DENSITY DEPENDENT PARASITISM AND HOST-KILLING OF LIRIOMYZA TRIFOLII (DIPTERA: AGROMYZIDAE) BY DIGLYPHUS INTERMEDIUS (HYMENOPTERA: EULOPHIDAE)

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Abstract

Liriomyza trifolii (Burgess) is an important leafmining pest of numerous ornamental and vegetable crops. The pest is attacked by many species of parasitoids which inflict heavy mortality in the absence of insecticides. The functional response, as well as parasitoid-induced mortality, of one major parasitoid, *Diglyphus intermedius* (Girault), was estimated over a range of densities of third instar *L. trifolii* at 25-27°C in the laboratory. The functional response of *D. intermedius* was given by the equation $Y = Kp \cdot n_2 \cdot (1-\exp(-n_1/Kh))$ where Y, the rate of parasitism, is the number of hosts parasitized per day; Kp is a constant of 7.3908 hosts parasitized per parasitoid-day; n_1 and n_2 are the densities of leafminer larvae and parasitoid adults (numbers/cm^2 leaf area), respectively, and Kh is a constant of 0.0144 leafminer larvae/cm^2 leaf area. The relationship between host and parasitoid density and parasitoid-induced host mortality was given by $Z = Cp \cdot n_2 \cdot (1-\exp(-n_1/Ch))$ where Z, the rate of parasitoid-induced mortality, is the number of leafminer larvae killed per day; Cp is a constant of 9.2064 hosts killed per parasitoid-day and Ch is a constant of 0.0165 leafminer larvae/cm^2 leaf area. The observed rate of parasitism at a particular parasitoid density was always lower than the observed rate of parasitoid-induced host mortality at that density. Lower leafminer larval densities resulted in increased multiple oviposition by *D. intermedius*. When eggs of the parasitoid were placed at increasing densities on leafminer larvae in artificial mines, the number of parasitoid eggs surviving to adulthood decreased while the number of individuals surviving per host tended to remain at about one.

Key Words: *Liriomyza*, *Diglyphus*, biological control, leafminer, parasitism, host-killing, functional response

Resumen

El minador de hojas, *Liriomyza trifolii* (Burgess) es una plaga importante de numerosas plantas ornamentales y de hortalizas. Varias especias de parasitoides atacan esta plaga inflijiendo una mortalidad alta en la ausencia de insecticidas. Se estimaron la respuesta funcional y la mortalidad inducida por parasitoides, en el parasitoide principal, *Diglyphus intermedius* (Girault), en varias densidades del *L. trifolii* en el tercer estadio a 25-27°C en el laboratorio. La respuesta funcional de *D. intermedius* fué dada por la ecuación $Y = Kp \cdot n_2 \cdot (1-\exp(-n_1/Kh))$ donde Y (la tasa de parasitismo) es el número de hospederos parasitados por día; Kp es un constante de 7.3908 hospederos parasitados por dia-parasitoid; n_1 y n_2 son las densidades de las larvas del minador y los adultos de parasitoides (numeros/area cm^2 de la hoja), respectivamente, y Kh es una constante de 0.0144 larvas de minador /area cm^2 de la hoja. La relación entre la densidad del hospedero y la densidad del parasitoide y la mortalidad inducida por el parasitoide ha sido dada por $Z = Cp \cdot n_2 \cdot (1-\exp(-n_1/Ch))$ donde Z (la tasa de mortalidad inducida por el parasitoid) es el número de larvas de minador matadas por día; Cp es una constante de 9.2064 hospederos matados por día-parasitoide y Ch es una constante de 0.0165 larvas de minador/area cm^2 de la hoja. La tasa de parasitismo observada en una densidad especifica del parasitoide siempre fué más baja que la tasa de mortalidad observada inducida por el parasitoide de la misma densidad. Las densidades menores de larvas de minador resultaron en un aumento de oviposiciones multiples por *D. intermedius*. Cuando los huevos del parasitoide fueron colocados en densidades crecientes sobre las larvas de minador en minas artificiales, el número de huevos parasitados que sobrevivieron hasta el estado adulto diminuyó mientras que el número de individuos quesobrevivieron por hospedero tendieron a permanecer aproximádamente uno por hospedero.

Liriomyza trifolii (Burgess) is an important pest of many ornamental and vegetable crops including tomato. Over 40 species of parasitoids have been recovered from *Liriomyza* spp. leafminers (Waterhouse & Norris 1987), including 20 in Florida (Schuster et al. 1991, Schuster & Wharton 1993) where, in the absence of insecticides, parasitism of the leafminer has ranged from about 65 to 75%. Applications of broad spectrum insecticides like methomyl have resulted in a decline in parasitism followed by an increase in leafminer density (Oatman & Kennedy 1976). Action thresholds for timing insecticide applications have been established for tomato (Pernezny et al. 1996, Schuster et al. 1996). While the extent of parasitism might be taken into account during the sampling process (Schuster et al. 1996), the relationship between leafminer and parasitoid density and subsequent parasitism and host death is not known.

Diglyphus intermedius (Girault) was one of the most abundant parasitoids found attacking *L. trifolii* on tomato in Florida (Schuster & Wharton 1993). The parasitoid is ectoparasitic and prefers third instar leafminers for oviposition. The lifetime fecundity (F) and the lifelong total number of hosts killed (Hm) were found to be functions of temperature (T) and were represented by $F = -196.11 + 42.65T - 1.1T^2$ and $Hm = 721.97 - 19.1T$, respectively (Patel & Schuster 1991). The temperature range used in these experiments was 15.6 to 31.1°C, which should be the limits for making interpretations and predictions. The peak 3 day moving averages of the number of eggs deposited and the number of hosts killed were highest at 23.3 and 26.7°C. The relationship between host and parasitoid densities was not addressed in these experiments. This relationship is often referred to as the functional response and can be either curvilinear (type 2 response) or sigmoid (type 3 response) (as summarized by Price 1997). The plateau of the type 2 response results from the limitation of prey handling at higher prey densities and is characteristic of invertebrate parasitism or predation. With the type 3 sigmoid response, the efficiency or rate of capture increases as the predator learns to find and recognize prey, with a resulting rapid increase in predation. Eventually, a plateau in the number of prey captured is reached as the limitation in prey handling is reached. The type 3 response is characteristic of vertebrate predation, although invertebrates can also demonstrate this response.

The leafminer-parasitoid interaction was a focus of the leafminer population dynamics model proposed by Smerage et al. (1980), which provides an excellent framework for the elucidation of the role of natural enemies in regulating leafminer populations. The model pertained to within-field populations of eggs, larvae, pupae and adults of leafminers and their parasitoids, broadly expressed as processes that contribute to the overall dynamics of the population. The rate of parasitism in the model was a function of host and parasitoid densities and the relationship between the rate of parasitism and host and parasitoid densities at constant temperature was hypothesized to be an exponential equation generating families of curves at different host and parasitoid densities.

The purpose of the present investigation was to obtain a mathematical description of the functional response of *D. intermedius* at various parasitoid densities when using *L. trifolii* as a host at a constant temperature.

MATERIALS AND METHODS

Several limitations were encountered in the experimental design. Ideally, observations on parasitoids should be made in a large arena which allows the parasitoids to move naturally in and out of the arena. This would enable the parasitoids to behave naturally and to have random access to hosts. Also, the likelihood of encountering the same host again would not be increased due to confinement to a restricted arena. Arena size would certainly be important if the period of observation was long and parasitoids were confined to a small region. Because of the small size of adult *D. intermedius*, it is not possible to monitor adult parasitoid densities in a large arena with confinement, nor is it possible to maintain uniformity in leafminer and parasitoid densities between observation plots and to maintain constant environmental conditions. To overcome these limitations, a compromise was made. Female *D. intermedius* were confined in $67 \times 67 \times 67$ cm cages within a controlled environment room for 12 h observation periods. There were several advantages to using cages. *D. intermedius* density on a per cage basis was easy to record and manipulate, and other parasitoid species could be excluded. The relatively small cage size permitted them to be maintained in a controlled environment room.

Tomato plants, *Lycopersicon esculentum* Mill. cv Hayslip, used in the experiments were approximately 30 days post transplanting, 50 to 60 cm tall with 10 to 13 leaves, and were just beginning to flower. Plants of this size just fit into the above cages and allowed the maximum amount of leaf area possible on one plant confined within a cage. The plants selected had approximately 2,000 to 3,000 cm² leaf area, although on occasion some plants were smaller or larger. Three selected plants were placed in each of two $67 \times 67 \times 67$ cm cages. The number of leafminer adults released into the cages ranged from as few as 10 to as many as 50 and the duration of exposure ranged from as little as one minute to as long as 4 h. By manipulating the number of adults and the exposure period, leafminer larval densities ranging from 0 to 0.06 larvae/cm² were obtained. The range then

was divided into six classes of equal size for experimentation. After exposure to leafminer adults, the plants were removed, examined for leafminer adults (which were removed, if present) and moved to cages of similar size in a temperature-controlled room at 25-27 °C and a photoperiod of 14:10 (L:D) h. After five d, the five plants most similar in height, quality and density of third instar leafminers were removed at 0800 h and placed individually into each of five 67 × 67 × 67 cm cages.

The parasitoid adults used for the experiments were collected from a laboratory colony maintained on *L. trifolii* on tomato (Patel 1987). Ten females and five males were confined in each of four, 150 × 15 mm Petri dishes. Each dish was provisioned daily with 40 to 60 third instar leafminers in tomato leaflets. On the fourth day, female parasitoids were isolated singly in 00 gelatin capsules and the males were discarded. Thus, the females were at the age of peak oviposition and peak host mortality inducement (Patel & Schuster 1991). One, two, three, four, or five parasitoid females were then released into each of the five cages holding the leafminer- infested plants. After 12 h (2000 h) the plants were removed from the cages, shaken to dislodge parasitoids and transferred to the laboratory where plant height and age, and the numbers of leaves and leaflets were recorded. The total leaf area, the area of leaflets containing leafmines and the area of leaflets containing parasitized leafminer larvae were measured (LI-3000, LiCor®, Lincoln, NE). The numbers of live and paralyzed (or dead) larvae were recorded in each of three categories: old leaves (usually the first three leaves which showed signs of yellowing), fully expanded leaves (the majority of leaves) and non-expanded leaves (usually the top three to four leaves, although occasionally there may have been several more in a small, tight bundle at the plant apex). Leafmines containing paralyzed (or dead) larvae were dissected and the number of parasitoid eggs deposited on each leafminer larva was recorded. Paralyzed or dead leafminer larvae on which no parasitoid eggs were deposited were categorized as parasitoid-induced mortality because in previous studies (Patel & Schuster 1991) no mortality of leafminer larvae was observed in the absence of parasitoid females.

The experiment was repeated four times. The assignment of parasitoid density to the cages was rotated so that the same cage had the same parasitoid density every fifth time. Because the plants varied in leaf area, and leafminer oviposition could not be made uniform on each plant, it was not possible to regulate leafminer density as uniformly as parasitoid density. The number of leafminer larvae on each plant, and, hence, in each cage, could have been kept the same by destroying some larvae on each plant; however, this would not have been appropriate for two reasons. Parasitoids searching a greater leaf area with the same number of leafminers per cage would take longer than for the same number of leafminers on a smaller leaf area. Also, destroying leafminer larvae may elicit its own response from the parasitoid adults, if the adults cue in to host plant damage in locating leafminer larvae.

To study the survival of parasitoid larvae to adulthood as influenced by the initial density of parasitoid eggs per third instar leafminer, parasitized third instar leafminers and associated parasitoid eggs were dissected from real leafmines obtained from the *D. intermedius* colony and were placed in artificial mines (Patel & Schuster 1983). The artificial mines consisted of a piece of construction paper with a 7 mm hole and a piece of filter paper, both equal in dimensions to a microscope slide, sandwiched between a glass microscope slide and a cover slip. Parasitoid eggs, less than 24 h old, were dissected from leafmines containing parasitized leafminer larvae and placed next to the larvae in the artificial mines at densities of one, two, three, or four eggs per larva. Each artificial mine was sealed with sticky tape and kept in a 100 × 15 mm Petri dish containing a water moistened filter paper to provide relatively high humidity in order to prevent desiccation of the leafminer larva and the parasitoid egg(s). The number of host larvae utilized was 12 with one egg per larva, six with two eggs per larva, four with three eggs per larva, and three with four eggs per larva. Thus, there were 12 eggs at each egg density. The Petri dishes were maintained at the same conditions as the leafminer per parasitoid density study and the filter paper in each Petri dish was moistened daily until no more parasitoid adults emerged. The experiment was replicated five times and the number of parasitoids emerging from each mine was recorded.

The NLIN procedure (SAS Institute 1982) was utilized to determine the parameters for the hypothesized exponential equations describing the relationships between leafminer larval density and the rate of parasitism and the rate of parasitoid-induced mortality at various parasitoid densities. Chi square tests were performed to determine if there was any effect of altering either leafminer or parasitoid density on the numbers of parasitoid eggs on paralyzed host larvae. The ANOVA procedure (SAS Institute 1982) was utilized to determine if any relationship existed between the initial total number of parasitoid eggs placed at each egg density and the total number of individuals reaching the adult stage at each egg density in the artificial mines.

Results

The exponential equation obtained using the nonlinear regression to express the relationship

between host and parasitoid density and parasitism was

$$Y = Kp \cdot n_2 \cdot (1-\exp(-n_1/Kh)) \qquad (r^2 = 0.79)$$

where Y, the rate of parasitism, is the number of hosts parasitized per day. Kp is a constant of 7.3908 hosts parasitized per parasitoid-day and n_1 and n_2 are the densities of leafminer larvae and parasitoid adults (numbers/cm² leaf area), respectively. Kh is a constant of 0.0144 leafminer larvae/cm² leaf area. The exponential equation expressing the relationship between host and parasitoid density and parasitoid-induced host mortality was

$$Z = Cp \cdot n_2 \cdot (1-\exp(-n_1/Ch)) \qquad (r^2 = 0.78)$$

where Z, the rate of parasitoid-induced mortality, is the number of leafminer larvae killed per day. Cp is a constant of 9.2064 hosts killed per parasitoid-day and Ch is a constant of 0.0165 leafminer larvae/cm² leaf area.

The hypothesized relationship between host density, parasitoid density and the rate of parasitism utilizing the above equation is depicted in Fig. 1 and the hypothesized relationship between the rate of parasitoid-induced mortality and host and parasitoid density is depicted in Fig. 2. The observed rate of parasitism at a particular parasitoid density was always lower than the observed rate of parasitoid-induced mortality. These results confirmed previous findings that *D. intermedius* killed more hosts than it parasitized (Patel & Schuster 1991); however, the proportion of hosts killed that were also parasitized was not the same at all leafminer densities. In the 0-0.0099 host larvae/cm² range, 24 of 38 observations (63%) had a 100% parasitization rate while only 5 of 19 (26%) and 3 of 33 (10%) observations had 100% parasitization of the killed hosts when leafminer larval densities ranged from 0.01 - 0.0199 and 0.02 - 0.06 larva/cm² leaf area, respectively.
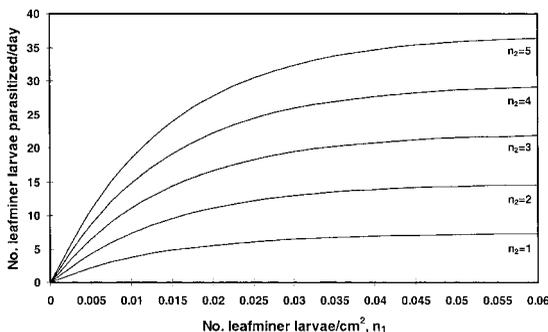

Fig. 1. The relationship between density of *Liriomyza trifolii* larvae (n_1) and parasitism rate at different densities of the parasitoid *Diglyphus intermedius* (n_2, number of females/plant).
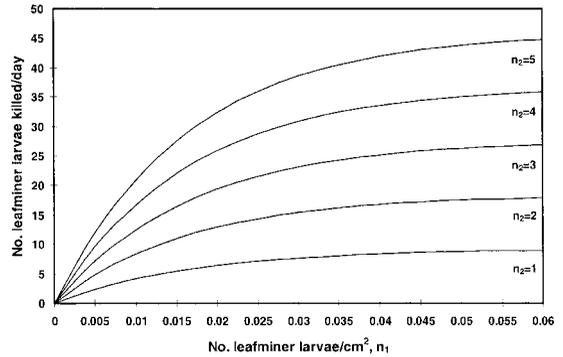

Fig. 2. The relationship between density of *Liriomyza trifolii* larvae (n_1) and rate of parasitoid-induced mortality at different densities (n_2) of the parasitoid *Diglyphus intermedius* (n_2, number of females/plant).

D. intermedius did not always deposit a single egg per host as was assumed by Smerage et al. (1980) (Table 1). A χ^2 test of the data in Table 1 suggested a significant relationship between the number of parasitoid eggs per host and host density ($\chi^2 = 67.62$; $df = 25$; $P < 0.001$), while grouping the data according to parasitoid density suggested no significant relationship between the number of parasitoid eggs and parasitoid density ($\chi^2 = 15.6$; $df = 20$; $P > 0.70$). Increasing the number of artificially established parasitoid eggs per host larva from one to four resulted in decreasing numbers of individuals (of 12) surviving to adulthood from about 10 to three (Table 2). The difference in the number of parasitoids surviving per leafminer larva was significantly different between initial egg densities of one and three eggs per leafminer larva; however, there was little difference biologically in the numbers surviving per larva. Regardless of the initial density of parasitoid eggs per leafminer larva, generally one parasitoid survived per leafminer larva.

DISCUSSION

The results of this investigation clearly demonstrate that both parasitism and parasitoid-induced mortality of *L. trifolii* by *D. intermedius* are representative of the type 2 functional response. This suggests that handling time becomes a limitation to parasitization and host-killing as host density increases. The curvilinear description of the functional response further suggests that increased experience of *D. intermedius* with its host did not result in an increased rate of host discovery or decreased rate of host handling, i.e. learning. However, the female parasitoids used in these experiments already had been exposed to leafminer larvae for four days when the experiments were initiated. It is possible that naive females would exhibit a type 3 functional response. Even if this were so, the effect would be expected to di-

TABLE 1. FREQUENCY DISTRIBUTION OF THE NUMBERS OF LARVAE OF THE LEAFMINER, *LIRIOMYZA TRIFOLII*, KILLED BY THE PARASITOID, *DIGLYPHUS INTERMEDIUS*, IN CLASSES OF DIFFERENT EGG DENSITIES OF THE PARASITOID AT DIFFERENT DENSITIES OF LEAFMINER LARVAE.

Leafminer larvae/cm² leaf area	No. parasitoid eggs/killed leafminer host larva						
	0	1	2	3	4	4+	Total
0.00 - 0.0099	19	108	60	19	11	16	233
0.01 - 0.0199	42	189	74	31	8	6	350
0.02 - 0.0299	49	163	50	11	10	3	286
0.03 - 0.0399	45	180	46	10	2	2	285
0.04 - 0.0499	43	135	43	9	1	0	231
0.05 - 0.0600	16	40	13	5	0	1	75
0.00 - 0.0600	214	815	286	85	32	28	1460

minish within at least four days, if not sooner. The functional response was studied in a room maintained at 25-27°C, using four-day-old parasitoids. These conditions of temperature and parasitoid age are ideal for estimating the maximum rate of parasitism. Both parasitoid age and temperature affect the rate of parasitism (Patel & Schuster 1991). Altering temperature and utilizing parasitoid females younger or older than four days old, unless naive females behave differently, would likely affect the observed rates of parasitism but not the exponential nature of the relationship between host and parasitoid density.

The term host-feeding was not used in this study to describe parasitoid-induced mortality because, as was shown in a previous study (Patel & Schuster 1991), *D. intermedius* kills more hosts than it parasitizes and because killed larvae can be used for oviposition or host-feeding or can be rejected, as was the case for *D. begini* (Heinz & Parrella 1989). In this latter study, the proportion of stung hosts in each category varied depending upon the host size distribution which the parasitoids were provided. When a large host size distribution (third instars) was encountered, 35% of the larvae were killed without oviposition (20% for host-feeding), while when a small host size distribution (late second and early third instars) was encountered, 62% were killed (18% for host feeding). Thus, the proportion of larvae used for host-

feeding remained fairly constant, while the proportion rejected increased as the frequency of small larvae increased. In a later study, Heinz & Parrella (1990a) observed that *D. begini* killed 1.3 *L. trifolii* larvae for every larva used for oviposition (about 23%) and made no distinction as to whether the excess larvae were used for host-feeding. Minkenberg (1989) determined that the proportion of *L. bryoniae* (Kaltenbach) larvae attacked by *Diglyphus isaea* (Walker) and used for host-feeding varied from 15 to 40%; however, he considered any stung host without oviposition to have been fed upon. In the present study, all *L. trifolii* larvae were large (third instars); nevertheless, the number of larvae killed per day always exceeded the number of larvae parasitized. About 15% of the larvae killed in the experiment were not used for oviposition (Table 1), which is lower than the total host-kill observed by Heinz & Parrella (1989) and Minkenberg (1989) but is about the same as the total host-kill observed by Heinz & Parrella (1990a) and about the same as the percentage used for host feeding observed by Heinz & Parrella (1989). The differences could be due to the larger arena used in the present study (67 × 67 × 67 cm cages) compared to the smaller arenas used by Heinz & Parrella (1989) (9 cm diam Petri dishes and 11.5 cm diam by 13.2 cm high cylindrical cages) and Minkenberg (1989) (7.5 cm diam by 61 cm high cylindrical cages). The cage size used

TABLE 2. SURVIVAL OF EGGS OF THE PARASITOID, *DIGLYPHUS INTERMEDIUS*, TO ADULTHOOD WHEN PLACED AT DIFFERENT DENSITIES OF LARVAE OF THE LEAFMINER, *LIRIOMYZA TRIFOLII*.

Initial egg density/host larva (12 eggs at each density)	Mean no. eggs surviving to adulthood	Survivorship of eggs/larva
1	9.6 a	0.80 b
2	6.6 b	1.10 ab
3	6.0 b	1.35 a
4	3.0 c	0.98 ab

Means in a column followed by the same letter are not significantly different at the *P* = 0.05 level, Duncan's multiple range tests.

by Heinz & Parrella (1990a) ($50 \times 50 \times 50$ cm) was similar to the cage size in the present study. Heinz & Parrella (1990a) also believed that the lower percentage of host-killing that they observed relative to other studies was due to the use of a larger cage. In the present study, the proportion of larvae killed in the absence of oviposition increased from 8 to 20% as the host density increased (Table 1). It is clear from the present study with *D. intermdius* and with the above studies with other species of *Diglyphus* that more hosts are killed than are needed for oviposition, that at least some are used for host-feeding, and that some may be rejected. While host-feeding can provide parasitoid females with necessary nutrients for egg development, the benefit of host rejection is less apparent, particularly in light of the energy and time expended in the process. Perhaps host rejection is a mechanism for managing the density of leafminer larvae on individual leaflets, thus ensuring that a leaflet containing parasitized larvae will not be lost to the leafmining of surviving, non-parasitized larvae on the same leaflet. Excessive leafmining can cause desiccation, necrosis and abscission of tomato leaflets, thus potentially resulting in reduced survival of parasitoid larvae.

Little is known regarding the ability of *Diglyphus* species to locate infested leaflets relative to non-infested leaflets; however, other species of parasitoids attacking *Liriomyza* spp. have been shown to have discriminatory behaviors. In flight tunnel and olfactometer studies, Petitt et al. (1992) demonstrated that females of *Opius dissitus* Musebeck responded preferentially to olfactory cues emanating from foliage infested with larvae of *L. sativae* Blanchard. A greater proportion of *Dacnusa sibirica* Telenga flew upwind in no-choice flight tunnel experiments when leafminer infested plants were placed upwind (Dicke & Minkenberg 1991). When given a choice, female *D. begini* landed on leaves mined by *L. trifolii* more than on leaves not mined (Heinz & Parrella 1990a). Although the present cage experiments were not designed specifically to study host-finding behavior, some deductions regarding the effect of spatial heterogeneity of host larvae on parasitism rate can be made. In 68 of 79 observations, the leaflet with the greatest number of leafmines was encountered by parasitoid adults as indicated by at least one leafminer larva being parasitized on that leaflet. In another four observations, the parasitoids similarly found and oviposited on larvae in the leaflet with the next highest leafminer density. In the remaining seven observations, the maximum number of leafminer larvae on the leaflets was four. These observations suggest that either the parasitoids were more attracted to leaflets that were more heavily mined or that, once landing on a leaflet, the parasitoids were more likely to encounter a host if the host density

on that leaflet was higher. Which behavior, or maybe both, that was exhibited cannot be determined because the area of each leaflet and the distance between individual leafminer larvae were not measured.

Heinz & Parrella (1990b) observed rates of superparasitism of 0 and 3.1% when *D. begini* was released in greenhouses for control of *L. trifolii*. These rates are much lower than the 35% superparasitism observed in the present study (Table 1). This much higher rate of superparasitism could have resulted from the confinement of *D. intermedius* in cages. Parrella et al. (1989) observed that superparasitism of *L. trifolii* by *D. begini* would occur in the rearing method they developed but that the extent was not known. They further observed that, if two parasitoid eggs were deposited adjacent to a third instar leafminer, two adults would be produced, although they would be smaller. In the present study, only one parasitoid generally completed development per leafminer larva, regardless of the initial parasitoid egg number per host (Table 2). Furthermore, the number of eggs surviving to adulthood declined as the initial parasitoid egg numbers per host increased. Thus, superparasitism by *D. intermedius* represents a waste of resources and an impediment to parasitoid population increase and, ultimately, to biological control of *L. trifolii*.

REFERENCES CITED

DICKE, M., AND O. P. J. M. MINKENBERG. 1991. Role of volatile infochemicals in foraging behavior of the leafminer parasitoid *Dacnusa sibirica* Telenga. J. Insect Behavior 4: 489-500.

HEINZ, K. M., AND M. P. PARRELLA. 1989. Attack behavior and host size selection by *Diglyphus begini* on *Liriomyza trifolii* in chrysanthemum. Entomol. Exp. Appl. 53: 147-156.

HEINZ, K. M., AND M. P. PARRELLA. 1990a. Holarctic distribution of the leafminer parasitoid *Diglyphus begini* (Hymenoptera: Eulophidae) and notes on its life history attacking *Liriomyza trifolii* (Diptera: Agromyzidae) in chrysanthemum. Ann. Entomol. Soc. Am. 83: 916-924.

HEINZ, K. M., AND M. P. PARRELLA. 1990b. The influence of host size on sex ratios in the parasitoid *Diglyphus begini* (Hymenoptera: Eulophidae). Ecol. Entomol. 15: 391-399.

MINKENBERG, O. P. J. M. 1989. Temperature effects on the life history of the eulophid wasp *Diglyphus isaea*, an ectoparasitoid of leafminers (*Liriomyza* spp.), on tomatoes. Ann. Appl. Biol. 115: 381-397.

OATMAN, E. R., AND G. G. KENNEDY. 1976. Methomyl induced outbreak of *Liriomyza sativae* on tomato. J. Econ. Entomol. 69: 667-668.

PARRELLA, M. P., J. T. YOST, K. M. HEINZ, AND G. W. FERRENTINO. 1989. Mass rearing of *Diglyphus begini* (Hymenoptera: Eulophidae) for biological control of *Liriomyza trifolii* (Diptera: Agromyzidae). 82: 420-425.

PATEL, K. J. 1987. Parasitization of *Liriomyza trifolii* (Burgess) by *Diglyphus intermedius* (Girault). Ph.D. dissertation, University of Florida, Gainesville.

PATEL, K. J., AND D. J. SCHUSTER. 1983. Influence of temperature on the rate of development of *Diglyphus intermedius* (Girault) (Hymenoptera: Eulophidae), a parasite of *Liriomyza* spp. leafminers (Diptera: Agromyzidae). Environ. Entomol. 12: 885-887.

PATEL, K. J., AND D. J. SCHUSTER. 1991. Temperature-dependent fecundity, longevity, and host-killing activity of *Diglyphus intermedius* (Hymenoptera: Eulophidae) on third instars of *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae). Environ. Entomol. 20: 1195-1199.

PERNEZNEY, K., D. SCHUSTER, P. STANSLY, G. SIMONE, V. WADDILL, J. FUNDERBURK, F. JOHNSON, R. LENTINI, AND J. CASTNER. 1996. Florida tomato scouting guide with insect and disease identification keys. Univ. of Fla., IFAS, Coop. Ext. Serv., Gainesville, SP-22.

PETITT, F. L., T. C. J. TURLINGS, AND S. P. WOLF. 1992. Adult experience modifies attraction of the leafminer parasitoid *Opius dissitus* (Hymenoptera: Braconidae) to volatile semiochemicals. J. Insect Behavior 5: 623-634.

PRICE, P. W. 1997. Insect Ecology Third Edition. John Wiley & Sons, Inc., New York, NY.

SAS INSTITUTE, INC. 1982. SAS user's guide: statistics, 1982 edition. Cary, NC.

SCHUSTER, D. J., AND R. A. WHARTON. 1993. Hymenopterous parasitoids of leaf-mining *Liriomyza* spp. (Diptera: Agromyzidae) on tomato in Florida. Environ. Entomol. 22: 1188-1191.

SCHUSTER, D. J., J. P. GILREATH, R. A. WHARTON, AND P. R. SEYMOUR. 1991. Agromyzidae (Diptera) leafminers and their parasitoids in weeds associated with tomato in Florida. Environ. Entomol. 20: 720-723.

SCHUSTER, D. J., J. E. FUNDERBURK, AND P. A. STANSLY. 1996. IPM in tomatoes, pp. 387-411. *In* D. Rosen, F. D. Bennett and J. L. Capinera [eds.], Pest Management in the Subtropics, Integrated Pest Management—A Florida Perspective. Intercept. Ltd, Andover, Hants, UK.

SMERAGE, G. H., C. A. MUSGRAVE, S. L. POE, AND W. D. ESHLEMAN. 1980. Systems analysis of insect population dynamics. Univ. of Fla., IFAS, Gainesville, IPM-3, 92 pp.

WATERHOUSE, D. F., AND K. R. NORRIS. 1987. *Liriomyza* species (Diptera: Agromyzidae) leafminers, pp. 159-176. *In* Biological Control: Pacific Prospects. Inaka Press, Melbourne, Australia.