day) and larval performance is poor ( $\leq 50\%$  survivorship); and (3) plants that receive relatively few eggs (<1.5 eggs per female per day) but have relatively high performance on these plants (60–100% larval survivorship; Fig. 3A). This same pattern is observed if we use growth rate or development time as the measure of larval performance.

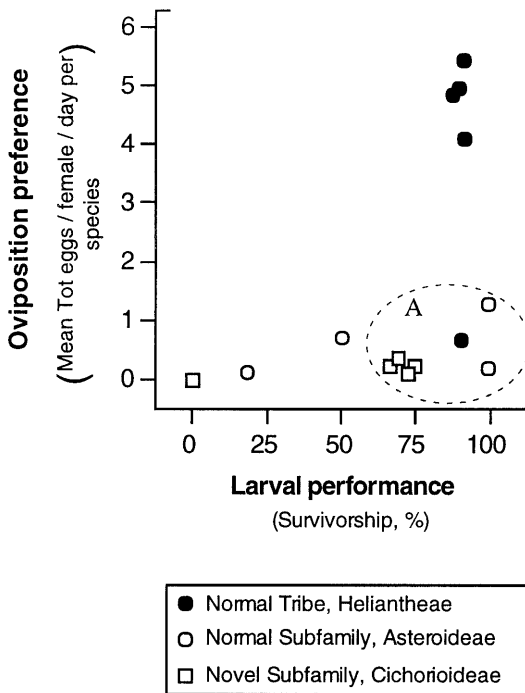


Fig. 3. Relationship between mean oviposition preference and larval performance for each species. Group A represents plants on which larval performance is high, but oviposition preference is low (see text for discussion).

### Discussion

**Relationship Between Oviposition Preference and Larval Performance.** For *L. helianthi*, there is no clear relationship between oviposition preference and larval performance on normal and novel plants. Our experiments have shown that there are potential host plants in which larval performance and oviposition preference are both high and novel plants which are avoided and larvae do not perform well (Fig. 3). However, there are also novel plants on which larvae perform as well as on the normal hosts, but are not used for oviposition by females (Fig. 3A).

As has been documented for other specialist herbivores, including a congeneric agromyzid (Strong et al. 1984, Peschken and Derby 1988, Spencer 1990), *L. helianthi* shows a decrease in oviposition on plants outside of the normal host tribe, Heliantheae, and normal subfamily, Asteroideae (Figs. 1b and 2). Peschken and Derby (1988) found similar results for the agromyzid *Liriomyza sonchi* Hendel, a specialist on sowthistle, *Sonchus arvensis* L. Oviposition into plants of the same genus (*Sonchus* spp.) as the normal host was  $\approx 40\%$  of the normal host. Oviposition into plants outside the genus (but in the same subfamily) ranged from 0.02 to 6.7% of the total of the normal host.

Preference for the *H. annuus* (cultivated) control over other normal hosts in choice experiments (Fig. 1b) suggests that prior experience with *H. annuus* (cultivated) may affect oviposition preference

(Minkenberg and Fredrix 1989, Papaj and Prokopy 1989). Flies were maintained on *H. annuus* (cultivated) for 2–3 d before commencement of experiments to increase survivorship because inexperienced, virgin flies placed directly on test plants suffered high mortality and laid few eggs (C.G., unpublished data). In addition, because flies originated from a laboratory colony reared on *H. annuus* (cultivated) for at least 40 generations (although field-collected adults were added to the colony during the summer months), there also may be a colony effect, with flies developing preferences over time for plants on which they are reared. The absence of any difference between *H. annuus* (cultivated), wild *H. annuus*, and *X. strumarium* in no-choice experiments (Fig. 1) suggests that any initial preference for the colony plant is overcome and normal hosts are used as often as the control plant.

Performance of *L. helianthi* larvae on novel plants suggests that, at least within the same plant family, taxonomic relatedness of novel species is not a good predictor of larval performance. Evidence that larval host ranges are greater than those of ovipositing adults has been documented for other herbivores (Wiklund 1975, Courtney and Forsberg 1988). Also using larval transfers, Sehgal (1971) demonstrated that larvae of the oligophagous agromyzid leafminer *Phytomyza matricariae* Hendel could develop and survive in novel hosts despite the lack of oviposition in those hosts by females. Examination of the performance of other specialist insects on novel hosts shows that larval development sometimes decreases (Prokopy et al. 1988, Hanks et al. 1995), but in other cases, development is equally as good as that on the normal host (Thompson 1988b, Kibota and Courtney 1991).

It has been proposed that the vast diversity of plant secondary chemicals has arisen in part to protect plants against insect attack (Fraenkel 1959, Berenbaum and Rosenthal 1992). Plant allelochemicals often have been shown to kill herbivorous insects not specialized to detoxify them (Berenbaum 1990). In our experiments, we can be reasonably certain that plants used represented a diverse array of chemical, nutritional, and morphological challenges to larvae (Heywood et al. 1977). Tribes of the Asteraceae are known to contain characteristic secondary plant compounds (e.g. sesquiterpene lactones in Heliantheae, monoterpenes in Anthemideae; Heywood et al. 1977) with known antiherbivore effects (Mabry et al. 1977, Jones et al. 1979, Mabry and Gill 1979, Landau et al. 1994), although Futuyama and McCafferty (1990) warn that generalizations at the tribal level may not be applicable at the species level. Nevertheless, leafminer larvae were able, in large part, to survive and develop to pupation in a wide variety of plants both normal and novel. One possibility is that leafminer larvae have broadly targeted detoxification systems that are able to cope with various plant chemistries (Isman 1992).

In addition, broad larval diet, compared with restricted oviposition behavior, supports the hypothesis that many plant chemicals are more effective in deterring oviposition and yet have few major posting-

**Table 3. Host affiliations and geographic distribution of flies in the *Liriomyza pusilla* complex**

Species	Tribes	Plant genera	Distribution
<i>Liriomyza pusilla</i>	Astereae Senecioneae Heliantheae Coreoideae Inulae	<i>Bellis</i> , <i>Aster</i> , <i>Solidago</i> , <i>Callistephus</i> , <i>Crassocephalum</i> , <i>Tithonia</i> , <i>Xanthium</i> , <i>Bidens</i> , <i>Epilobium</i>	Europe, India, E and SE Asia
<i>L. helianthi</i>	Heliantheae	<i>Helianthus</i> , <i>Xanthium</i>	California, Washington
<i>L. eupatorii</i>	Astereae Eupatorieae Heliantheae	<i>Aster</i> , <i>Eupatorium</i> , <i>Helianthus</i> , <i>Galeopsis</i> <sup>a</sup>	Europe, N. America
<i>L. spencerella</i>	Calenduleae Heliantheae Anthemidae Coreoideae	<i>Calendula</i> , <i>Bidens</i> , <i>Chrysanthemum</i> , <i>Helianthus</i>	Argentina
<i>L. sabazia</i>	Astereae Carduaceae Helenieae Inulae	<i>Sabazia</i> , <i>Galinsoga</i> , <i>Baccharis</i> , <i>Carduus</i> , <i>Cirsium</i> , <i>Silybum</i> , <i>Dahlia</i> , <i>Gnaphalium</i>	Venezuela, California
<i>L. heringi</i>		<i>Euphorbia</i> <sup>b</sup>	Europe

Tribes and plant genera are within the Asteraceae unless otherwise indicated.

<sup>a</sup> Lamiaceae.

<sup>b</sup> Euphorbiaceae.

estive effects on larvae (for those that were not killed by secondary plant compounds) (Dethier 1954, Bernays and Chapman 1987). Alternatively, the broader diet of larvae, compared with the narrow oviposition behavior of female flies, may be the residual of a recently restricted behavioral repertoire that has responded to selection for discrimination against marginally less favorable hosts (Wiklund 1975, Fox and Lalonde 1993, Larsson and Ekblom 1995). For plant-herbivore systems in which this pattern prevails, the evolution of insect oviposition behavior may be the primary determinant of host-use patterns, with larval performance adjusting and fine tuning to the host after it has been accepted as a host suitable for oviposition (Futuyma 1983).

This asymmetry between oviposition preference and larval performance allows for the possibility that some oviposition mistakes by adult flies may occur on a novel host that is suitable for larval development. For example, *L. helianthi* was shown to occasionally oviposit, although at highly reduced rates, in novel hosts such as *C. solstitialis*, which are suitable for larval development. It is postulated that such oviposition mistakes are regular features of insect oviposition behavior and, given the potential suitability of some novel hosts for larval development, may be the source of host range expansions (Courtney and Kibota 1990, Kibota and Courtney 1991). In addition, for novel hosts in which performance is not as good as the normal host, other benefits, such as escape to enemy-free space (Gilbert and Singer 1975, Jeffries and Lawton 1984, Feder 1995, Gratton 1997), may counterbalance some of the incurred developmental costs and thus facilitate a diet-breadth expansion.

**Host Utilization Patterns.** Oviposition and larval performance patterns of *L. helianthi* can be viewed in a broader context by comparing the host utilization of closely related species. Host affiliations within groups of related herbivores (i.e., genera, tribes, families) are

often remarkably similar and highly conserved (Mitter and Farrell 1991), a pattern which also is apparent for *L. helianthi* and its closest relatives. Despite our limited knowledge of evolutionary relationships within the Agromyzidae and *Liriomyza* in particular, Spencer (1990) placed *L. helianthi* in a species group, the *Liriomyza pusilla* complex, based on shared morphological features of the male aedeagus (Table 3). Given the morphological similarities of this group, we can infer some degree of shared ancestry of the species. Rearing records have found species in this group restricted primarily to plants in the sub-family Asteroideae of the Asteraceae (Spencer 1990). That *L. helianthi* can oviposit in other plants of the Heliantheae and shows significantly decreased oviposition in the Cichorioideae is consistent with host use of related species in the *L. pusilla* complex. It is possible that lack of oviposition into the Cichorioideae may represent the absence of genetic variability to respond to chemical stimuli from plants in that subfamily (Futuyma et al. 1995). Nevertheless, we must be cautious about generalizations from the literature because there may be factors that vary with geography, such as host availability or unevenness in collecting, that may present an incomplete picture of the actual host-use patterns.

Given the ability of *L. helianthi* larvae to successfully utilize some plants in the Cichorioideae, it would be important to test if its closest relatives also have this ability despite their apparent reluctance to oviposit in those plants. Although it is difficult to infer potential larval diet breadth of other species in the *L. pusilla* complex from the literature, it is possible that ancestors of this group were readily able to feed on plants in the Cichorioideae, with the ability retained by their descendants in the *L. pusilla* complex (e.g., Futuyma et al. 1993). In any event, such latitude in larval performance across hosts, coupled with occasional, genetically based oviposition mistakes, may predispose some phytophagous insect groups to be more likely to

successfully incorporate novel plants into their diet. The lack of relationship between preference and performance may be partly responsible for the great taxonomic diversity of such groups (*sensu* Bush 1975).

If oviposition into novel hosts sometimes occurs, and larval performance is often permitted on such unusual hosts, then why are host shifts so rare in nature (Bush 1975)? To predict how preference and performance relationships affect the incorporation of novel hosts into the herbivore diet will require a more detailed study of other potential constraints that may retard the incorporation of newly encountered hosts. Constraints may include genetic aspects of feeding and oviposition (i.e., trade-offs, difficult to do with these agromyzids because of mating constraints), and interactions with other organisms, such as natural enemies and competitors which may, depending on their relative magnitude and their persistence, either facilitate or retard the acquisition of novel hosts (Via 1984, Karowe 1990, Thompson et al. 1990, Futuyma et al. 1993, Denno et al. 1995, Gratton 1997, Hawthorne 1997).

In summary, for *L. helianthi*, it appears that females are relatively restricted in their oviposition behavior, confining most of their egg laying to plants in the same tribe as the normal hosts, Heliantheae. In contrast, by using larval transfers, we were able to demonstrate that leafminer larvae show more breadth and variability in their ability to survive and develop successfully in novel hosts, including plants in the distantly related subfamily Cichorioideae. The reduction in larval performance in novel plants is not as pronounced as the decline in oviposition. Thus, there is an asymmetry between oviposition preference and larval performance in novel hosts.

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