

Parasitism of Natural Populations of *Liriomyza helianthi* Spencer and *Calycomyza platyptera* (Thomson) (Diptera: Agromyzidae)

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The population dynamics and parasitoid assemblages of two leafminers, *Liriomyza helianthi* Spencer and *Calycomyza platyptera* (Thomson) (Diptera: Agromyzidae), were examined over a 3-year period. Leafminers were sympatric and occurred together on the same two host plants, *Helianthus annuus* L. and *Xanthium strumarium* L., at our study sites in northern California. Sixteen species of parasitoids were reared from the two leafminers and mortality from parasitoids was substantial, averaging about 74%. The most common species, such as *Diglyphus* spp. and *Neochrysocharis arizonensis* Crawford, show no bias in association with a particular leafminer or plant species. Of the remaining parasitoids, most were usually associated with a particular leafminer species (e.g., *Opius dimidiatus* [Ashmead] on *L. helianthi*). Only one parasitoid of the seven most common taxa (*Chrysocharis ainsliei* Crawford) was strongly associated with a particular host plant species (*H. annuus*) in either leafminer host. In addition, a review of the literature found that parasitoid assemblages in natural, unmanaged habitats tended to be more species rich than assemblages of parasitoids on leafminers in agricultural habitats, although significant heterogeneity occurs among studies. Nevertheless, the most common genera of parasitoids attacking leafminers (*Diglyphus*, *Chrysocharis*, *Neochrysocharis*, *Opius*) are prevalent in both habitats. Given the similarity in assemblages of many of the parasitoids attacking leafminers in managed and natural habitats and frequent proximity of the two habitats, there exists the potential for exchange of natural enemies among habitats, potentially enhancing pest control in agricultural areas.

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Key Words: *Liriomyza helianthi*; *Calycomyza platyptera*; *Diglyphus*; *Neochrysocharis*; *Opius*; *Chrysocharis*; *Helianthus annuus*; *Xanthium strumarium*; leafminer population dynamics; parasitoid com-

munities; host-plant effects; managed vs natural habitats.

INTRODUCTION

Agromyzid leafminers in the genus *Liriomyza* Mik (*L. sativae* Blanchard, *L. trifolii* [Burgess], and *L. huidobrensis* [Blanchard]) are serious economic pests of a variety of crops in North America and Hawaii (Spencer, 1973; Parrella, 1982; Johnson, 1987, 1993), and more recently in Europe and the Mediterranean (Minkenberg and van Lenteren, 1986; Parrella, 1987). The combination of broad host range (e.g., >400 species of host plants used by *L. trifolii*) and rapid development of resistance to insecticides has necessitated the use of biological control methods for the control of these leafminers in both greenhouse and field crops (Parrella *et al.*, 1982). As a result, a wealth of information exists on the biology of economically important *Liriomyza* species as well as data on the natural enemies that attack them (Minkenberg and van Lenteren, 1986; Johnson and Hara, 1987). In contrast, little is known of the natural history, population dynamics, and natural enemy assemblages attacking native *Liriomyza* species and other noneconomically important agromyzids.

Recent surveys have documented that economically important *Liriomyza* species are attacked by a cumulative total of at least 40 species of parasitic Hymenoptera in 4 different families (Johnson and Hara, 1987). A study of *L. sativae* on agricultural crops in one geographic area found 21 parasitoid species over a 2-year period (Harding, 1965). Extensive surveys of natural populations of leafminers have found similarly highly diversified parasitoid assemblages, with as many as 25 parasitoids reared from a single leafminer species (Kato, 1994a, 1996). In large part, parasitoid assemblages of dipteran leafminers are dominated by eulophids, braconids and pteromalids that attack the larval and pupal stages of the flies (Askew and Shaw, 1974;

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Salvo and Valladares, 1998, 1999; Valladares and Salvo, 1999).

In managed agricultural ecosystems, the proportion of leafminer mortality attributed to parasitoid attack can be significant. In tomato fields in California, outbreaks of *L. sativae* have been attributed to the decline of key parasitoids following applications of insecticides (Oatman and Kennedy, 1976), suggesting the importance of parasitoids in controlling leafminer pests. In addition, Johnson *et al.* (1980a) proposed that *Chrysocharis oscinidis* (Crawford) acting in a density-dependent manner was responsible for controlling populations of *L. sativae* in tomatoes. Beanfly, *Ophiomyia phaseoli* (Tyron), outbreaks in Hawaii have been controlled by importation and release of exotic parasitoids (Greathead, 1975). Parasitoids also have been used successfully to control leafminer infestations in greenhouses (van Lenteren and Woets, 1988; Heinz and Parrilla, 1990a). Other natural enemies such as fungal pathogens or generalist predators have not been examined in detail, but their effects appear to be negligible for many leafminer species (Harcourt *et al.*, 1987; Johnson, 1993). Overall, data from agricultural ecosystems suggest that agromyzid leafminers are attacked by a diverse assemblage of hymenopteran parasitoids that often are responsible for significant levels of leafminer mortality. Nevertheless, little information is available from noneconomically important agromyzid leafminers in natural habitats (but see Kato, 1994a, 1996).

For our first objective, we documented the population dynamics of two agromyzid leafminers under natural conditions and evaluated attack rates from natural enemies. Over a 3-year period, we followed a population of the specialist leafminer, *Liriomyza helianthi* Spencer (Diptera: Agromyzidae), a leafminer endemic to the west coast of the United States (Spencer, 1981). Larvae of *L. helianthi* feed only on *Helianthus annuus* L. (common wild sunflower) and *Xanthium strumarium* L. (cocklebur) (Asteraceae, Heliantheae) in natural habitats. In addition, we surveyed populations of the oligophagous *Calycomyza platyptera* (Thomson) as this species co-occurred with *L. helianthi* on the same host plants.

Since both leafminers occur sympatrically and utilize the same two host plants, our second objective was to evaluate to what extent the parasitoid assemblages of the two leafminers are differentiated on the basis of plant or leafminer hosts. Although host plants have often been shown to influence parasitoid foraging and attack on herbivorous insects (Barbosa, 1988), specificity of parasitoids to a particular insect species often explains significant variation in parasitoid assemblages (Mills, 1993). The 2 leafminer \times 2 host plant combination present at our study site provided us the opportunity to examine the relative strength of factors

that may influence differences in parasitoid assemblages.

Finally, since most information on leafminer parasitoids comes from studies of polyphagous leafminers in agricultural settings, we expanded the review of Johnson and Hara (1987) to include what is known of parasitoid assemblages of noneconomically important agromyzid leafminers. Our objective was to compare parasitoid species richness and level of attack among agromyzid leafminers in managed ecosystems to leafminers in natural habitats—a principal characteristic that differs between this study of *L. helianthi* and *C. platyptera* and the multitude of studies of economically important agromyzids.

MATERIALS AND METHODS

Natural History

Liriomyza helianthi is a specialist leafminer found exclusively in native wild sunflower (*H. annuus*) and cocklebur (*X. strumarium*) (Spencer, 1981; C. Gratton, personal observation) in roadside ditches, disturbed and low-lying areas in Pacific Coast states (Washington through California) of the United States (Whitson, 1992; Hickman, 1993). *L. 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 leaf. Larvae progress through 3 instars in approximately 5–6 days 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 days and return to host plants to mate and oviposit. *L. helianthi* is multivoltine during the summer months with an egg to adult cycle of approximately 3–4 weeks.

C. platyptera has a broader diet breadth than *L. helianthi*, forming whitish blotch mines on plants in at least 7 tribes of the Asteraceae, though it is found feeding primarily in the tribe Astereae (*Aster*, *Baccharis*, *Conyza*, *Erigeron*, *Grindelia*, *Heterotheca* and *Solidago*) and Heliantheae (*Helianthus*, *Xanthium*, *Zinnia*, *Ambrosia*) (Spencer, 1981). This blotch-miner is found throughout North and South America and in the Caribbean (Spencer, 1990; Valladares and Salvo, 1999). At our California field sites and in surrounding areas (50 km radius), surveys found *C. platyptera* only in *H. annuus* and *X. strumarium*, although some of their other host plant species were occasionally present. The duration of the larval stage is \approx 10–14 days. Unlike *L. helianthi*, *C. platyptera* pupates within the mine on the plant where the puparium is firmly glued. Adult emergence occurs 10–14 days after pupation. Egg development time is unknown for this species, but egg-adult generation time in the laboratory is approximately 4–5 weeks.

Field Sites and Sampling

Between 1993 and 1995, populations of leafminers and their parasitoids were studied in a 0.25 ha abandoned field, 1 km east of Rio Vista, Sacramento County, in the Sacramento River Delta of California. This site remained flooded until early June after which *H. annuus* and *X. strumarium* seeds germinated. Plants began flowering in late July, set seed, and senesced by late September-October. *L. helianthi* and *C. platyptera* co-occurred on plants at this site and their parasites were present throughout this period for all 3 years of the study.

Between 1993 and 1995, *L. helianthi* and *C. platyptera* populations were sampled weekly after germination of host plants in mid-June through senescence in late September. In 1993, only *H. annuus* plants were sampled, whereas in 1994 and 1995 both *H. annuus* and *X. strumarium* plants were sampled. On each sampling date, 6–12 plants of each species were haphazardly selected and all leaves were counted and examined for the presence of leafmines. All leaves with mines were removed, placed in plastic bags, stored on ice, and returned to the laboratory. Using a dissecting microscope (10–60X), all leafmines were dissected to determine the fate of leafminer larvae. Mines in which a leafminer was contained within the mine and was either still alive (A) or currently parasitized (P) were recorded. Mines that had been vacated by either the leafminer or parasitoid were not counted.

Leafminer densities were calculated for both leafminer species (*L. helianthi* and *C. platyptera*) on the two host plants (*H. annuus* and *X. strumarium*). For each replicate plant, the total number of occupied mines (A+P) of each leafminer species was summed and divided by the total number of leaves per plant as a measure of leafminer density. Although average leaf area of *X. strumarium* ($42.3 \pm 1.08 \text{ cm}^2$) is smaller than *H. annuus* ($65.3 \pm 1.08 \text{ cm}^2$) ($t = 8.09$, $df = 1022$, $P < 0.0001$), differences between plant species explains only 6% of the variance in leaf size. Hence, leafminer density estimates (No./leaf) between the two plant species are generally comparable. Percentage parasitism was estimated as $P/(A+P) \times 100$. Means are reported \pm standard errors. Differences in leafminer density and percentage parasitism among host plant species and among years were examined using *t* test or nonparametric Wilcoxon and Signed-ranks test when assumptions of homoscedasticity could not be met.

Characterization of Parasitoid Assemblage Attacking Leafminers

From samples collected in 1994 and 1995, attempts were made to rear all live leafminers and parasitoids collected from the plant sampling to adulthood. Since leafminers were usually scarce early in the season, an additional set of leaves with mines was collected in

order to increase the sample size for parasitoid identifications. Leaf petioles were cut with a razor blade and placed in vials with water. Vials with cut leaves were in turn placed individually in 473-ml plastic cups to catch any pupating leafminers (*L. helianthi*). Most actively mining leafminers completed larval development in less than 1 week. *L. helianthi* emerged from cut leaves and fell into the plastics cups. On the other hand, *C. platyptera* puparia were manually removed from inside mines as leaves began to dry out (≈ 1 week). Leafminer puparia were placed individually into 4-ml vials plugged with cotton to collect emerging adult leafminers and parasitoids.

Since leaves could usually not be kept alive long enough for parasitoid development to be completed (≈ 1 –3 week), paralyzed leafminer larvae with developing parasitoids were removed and placed in an artificial mine as described in Hendrickson and Barth (Hendrickson and Barth, 1978; Heinz, 1996). Briefly, a small paper square ($2 \times 2 \text{ cm}$) cut from an index card was lightly moistened with water and placed on a microscope slide. A hole (6 mm diameter) was punched in the middle of the square. An individual leafminer carcass with its parasitoid was placed in the circular arena and a square glass coverslip was placed over the paper square, sandwiching the leafminer and parasitoid between the coverslip and the microscope slide. The slide was placed in a closed petri dish lined with moistened filter paper. The artificial mine prevented the leafminer carcass from desiccating allowing the parasitoid larva to develop to pupation. A significant fraction of larvae succumbed to mold during development in the artificial mine. However, it is assumed that mortality was random with respect to parasitoid species and therefore did not bias emergence data. Parasitoids emerging from both artificial mines and leafminer puparia were stored in 70% ethanol for later identification.

Parasitoids were categorized as idiobionts if they suspended leafminer development or as koinobionts if the parasitized host was allowed to continue to develop (before eventual host death) (Askew and Shaw, 1986). Parasitoids were categorized further as endo- or ectoparasitoids depending on where parasitoid larvae developed relative to the leafminer host. All parasitoids that were successfully reared from leafminer hosts in 1994 and 1995 were identified to species ($n = 364$). However, almost half (7) of the total 16 species reared were scarce among the total number of parasitoid individuals reared (<3% of all parasitoids) and were not included in analyses of parasitoid assemblages. To increase the power of the analysis, some taxonomically similar groups were combined: *Diglyphus begini* (Ashmead) and the less common *Diglyphus pulchripes* (Crawford), both solitary ectoparasitoids, were combined and are hereto referred to as *Diglyphus* spp.; *Closterocerus cinctipennis* (Ashmead) and *Clostero-*

TABLE 1

Percentage of Parasitoid Species Reared from *Liriomyza helianthi* and *Calycomyza platyptera*

Family	Superfamily Species	Mode of parasitism ^a — endo/ecto ^b	Host stages of oviposition—emergence ^c	Leafminer hosts	
				<i>L. helianthi</i>	<i>C. platyptera</i>
Ichneumonoidea					
Braconidae	<i>Opius dimidiatus</i> (Ashmead) ^d	K-endo	L-P	16.54	2.88
Chalcidoidea					
Eupelmidae	<i>Macroneura</i> sp.	I-endo	?-P	0.00	0.96
Pteromalidae	<i>Halticoptera microstipes</i>	K-endo	L-P	0.77	0.00
	<i>Thinodytes</i> sp. ^d	K-endo	L-P	0.77	17.31
Eulophidae	<i>Cirrospilus</i> sp.	I-ecto	L-L	1.15	1.92
	<i>Diglyphus begini</i> (Ashmead) ^d	I-ecto	L-L	24.23	16.35
	<i>Diglyphus pulchripes</i> (Crawford) ^d	I-ecto	L-L	1.54	2.88
	<i>Diglyphus websteri</i> (Crawford)	I-ecto	L-L	0.38	0.00
	<i>Diglyphus</i> sp.	I-ecto	L-L	0.38	0.00
	<i>Diaulinopsis callichroma</i> Crawford	?	?	0.77	0.96
	<i>Pnigalio</i> sp. ^d	K-endo	L-L	0.77	4.81
	<i>Chrysocharis ainsliei</i> Crawford ^d	K/I-endo	L-P	6.15	11.54
	<i>Closterocerus cinctipennis</i> (Ashmead) ^d	I-endo	L-L	3.85	0.00
	<i>Closterocerus utahensis</i> (Crawford) ^d	I-endo	L-L	17.31	4.81
	<i>Neochrysocharis arizonensis</i> Crawford ^d	I-endo/ecto	L-L	25.38	33.65
	<i>Baryscapus</i> sp.	K-endo	L-P	0.00	1.92
	Total number emerged ^e			260	104

Note. Leafminers were collected from *Helianthus annuus* and *Xanthium strumarium* in 1994 and 1995 in northern California (Sacramento County).

^a I, idiobiont; K, koinobiont.

^b endo, develops internally; ecto, develops externally.

^c L, larva; P, pupa.

^d Used in analyses of parasitoid assemblage.

^e Data combined across both host plant species, *Helianthus annuus* and *Xanthium strumarium*, and across 1994 and 1995.

cerus utahensis (Crawford) were combined as *Closterocerus* spp. The resulting 7 taxonomic groups (Table 1), representing 95.9% of all emerging parasitoids, were used in ensuing analyses: *Opius dimidiatus* (Ashmead), *Thinodytes* sp., *Diglyphus* spp., *Pnigalio* sp., *Chrysocharis ainsliei* Crawford, *Closterocerus* spp., and *Neochrysocharis arizonensis* Crawford.

Associations between parasitoid species (PAR), leafminer host (H), and plant species (PL) were analyzed by comparing different log-linear models of the frequency data (Table 2). Models were compared by sequentially eliminating higher order terms and examining goodness-of-fit *G* statistics and by *G* tests between nested models (Sokal and Rohlf, 1995). Models were also compared using the Raftery's Bayesian Information Criterion (BIC) which adjusts goodness-of-fit statistics by the number of parameters estimated. Lower BIC values indicate an overall better fit of the model to the observed data (Wilkinson, 1989; Sokal and Rohlf, 1995).

Literature Survey

We surveyed the available literature to find studies that examined parasitoid attack of agromyzid leafminers. We evaluated how parasitoid assemblages differ between agromyzid leafminers typically found in man-

aged (i.e., agricultural and urban) habitats compared to leafminers in natural (unmanaged) habitats. Habitats were classified as "urban" for studies that examined leafminers in naturally occurring or ornamental plants growing in or near residential areas. Studies were included in our survey if an explicit attempt was made to characterize the parasitoid assemblage attacking a specific leafminer and if the relative abundances of parasitoid species were reported. Although some earlier studies of leafminers in agricultural systems may not have been included in this summary, we feel that the abundance of recent information is probably representative of the general patterns of parasitism for those species.

For each study, we recorded the total number of parasitoids species reared from each leafminer host. We also attempted to quantify, when possible, the degree of parasitoid attack (percentage parasitism) from each study. When not directly given in a paper, estimates of percentage parasitism were calculated from tables and graphs. Figures were digitized using a scanner and values from graphs were measured using Scion NIH Image (ver. Beta 3b, Scion Corp., Frederick, MD). Parasitism was calculated as number parasites emerging/(number leafminer + number of parasites) × 100. As a result, mortality caused by host feeding of adult

TABLE 2

Log-Linear Analysis of Parasitoid (PAR) Frequency Counts in Leafminer (H) and Plant (PL) Species

Model	df	G ^a	P ^b	BIC ^c
<i>Saturated model</i>				
$\mu + H^d + PL^e + PAR^f + H \times PL + H \times PAR + PL \times PAR + H \times PL \times PAR$				
<i>Partial association</i>				
1 $\mu + H + PL + PAR + H \times PL + H \times PAR + PL \times PAR$	6	5.36	0.499	-29.36
<i>Conditional independence</i>				
2 $\mu + H + PL + PAR + H \times PAR + PL \times PAR$	7	5.43	0.608	-35.08
3 $\mu + H + PL + PAR + H \times PL + PL \times PAR$	12	73.95	<0.0001	4.50
4 $\mu + H + PL + PAR + H \times PL + H \times PAR$	12	32.61	0.0011	-36.83
<i>Partial independence</i>				
5 $\mu + H + PL + PAR + PL \times PAR$	13	75.25	<0.0001	0.03
6 $\mu + H + PL + PAR + H \times PAR$	13	33.92	<0.0001	-41.31
7 $\mu + H + PL + PAR + H \times PL$	18	102.4	0.0002	-1.73
<i>Complete independence</i>				
8 $\mu + H + PL + PAR$	19	103.7	<0.0001	-6.21

Note. Each model (1–8) is nested within the full model by successively removing different interaction terms. Models that excluded the H×PAR or PL×PAR terms (3–8) did not adequately describe observed frequencies ($P < 0.05$). Moreover, models that included only the H×PAR interaction (4 and 6) better represented the data than models that included only the PL×PAR interaction (3 and 5), suggesting that leafminer species was a better predictor of parasitoid species than host plant species.

^a Goodness-of-fit statistic.

^b $P < 0.05$ indicates an inadequate fit of expected frequencies when compared to full (saturated) model.

^c Bayesian Information Criterion was used to examine the relative fit of different models adjusting for the number of estimated parameters. Smaller BIC indicates an overall better fit of the model to the observed data.

^d H, leafminer species.

^e PL, plant species.

^f PAR, parasitoid species.

parasitoids of some species (e.g., *D. begini*, *C. oscinidis*) is not evident in estimates of mean parasitism values. From all available data in a study, an overall mean parasitism was calculated for each leafminer in a particular habitat. In general, caution should be used in equating percentage parasitism with mortality caused by parasitoids (Van Driesche, 1983). However, the purpose of this review was to qualitatively assess the relative impact of parasitoids on different leafminer species in different habitats among studies and did not focus on whether parasitoids were regulating host populations or if parasitoids were the most significant source of mortality. Studies that did not differentiate between habitat types were not used in the survey. For studies that examined parasitoid attack in agricultural systems, only data on leafminer attack in untreated controls (i.e., no insecticides) were used. For leafminer species with multiple studies reporting parasitoid species richness and percentage parasitism a single pooled mean across all studies was calculated. For example, only one estimate of parasitoid species diversity and percentage parasitism was calculated from the 4 studies of *Agromyza frontella* (Rondani) in agricultural habitats (Table 3). This was done so as not to bias results in favor of frequently studied species (e.g., *L. sativae*, *L. trifolii*). In addition, a single pooled average was calculated for all studies that did discriminate between different *Liriomyza* species (e.g., Jensen and Koehler, 1970; Schuster and Wharton, 1993). Our lit-

erature survey found 50 independent studies (including this study) that examined leafminer parasitism with 30 unique leafminer species by habitat type combinations, 25 of which provided information on percentage parasitism. Because of the high variability in the data, summary statistics for species richness and percentage parasitism are reported as medians with interquartile ranges (25–75% percentile rank of observations). The effects of habitat type (agricultural, urban, or natural) on parasitoid species richness and mean percentage parasitism were compared using a Kruskal-Wallis nonparametric test.

RESULTS

L. helianthi and *C. platyptera* Population Dynamics and Mortality

In all years of the study, *L. helianthi* populations grew steadily throughout the season and peak abundance occurred in August or September (late September in 1995) (Figs. 1–3). *C. platyptera* reached peak densities a few weeks before *L. helianthi* in 1993 (early-mid August) (Fig. 4) but peaked in abundance at the same time as *L. helianthi* in 1994 (Fig. 5). *C. platyptera* populations were extremely low and relatively constant in 1995 (Fig. 6). On average, *L. helianthi* densities were about 5 times higher than *C. platyptera* ($t = 7.67$, $df = 36$, $P < 0.01$). In addition,

TABLE 3
 Summary of Literature Survey of Parasitoid Assemblages of Agromyzid Leafminers in Agricultural, Urban, and Natural Habitats

Habitat	Leafminer species	Host Range ^a	Host plant(s)	Native range	Study locality	Number of parasitoids	Most common parasitoids			Parasitism (percentage)		
							Dominant parasitoid 1	Dominant parasitoid 2	Mean	Min-max	Reference	
Agricultural	<i>Agromyza frontella</i> (Rondani)	M	<i>Medicago sativa</i>	Europe	Europe	17	<i>Chrysocharis punctifacies</i> ^b Delucchi	<i>Diglyphus isaea</i> ^b (Walker)	64	33-90	Drea <i>et al.</i> , 1982	
			<i>M. sativa</i>	Europe	Europe	6	<i>C. punctifacies</i>	<i>Dacnusa dryas</i> ^c (Nixon)	26 ^c	—	Hendrickson and Barth, 1979	
			<i>M. sativa</i>	Delaware ^h	Delaware ^h	14	<i>Diglyphus intermedius</i> (Girault)	<i>Diglyphus pulchripes</i> (Crawford)	36	0-91	Hendrickson and Barth, 1979	
			<i>M. sativa</i>	Canada ^h	Canada ^h	3	<i>Diglyphus</i> spp.	<i>Crytogaster vulgaris</i> ^d (Walker)	37	17-58	Harcourt <i>et al.</i> , 1987	
		<i>Agromyza nana</i> Meigen	O	<i>M. sativa</i>	Europe	Europe	12	<i>Miscogaster</i> ^d spp. <i>Dacnusa</i> spp.	75	71-100	Drea <i>et al.</i> , 1982	
		<i>Chromatomyia fuscula</i> (Zetterstedt)	O	<i>Hordeum vulgare</i>	N. Europe Canada	Norway	14	<i>Diglyphus begini</i> (Ashmead)	39	17-52	Darvas <i>et al.</i> , 1999	
		<i>Chromatomyia horticola</i> (Gour.)	P	<i>H. vulgare</i>	Norway	Norway	15	<i>D. begini/C. vulgaris vulgaris</i>	—	—	Hågvar <i>et al.</i> , 1998	
		<i>Liriomyza brassicae</i> (Riley)	O	<i>Brassica oleracea campestris</i>	Ethiopian	India	12	<i>Opisus turcicus</i> ^e Fischer	36	9-58	Kumar, 1989	
		<i>L. congesta</i> (Becker)	O	<i>Medicago sativa</i>	Europe	California	11	<i>D. begini</i>	68	27-84	Oatman and Platner, 1969	
		<i>L. huidobrensis</i> (Blanchard)	P	<i>Phaseolus vulgaris</i> , <i>Vicia faba</i> , <i>Spinacea oleracea</i>	Nearctic/ Neotropic	Europe Argentina	8	<i>Phaenotoma scabriventris</i> ^f (Nixon)	—	—	Drea <i>et al.</i> , 1982 Valladares and Salvo, 1999	
	<i>L. marginalis</i> (Malloch)	M	<i>Solanum tuberosum</i> , <i>Allium</i> , <i>Brassica</i> <i>Zea mays</i>	Neotropic	Honduras	2	<i>Chrysocharis tonones</i> (Walker)	—	—	Shepard <i>et al.</i> , 1998; Shepard and Barrion, 1998 Acosta and Cave, 1994		
	<i>L. sativae</i> Blanchard	P	<i>Lycopersicon esculentum</i>	Nearctic/ Neotropic	California	4	<i>Chrysocharis oscinidis</i> (Crawford)	27	7-60	Zehnder and Trumble, 1984		
	<i>L. esculentum</i>	P	<i>Cucumis melo</i>	California	California	19	<i>D. begini</i>	29	0-82	Oatman, 1959		
					California	5	<i>Neochrysocharis arizonensis</i> ^b Crawford	54	19-89	Johnson <i>et al.</i> , 1980a		

TABLE 3—Continued

Habitat	Leafminer species	Host Range ^e	Host plant(s)	Native range	Study locality	Most common parasitoids			Parasitism (percentage)		
						Number of parasitoids	Dominant parasitoid 1	Dominant parasitoid 2	Mean	Min-max	Reference
	<i>L. esculentum</i>				California	6	<i>D. begini</i>	<i>C. oscinidis</i>	—	—	Johnson <i>et al.</i> , 1980b, c
	<i>L. esculentum</i>				California	9	<i>D. begini</i>	<i>N. arizonensis</i>	72	35-99	Oatman and Kennedy, 1976
	Various				Texas	21	<i>H. patellana</i>	<i>Clasterocerus cinctipennis</i> ^b Ashmead	22 ^s	6-39	Harding, 1965
	<i>Lactuca sativae</i>				Arizona	6	<i>Chry. oscinidis</i>	<i>D. intermedius</i> / <i>D. begini</i>	19	8-26	Palumbo <i>et al.</i> , 1994
	Various				Honduras	14	<i>N. arizonensis</i> / <i>Opius dissitus</i>	—	—	—	Acosta and Cave, 1994
	<i>Apium graveolens</i>	P		Nearctic/ Neotropic	California	4	Muesebeck <i>D. begini</i>	<i>D. intermedius</i>	26	7-60	Zehnder and Trumble, 1984
	<i>Capsicum annuum</i>				Texas	6	<i>Ganaspidium hunteri</i> ^s (Crawford)	<i>Opius</i> sp.	35	12-64	Chandler and Gilstrap, 1989
	<i>Phaseolus</i> , <i>Solanum</i> , <i>Lycopersicon</i>				Japan ^h	12	<i>Neochrysocharis formosa</i> (Westwood)	<i>Chrysocharis pentheus</i>	35	19-44	Arakaki and Kinjo, 1998
	Various				Japan ^h	16	<i>Chrysocharis pentheus</i> (Walker)	<i>Neochrysocharis formosa</i> / <i>isaea</i>	50	2-94	Saito <i>et al.</i> , 1996
	<i>L. esculentum</i>	P		Nearctic/ Neotropic	Florida	14	<i>D. intermedius</i>	<i>D. begini</i>	50	0-83	Schuster and Warton, 1993
	<i>Apium graveolens</i>				California	7	<i>D. intermedius</i>	<i>D. begini</i>	45	0-91	Trumble and Nakahihara, 1983
	<i>Cucumis melo</i> , <i>Lactuca sativa</i>				Arizona	13	<i>H. patellana</i>	<i>N. arizonensis</i>	36	10-53	Hills and Taylor, 1951
	<i>Cucumis melo</i>				Texas	8	<i>Chrysonotomyia</i> sp.	<i>Opius</i> sp.	60	0-100	Chandler, 1982
	<i>Cucumis melo</i>	P/O		Nearctic	Hawaii ⁱ California	15	<i>N. arizonensis</i>	<i>G. hunteri</i>	19	0-96	Johnson, 1987
	<i>Medicago sativa</i>				California	6	<i>Chrysocharis ainsliei</i> ^b Crawford	<i>H. patellana</i>	65	32-91	Jensen and Koshler, 1970
	<i>M. sativa</i>	O		Nearctic	Delaware	12	<i>D. intermedius</i>	<i>Opius dimidiatus</i> (Ashmead)	55	28-79	Hendrickson, 1979
	<i>Melanagromyza sojae</i> (Zehntner)	O		Asia	Sumatra	7	<i>Gronotoma</i> sp. ^f	<i>Clorocyclus</i> sp. ^d	51	25-90	van den Berg <i>et al.</i> , 1995
	<i>Glycine max</i>				Indonesia	10	<i>Cynipidae</i> sp. ^{* /} <i>Eurytoma poloni</i> ^f Girault	—	—	—	Shepard and Barrion, 1998
	<i>Ophiomyia phaseoli</i> (Tyron)	O		Ethiopian	Ethiopia	17	<i>Opius phaseoli</i> Fischer	<i>Sphegaster stepicola</i> ^d (Bouc.)	29	0-93	Abate, 1991

TABLE 3—Continued

Habitat	Leafminer species	Host Range ^a	Host plant(s)	Native range	Study locality	Most common parasitoids			Parasitism (percentage)		
						Number of parasitoids	Dominant parasitoid 1	Dominant parasitoid 2	Mean	Min-max	Reference
Urban			<i>P. vulgaris</i>		Hawaii ^f	3	<i>Opius importatus</i> (Fischer)	—	36	0-51	Greathead, 1975
	<i>O. spencerella</i> (Greathead)	O	<i>P. vulgaris</i>	Ethiopian	Malawi	1	<i>O. phasoli</i>	—	81	10-99	Letourneau, 1995
	<i>Chromatomyia horticola</i> (Gour.)	O	<i>P. vulgaris</i>	Ethiopian	Malawi	1	<i>Eucoilidea sp.</i> ^g	—	23	0-29	Letourneau, 1995
	Median (Range) ^h		<i>P. vulgaris, Vicia faba</i>	Ethiopian	Indonesia	4	<i>H. varicornis</i>	—	—	—	Shepard and Barrion, 1998
	<i>Hexomyza schineri</i> (Giraud)	M	<i>Populus</i> spp.	W. Europe North America	Colorado	1	<i>Eurytoma contractura</i> ^f (Bugbee)	—	22	3-94	Eckberg and Cranshaw, 1995
	<i>Phytomyza jacarandae</i> Spencer	O	<i>Jacaranda mimosifolia</i>	Neotropic	Argentina	10	<i>Chrysonomyia thysanoides</i> (De Santis)	<i>D. websteri</i>	33	0-90	Salvo and Valladares, 1997
	<i>Phytomyza ilicicola</i> Loew	M	<i>Ilex opaca</i>	North America	Kentucky	2	<i>Opius striativentris</i> Gahan	<i>Sphegigaster</i> sp.	23	3-58	Potter, 1985
	<i>Phytomyza ilicis</i> Curtis	M	<i>I. opaca</i>	Europe	Kentucky Georgia	2 7	<i>O. striativentris</i>	<i>Sphegigaster</i> sp.	66 80	53-78 —	Potter and Gordon, 1985 Braman and Pendley, 1993
	Median (Range) ^h		<i>I. opaca, Ilex aquifolium</i>	Europe	Delaware England	5 4	<i>O. striativentris</i> gemma (Curt.)	<i>Sphegigaster pallicornis</i> (Spinola)/ <i>Chrysocharis pubicornis</i> (Zett.)	72 43	50-95 0-43	Kahn and Cornell, 1989 Heads and Lawton, 1983
	Natural			<i>I. aquifolium</i>		England	9	<i>C. gemma</i>	<i>Sphegigaster flavicornis</i> Walker	—	—
			<i>I. aquifolium</i>		England	6	<i>C. gemma</i>	<i>Pediobius acantha</i> (Walker)	—	—	Askew and Shaw, 1974
Median (Range) ^h						5 (2-9)			38 (25-56)		
<i>Calycomyza platyptera</i> (Thomson)		O	<i>H. annuus</i> <i>X. strumarium</i>	W. USA	California	14	<i>N. arizonensis</i>	<i>D. bogini</i>	71	18-100	This study
<i>Chromatomyia suikazurae</i> Sasakawa		M	<i>Lonicera gracilipes</i>	Japan	Japan	24	<i>C. penitheus</i>	<i>Chrysocharis pubens</i> (Delucchi)	85	75-93	Kato, 1985; 1994a, b
<i>Chromatomyia syngenesiae</i> Hardy		O	<i>Chrysanthemum, Sonchus</i>	Europe	England	22	<i>Dacnusa areolaris</i> Nees	<i>Chrysocharis pubicornis</i> Zett.	45	14-62	Cornelius and Godfrey, 1984
<i>L. commelinae</i> (Frost)		M	<i>Commelina diffusa</i>	Neotropic	Jamaica	10	<i>Chrysocharis majorani</i> Girault	—	41	32-57	Freeman and Smith, 1990

TABLE 3—Continued

Habitat	Leafminer species	Host Range ^a	Host plant(s)	Native range	Study locality	Number of parasitoids	Most common parasitoids			Parasitism (percentage)	
							Dominant parasitoid 1	Dominant parasitoid 2	Mean	Min-max	Reference
	<i>L. huidobrensis</i> (Blanchard)	P	<i>C. diffusa</i> <i>Lycium cestroides</i>	Nearctic/ Neotropic	Honduras Argentina	6 3	— <i>P. scabriventris</i>	— —	— —	— —	Acosta and Cave, 1994 Valladares and Salvo, 1999
	<i>L. helianthi</i> Spencer	M	<i>H. annuus</i> , <i>X. strumarium</i>	W. USA	California	14	<i>N. arizonensis</i>	<i>D. begini</i>	77	30–100	This study
	<i>L. sativae</i> Blanchard	P	Various	Nearctic/ Neotropic	Honduras	20	<i>N. diastatae</i> (Howard) <i>Opius dissitus</i> Muesebeck	—	—	—	Acosta and Cave, 1994
	<i>O. phaseoli</i> (Tyron)	O	<i>Crotalaria laburnifolia</i>	Ethiopian	Ethiopia	17	<i>S. stepicola</i>	<i>O. phaseoli</i>	41	5–71	Abate, 1991
	<i>P. ilicicola</i> Loew	M	<i>I. opaca</i>	North America	Delaware	5	<i>O. striativentris</i>	—	84	60–100	Kahn and Cornell, 1989
	<i>Phytomyza ranunculi</i> (Schrank)	M	<i>Ranunculus glaber</i>	Europe California, Japan	Japan	2	<i>C. pentheus</i>	<i>Diglyphus pusztenis</i> (Erdős and Novicky)	36	0–87	Sugimoto <i>et al.</i> , 1982
	Median (Range) ^y					14 (5–21)			57 (41–82)		

For each study, overall species richness, dominant parasitoids reared from leafminers, and an estimate of percentage parasitism of leafminer hosts are reported.

^a M, monophagous; O, oligophagous; P, polyphagous.

^b Eulophidae.

^c Braconidae.

^d Pteromalidae.

^e Eucilidae.

^f Eurytomidae.

^g Pupal parasitism only (not used in analysis).

^h Leafminer introduced.

ⁱ Leafminer and parasitoids introduced.

^j Interquartile range, 25%–75% of observations.

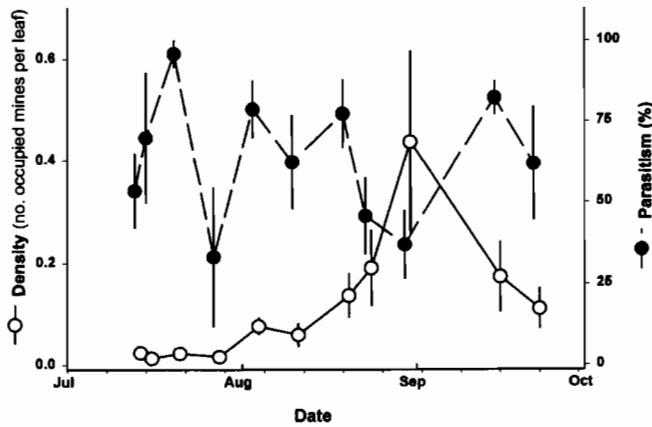


FIG. 1. *Liriomyza helianthi* population density and parasitism in *Helianthus annuus* in 1993.

leafminer densities were significantly greater overall in 1994 compared to 1995 for both *L. helianthi* (0.21 ± 0.02 mines/leaf vs 0.09 ± 0.02 mines/leaf, Wilcoxon $\chi^2 = 9.97$, $df = 1$, $P < 0.01$) and for *C. platyptera* (0.041 ± 0.007 mines/leaf vs 0.01 ± 0.02 mines/leaf, $\chi^2 = 14.5$, $df = 1$, $P < 0.01$).

There were no consistent differences in leafminer abundance between the two host plants. *L. helianthi* densities were greater in *X. strumarium* in 1994 (Figs. 2A and B, $\chi^2 = 4.46$, $df = 1$, $P < 0.05$), but were equal between the two host plant species in 1995 (Figs. 3A and B, $\chi^2 = 0.2$, $df = 1$, $P > 0.10$). *C. platyptera* densities were similar in the two host plants in 1994 (Figs. 5A and B, $\chi^2 = 8.4$, $df = 1$, $P > 0.10$), but tended to be higher in *X. strumarium* in 1995 (Figs. 6A and B, $\chi^2 = 4.18$, $df = 1$, $P < 0.05$).

Estimates of natural enemy-caused mortality (% parasitism) were consistently high in all 3 years and comparable for both leafminer species ($t = 1.48$, $df = 109$, $P > 0.10$). On average *L. helianthi* suffered $77.1\% \pm 2.6\%$ ($n = 56$) mortality from parasitoids (Figs. 1–3) and percentage parasitism in *C. platyptera* was $71.1\% \pm 2.9\%$ ($n = 55$) (Figs. 4–6). Similarly, there was no difference in percentage and mortality across host plants ($t = 1.92$, $df = 109$, $P > 0.05$).

Parasitoid Assemblages of *L. helianthi* and *C. platyptera*

Sixteen species of parasitic Hymenoptera belonging to 4 different families were reared from *L. helianthi* and *C. platyptera* between 1994 and 1995 (Table 1). *L. helianthi* harbored 14 of the 16 species reared, whereas 12 of the 16 species were found in *C. platyptera*. Almost half of the species, 7/16 were relatively scarce (<3%), represented by a total of 16 individuals. The most common parasitoids found in both *L. helianthi* and *C. platyptera* were the solitary larval parasitoids *D. begini* (ectoparasitoid) and *N. arizonensis* (endoparasitoid) representing about half of all parasitoids reared

from both leafminers (Table 1, Fig. 7). Also relatively common in *L. helianthi* were the endoparasitoids *Closterocherus* spp. and the *O. dimidiatus*. *C. platyptera*, on the other hand, was host to *Thinodytes* sp., a larval-pupal parasitoid that was rarely reared from *L. helianthi* (Table 1, Fig. 7).

Parasitoid assemblages from leafminer hosts co-occurring on *H. annuus* and *X. strumarium* differed. A log-linear analysis of the frequency counts (Table 2) found that models that excluded the leafminer host \times plant species \times parasitoid species (model 1, $G = 5.36$, $df = 1$, $P = 0.50$) or additionally the H \times PL interaction (model 2, $G = 5.43$, $df = 7$, $P = 0.61$) did not differ significantly from a saturated model. However, models that excluded the second order interactions involving H \times PAR (model 3, $G = 73.95$, $df = 6$, $P < 0.0001$) and PL \times PAR (model 4, $G = 32.61$, $df = 6$, $P < 0.0001$) in addition to the 3-way interaction did not adequately describe the observed frequencies. This analysis, therefore, shows an association between particular parasitoids and leafminer species as well as an association between parasitoids and plant species. Es-

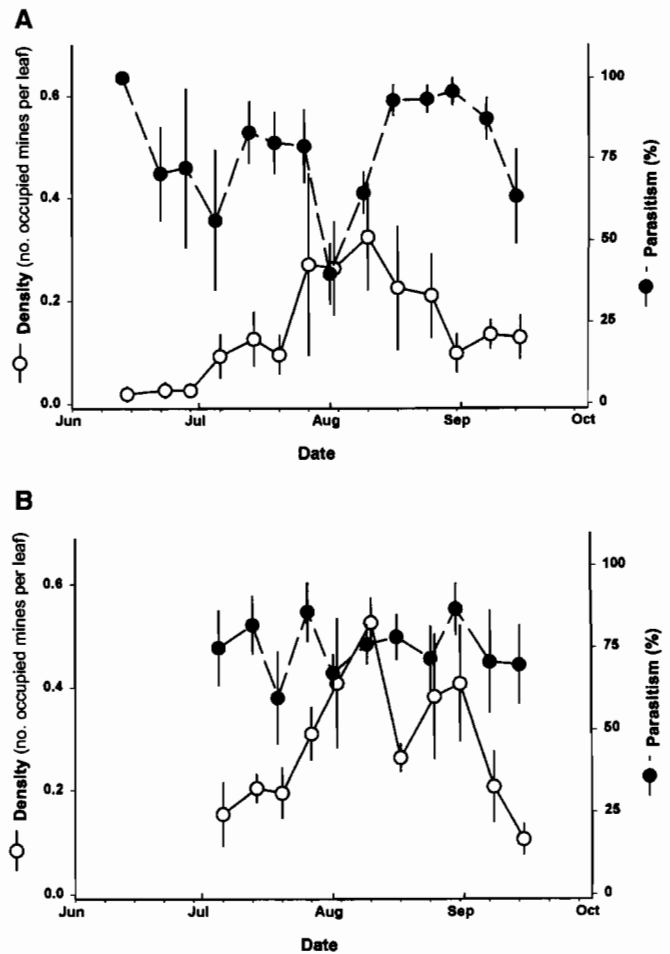


FIG. 2. *Liriomyza helianthi* population density and parasitism in *Helianthus annuus* (A) and *Xanthium strumarium* (B) in 1994.

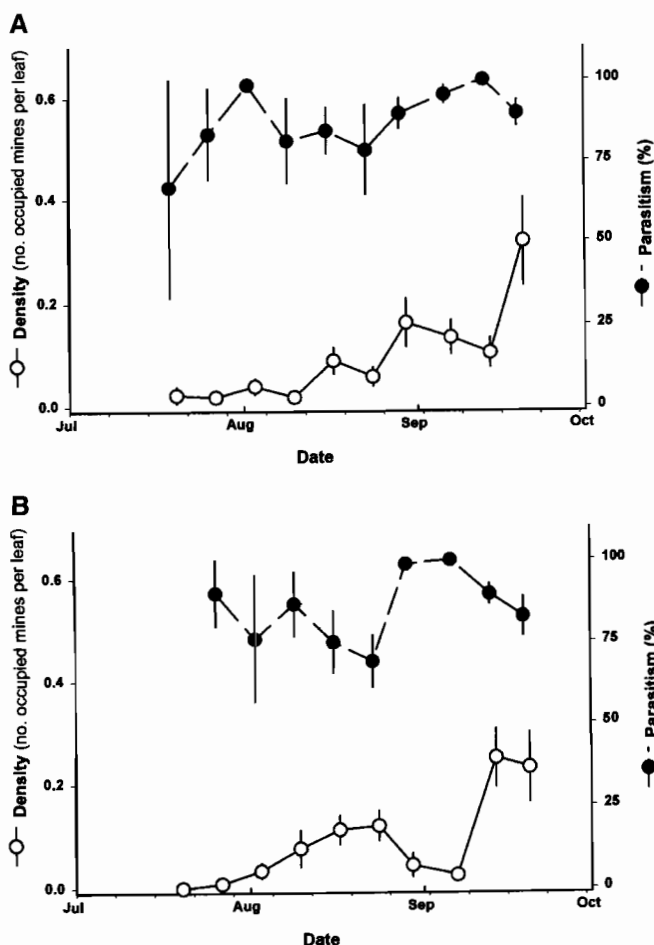


FIG. 3. *Liriomyza helianthi* population density and parasitism in *Helianthus annuus* (A) and *Xanthium strumarium* (B) in 1995.

estimated parameters from the model using both interactions (model 2) suggest that *Closterocerus* and *Opius* have significant positive associations with *L. helianthi* ($\lambda = 0.984$ and 1.015 , respectively), while *Pnigalio* and *Thinodytes* have positive associations with *C. platyptera* ($\lambda = 0.96$ and 1.307 , respectively). The PL \times PAR interaction indicates a positive association between *Chrysocharis* and *H. annuus* ($\lambda = 0.876$), while *Closterocerus* tended to be relatively more common in *X. strumarium* ($\lambda = 0.530$). Parameter estimates for *Diglyphus* and *N. arizonensis* were close to zero and similar among the different factors, suggesting no association among leafminer host or host plant species.

A comparison of the various models describing leafminer, plant, and parasitoid associations (Table 2) found that models that included a H \times PAR interaction provided for an improved fit to the observed data (models 4 and 6, BIC = -36.83 and -41.31 , respectively) than did models with PL \times PAR interaction (models 3 and 5, BIC = 4.5 and 0.03 , respectively). In fact, model 6 was a more parsimonious description of the observed

data compared to the model with both H \times PAR and PL \times PAR interactions included (model 2, BIC = -35.08). This analysis suggests that leafminer species is a relatively better predictor of parasitoid species than host plant species.

In summary, the parasitoid assemblages of *L. helianthi* and *C. platyptera* on two shared host plants were differentiated with respect to both plant- and leafminer-related factors. The most abundant parasitoid species, *Diglyphus* spp. and *N. arizonensis*, were common to both leafminers on both host plant species (Fig. 7). Some parasitoids, in contrast, were more likely to be reared from *L. helianthi* (*Closterocerus* spp. and *Opius* sp.), whereas others (*Pnigalio* sp. and *Thinodytes* sp.) were more typically reared from *C. platyptera*. Although most of the variation in parasitoid assemblage appeared to be related to leafminer species, some parasitoids, such as *C. ainsliei*, and to a lesser extent *Closterocerus*, were more likely to be found attacking leafminers in a particular host plant (*H. annuus* and *X. strumarium*, respectively).

Literature Survey

The survey of agromyzid parasitoid literature found a high degree of variability in species richness and percentage parasitism of parasitoid assemblages across the different habitat types (Table 3). No statistical differences were found among agricultural, urban, and natural habitats for either parasitoid species richness (Kruskal-Wallis $\chi^2 = 4.21$, $df = 2$, $P = 0.12$) or percentage parasitism ($\chi^2 = 3.3$, $df = 2$, $P = 0.19$). Given the relative paucity of studies of agromyzid leafminer parasitoid assemblages and large variation among studies, the ability to detect a statistical difference among habitat types in this analysis was small (Power = 0.31 – 0.34). While we cannot conclude with statistical confidence that these differences are real, the effect of lowest parasitoid richness in urban habi-

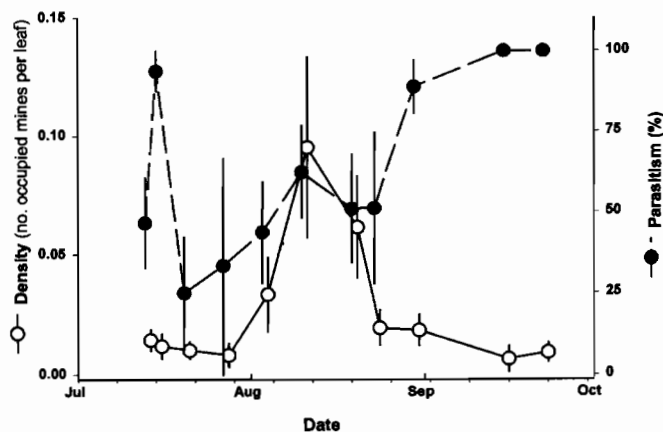


FIG. 4. *Calycomyza platyptera* population density and parasitism in *Helianthus annuus* in 1993.

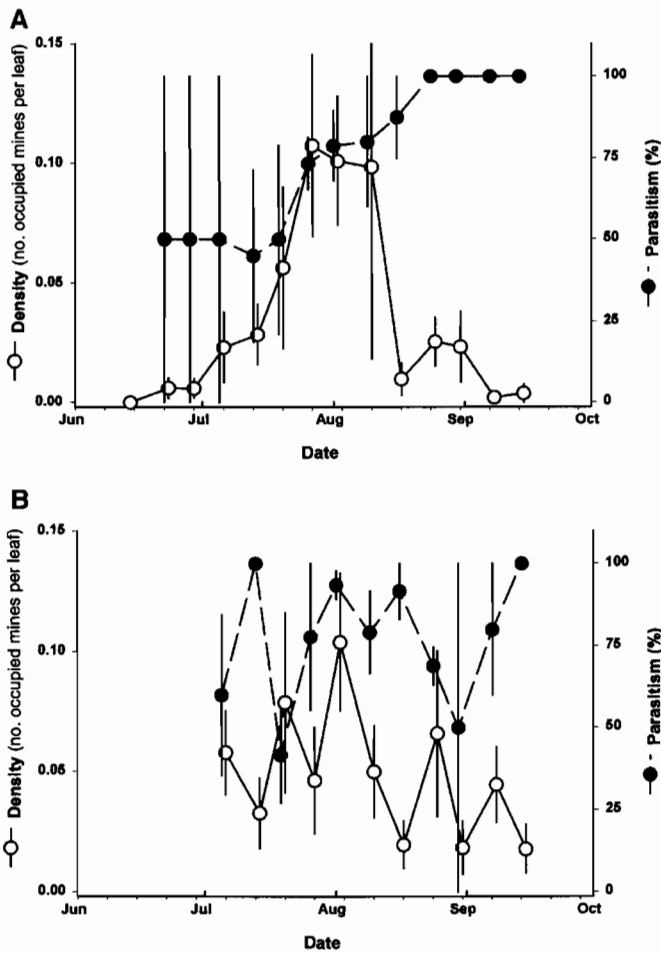


FIG. 5. *Calycomyza platyptera* population density and parasitism in *Helianthus annuus* (A) and *Xanthium strumarium* (B) in 1994.

tats (median = 5 parasitoid species per leafminer), followed by agricultural habitats (median = 9 parasitoid species per leafminer) with the greatest richness found in natural habitats (median = 14 parasitoid species per leafminer), appears to be large, with almost double the number of parasitoid species attacking leafminers in natural habitats. Percentage parasitism also tended to be lower in urban environments (median = 38%) followed by agricultural habitats (median = 51%) with the highest percentage parasitism seen in natural habitats (median = 58%).

The large heterogeneity in parasitoid assemblages and parasitism rates among studies within the same habitat type may in part reflect differences in sampling practices, geographic variation, and inclusion of studies of introduced leafminer species. Because unequal sampling among studies in different habitats should influence estimates of species richness, we expected that relatively understudied leafminers in natural habitats would have lower parasitoid richness since rare species would be underrepresented. However, studies from natural habitats had 50% greater species

richness than studies from agricultural habitats, suggesting that this pattern may be accentuated with increased sampling.

If we examine the relationship between mean parasitoid species richness per leafminer and percentage parasitism across all leafminer \times habitat combinations we find a significant correlation ($r = 0.41$, $P = 0.04$, Fig. 8). Excluding the study of Kahn and Cornell (1989), which found high levels of parasitism of the holly leafminer, *Phytomyza ilicicola* (Loew), in natural areas with only 5 parasitoids, a highly significant relationship between species richness and percentage parasitism was found ($r = 0.53$, $P = 0.01$).

DISCUSSION

Parasitoid Assemblages on L. helianthi and C. platyptera

Parasitoid assemblages attacking *L. helianthi* and *C. platyptera* were diverse and differentiated to some extent between the two species. In contrast to idobionts such as *Diglyphus* spp. and *N. arizonensis*, koinobiont parasitoids, emerging from either pupal or larval stages, showed the greatest degree of specificity to a particular leafminer species. Only one species (of 6) that emerged from leafminer puparia was shared to any significant extent by both leafminers (*C. ainsliei*). For example, *L. helianthi* was attacked by the larval-pupal *O. dimidiatus*, a species which rarely attacked *C. platyptera*. This result is consistent with other studies that have found that koinobiont braconid parasitoids attacking leafminers often have more restricted host-ranges than idiobiont parasitoids (Askew and Shaw, 1986; Sato, 1990; Sheehan and Hawkins, 1991). A study of the closely related *A. frontella* and *A. nana*, both found sympatrically in alfalfa in Europe, found discrimination among leafminer species by a larval-pupal parasitoid (Drea *et al.*, 1982). Host pupation site may also contribute to the partitioning of the larval-pupal parasitoid guild. *C. platyptera* pupates within the mine, whereas *L. helianthi* emerges from the leaf and falls to the soil for pupation. The location of pupation site, therefore, may offer an additional suite of challenges (e.g., microhabitat) to a parasitoid that may further promote parasitoid specialization (Mills, 1993):

Despite demonstrated effects of plant morphology and chemistry on the foraging behavior and success of natural enemies (Casas, 1989; Barbosa *et al.*, 1991; Dicke and Minkenbergh, 1991; Rowell-Rahier and Pasteels, 1992; Finidori-Logli *et al.*, 1996; Barbosa and Benrey, 1998; Barbosa and Wratten, 1998) there was little evidence for plant-associated differences in parasitoid attack of *L. helianthi* or *C. platyptera*. The taxonomic and chemical similarity of the two host plants (Heywood *et al.*, 1977; Bohlmann, 1990) suggests that these plants may be indistinguishable from the point of

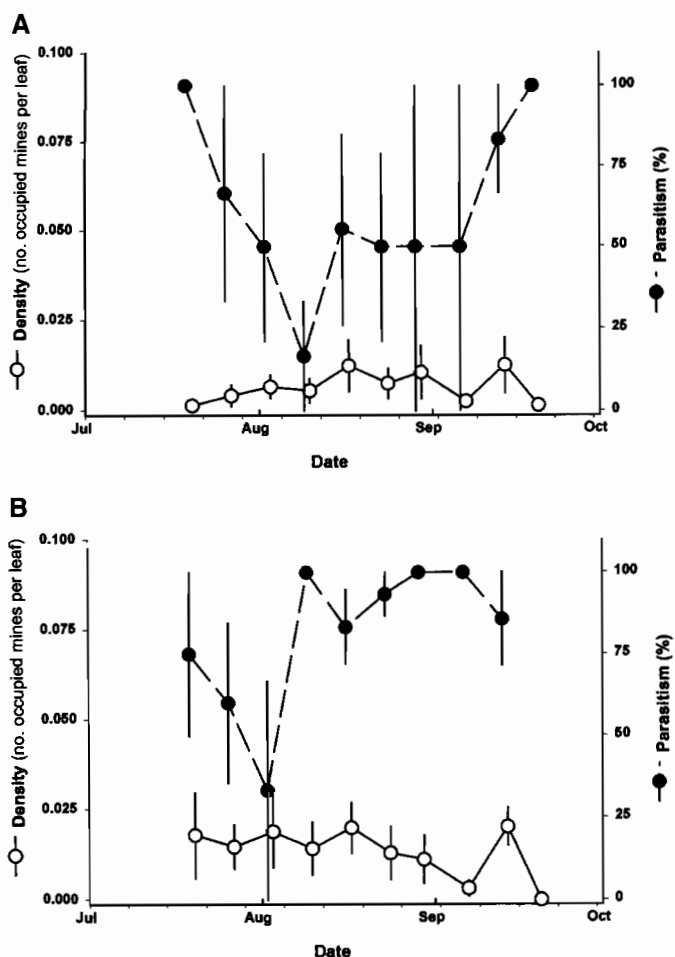


FIG. 6. *Calycomyza platyptera* population density and parasitism in *Helianthus annuus* (A) and *Xanthium strumarium* (B) in 1995.

view of the parasitoids. In fact, in an experimental study of *L. helianthi*, Gratton and Welter (1999) found that parasitoid attack was significantly lower when leafminer larvae were manually transplanted to novel host plants outside of the normal host plant tribe, suggesting that parasitoids can be influenced by differences among host plants if these differences are sufficiently large.

Leafminer Parasitism in Managed and Natural Habitats

Agromyzid leafminers in natural, unmanaged, habitats tend to have higher parasitoid species richness and greater degree of parasitoid attack than leafminers in agricultural or urban habitats (Table 3). Habitat differences *per se* may explain part of the variation in parasitism. Natural habitats may represent more stable and diverse communities with respect to microhabitat, alternate hosts, or host phenology such that a greater number of parasitoid species can accumulate over time on a greater array of resources. Agricultural

habitats, on the other hand, are relatively simple both structurally and in terms of leafminer host and plant diversity. In addition, these habitats are periodically destroyed and all inhabitants must either emigrate or perish. As a result, managed communities may simply not have enough resources or time to accumulate the same number of natural enemies and, therefore, only species with highly developed dispersal capabilities are relatively common.

Parasitoid assemblages of agromyzid leafminers appear to be relatively consistent across broad geographic areas. Many of the common leafminer parasitoids found in agricultural settings are generally polyphagous and have been reared from leafminers in many different host plants and even from leafminers in different insect orders (Hansson, 1985, 1995; Heinz and Parrella, 1990b; LaSalle and Parrella, 1991). Similar to parasitoid assemblages in natural areas, polyphagous *Diglyphus* spp. (Heinz and Parrella, 1990b) represented primarily by *D. begini* and *D. intermedius* were the most common parasitoids in agricultural habitats, followed by *Opius* spp. and *Chrysocharis* spp. The most common parasitoids in this study, *D. begini*, *N. arizonensis*, and *O. dimidiatus*, are common parasitoids of polyphagous *Liriomyza* species (*L. sativae*, *L. trifolii*) in the western United States and Florida (Table 3; Johnson and Hara, 1987). Salvo and Valladares (1998) found that eulophids were the most diverse and abundant parasitoids reared from agromyzid leafminers in Argentina. The most common genera included *Chrysonotomyia*, *Chrysocharis*, and *Diglyphus*. However in the same survey, Salvo and Valladares (1998) found that despite their low species diversity braconids were numerically dominant in agricultural habitats.

The proximity of our study sites to many agricultural areas in the Central Valley of California may in part explain the abundance of the common parasitoids reared from *L. helianthi* and *C. platyptera* and their similarity to assemblages in agricultural systems. Both *D. begini* and *N. arizonensis* are common and dominant parasitoids attacking *L. sativae* in tomatoes in central and southern California (Oatman, 1959; Oatman and Platner, 1969; Jensen and Koehler, 1970; Johnson *et al.*, 1980b,c). *Chrysocharis ainsliei*, *C. utahensis*, and *Opius* sp. are often recovered from *Liriomyza* spp. in California, but never represent a significant proportion of the assemblage in agricultural systems. In contrast, *Halticoptera patellana* (Dalman) was often a dominant parasitoid of *Liriomyza* spp. in tomatoes and cabbage in southern California (Oatman, 1959; Oatman and Platner, 1969; Jensen and Koehler, 1970) but was never found attacking *L. helianthi* or *C. platyptera* in natural habitats, suggesting that some parasitoids may be more habitat specific.

The similarity in parasitoid assemblages among native and economically important *Liriomyza* species in California suggests the possibility of exchange of nat-

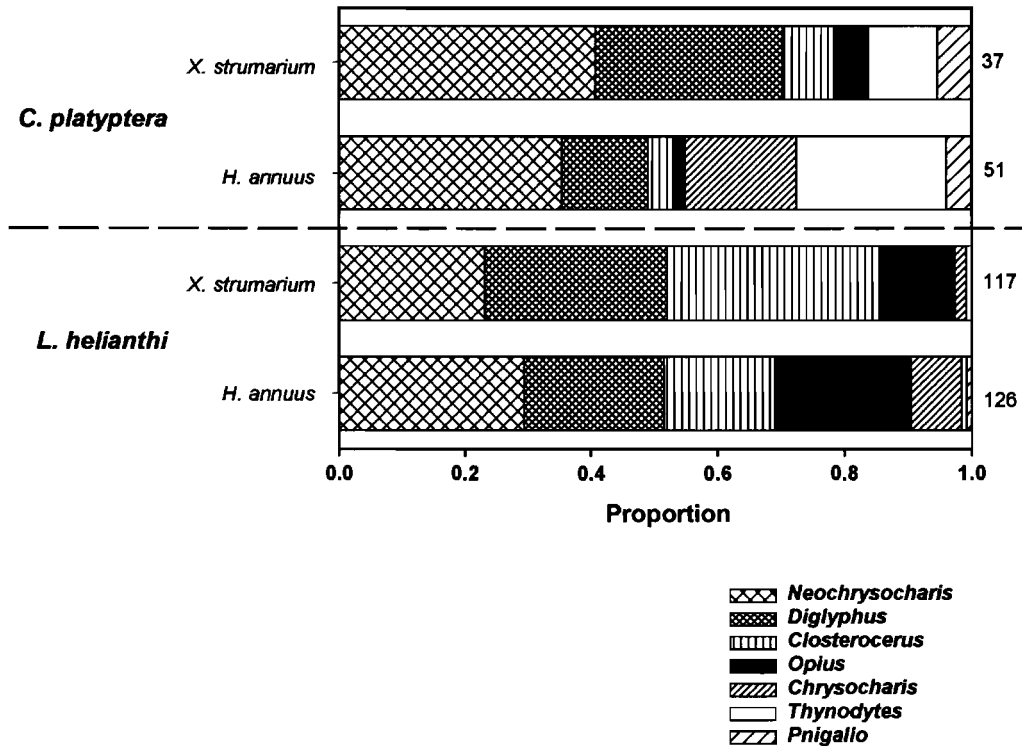


FIG. 7. Proportions of main parasitoid species emerging from each leafminer and host plant species. Numbers next to each bar represent total number emerging.

ural enemies among different habitats during the course of a growing season. Such interchanges of natural enemies between natural habitats and agroecosys-

tems have been documented in the utilization of introduced leafminers by native parasitoid faunas. *Liriomyza trifolii* recently invaded Japan (1990) and is

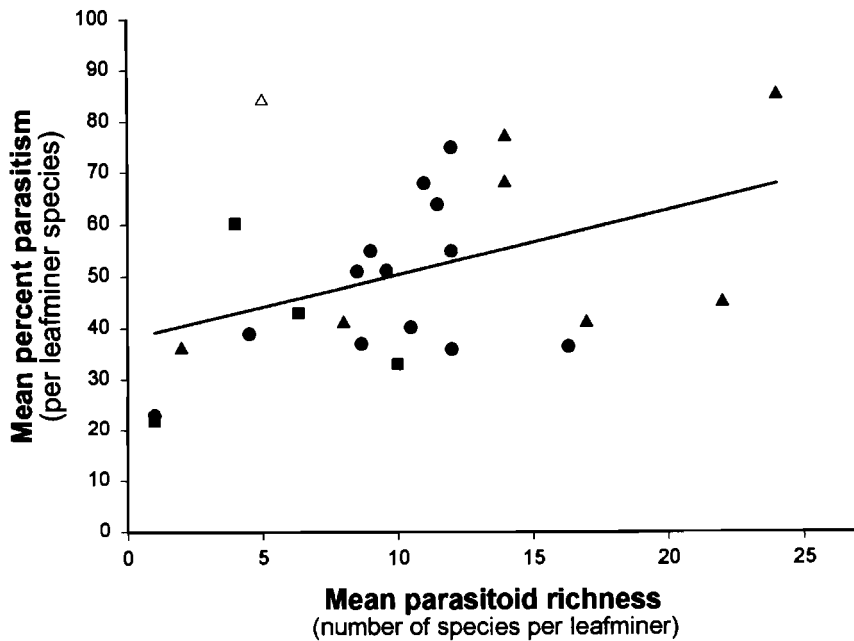


FIG. 8. Relationship between mean parasitoid richness (number of species) and mean percentage parasitism for studies of agromyzid leafminers in urban (square), agricultural (circles), and natural habitats (triangles). There is a significant relationship ($r = 0.41, P = 0.04$). Excluding the open triangle (see text for discussion) results in a highly significant relationship ($r = 0.53, P = 0.01$).

already a host to 12 native parasitoid species (Arakaki and Kinjo, 1998). Likewise, the alfalfa blotch miner, *A. frontella*, introduced from Europe to the eastern United States, was rapidly colonized by the naturally occurring parasitoid fauna (Hendrickson and Barth, 1979).

Exploiting such rich and diverse parasitoid communities in natural habitats may be a way of enhancing pest control in adjacent agricultural areas (Landis *et al.*, 2000). The positive relationship between parasitoid species richness and percentage parasitism of leafminers (Fig. 8) suggests that enhancing the colonization and retention of a more diverse array of leafminer parasitoids into agricultural areas may result in a higher degree of parasitism of a pest population. Proximity of natural or constructed habitats that can harbor relatively constant and abundant populations of native leafminers may provide a source of a wide array of natural enemies available for movement into agricultural fields (Wissinger, 1997; Landis *et al.*, 2000). Nevertheless, there remains a significant amount of unexplained variation ($\approx 72\%$) in the relationship between the richness of parasitoid assemblages and relative levels of attack that warrants further investigation.

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