Interactions Between *Encarsia pergandiella* (Hymenoptera: Aphelinidae) and its Host *Bemisia argentifolii* (Homoptera: Aleyrodidae): Effects of Parasitoid Densities and Host-Parasitoid Ratios

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ABSTRACT

Laboratory experiments were conducted to measure the functional response of *Encarsia pergandiella* Howard to *Bemisia argentifolii* Bellows and Perring and the effects of different densities of parasitoids on mutual interference. When host density was held constant (100 third instars) and parasitoid density maintained at 1, 5, and 15 females, the percentage of total host mortality (parasitized + desiccated nymphs) was significantly lower at the lower parasitoid densities. The number of parasitized host nymphs per parasitoid female decreased 15-fold with increased parasitoid density (from 1 to 15). The interference between parasitoids, which detracts from their searching efficiency, increased with parasitoid density. The emergence rate, development time, and body lengths of progeny were significantly greater at parasitoid densities of 1 and 5 than at 15. When the number of parasitoids was held constant (*n* = 5) and the number of hosts varied (5, 25, 50, 100, and 250), the total percentage of nymph mortality decreased from 91.3% (1 : 1 parasitoid - host ratio) to 19.1% (1 : 50). The data was described as a Type II functional response. To summarize and compare the effects of parasitoid - host ratios, we propose a generalized index of efficacy, calculated by multiplying the proportions of total host mortality and emergence of parasitoids under each treatment. The index showed that the most efficient parasitoid - host ratio was 1 : 10.

RESUMEN

Se condujeron experimentos en laboratorio para medir la respuesta funcional de *Encarsia pergandiella* Howard a *Bemisia argentifolii* Bellows y Perring así como los efectos de diferentes densidades de parasitoides en interferencia mutua. Cuando la densidad del hospedero se mantuvo constante (100 individuos en tercer instar) y la densidad del parasitoide se mantuvo en 1, 5, y 15 hembras, el porcentaje de mortalidad total del hospedero (ninfas parasitadas y disecadas) fue significativamente menor con las densidades del parasitoide más bajas. El número de ninfas parasitadas por hembras del parasitoide disminuyó 15 veces cuando aumentó la densidad del parasitoide (de 1 a 15). La interferencia entre parasitoides, la cual reduce su eficiencia de búsqueda, se incrementó con la densidad del parasitoide. La tasa de emergencia, el grado de desarrollo, y las longitudes del cuerpo de la progenie, fueron significativamente mayores a densidades de parasitoides de 1 y 5 que a 15. Cuando el número de parasitoides se mantuvo constante (*n* = 5) y el número de hospederos varió (5, 25, 50, 100, y 250), el porcentaje total de mortalidad de ninfas disminuyó de 91.3% (radio parasitoide hospedero de 1:1) a 19.1% (1:50). Los datos fueron descritos como una respuesta funcional de Tipo II. Para resumir y comparar los efectos de radios parasitoide - hospedero, propusimos un índice generalizado de eficiencia, calculado por la multiplicación de las proporciones de la mortalidad total del hospedero y la emergencia de los parasitoides bajo cada tratamiento. El índice mostró que el radio parasitoide-hospedero más eficiente fue 1:10.

Additional Index Words: parasitoid, mutual interference, functional response, generalized index of efficacy

The silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring (=sweetpotato whitefly, *Bemisia tabaci* [Gennadius], Biotype B) is a polyphagous pest species in the tropics and subtropics on all continents. Since 1987, annual losses in the USA have exceeded $US 200 million (Brown et al., 1995). *Encarsia pergandiella* Howard (Hymenoptera: Aphelinidae) is a solitary parasitoid indigenous to North America. It is a heteronomous, biparental endoparasitoid whose females develop

as primary parasitoids on immature whiteflies. Males develop as secondary parasitoids on females of their own and related species (Hunter, 1989).

The research reported here is part of a long-range study to understand the host-parasitoid interrelationships between co-existing parasitoid species, and to develop efficient methods for augmentative biological control of *B. argentifolii*. Cost effective mass rearing and release of parasitoids against *B. argentifolii* will depend on our knowledge of many factors, including quantitative data on the parasitoid-host relationships. However, these data are limited. The level of mortality inflicted on a host population is often determined by the response of the parasitoid to host density, while population stability is maintained as a result of both density-dependent parasitoid progeny production and parasitoid-inflicted host mortality (Holling, 1959). To improve biological control of *B. argentifolii* and to obtain a better understanding of the host-parasitoid interactions, more detailed studies are necessary. Knowledge of functional response and mutual interference relationships are helpful for understanding basic mechanisms underlying parasitoid-host interactions and for predicting parasitoid potential in biological pest control (Houck and Strauss, 1985). The objectives of this study were to determine the response of *E. pergandiella* to various *B. argentifolii* densities, and measure the effects of variable parasitoid densities on host mortality and parasitoid reproduction.

MATERIALS AND METHODS

Parasitoid and host cultures. The *E. pergandiella* used in

Table 1. Effects of parasitoid densities on *B. argentifolii* mortality and parasitoid progeny[1].

Parasitoid density	Percentage of host nymphs			No. per female parasitoid			
	Parasitized	Desiccated	Total mortality[2]	Hosts killed[3]	Hosts parasitized[3]	Hosts desiccated[3]	Parasitoid progeny[3]
15	19.0 ± 10.2 b	67.1 ± 5.7 a	86.1 ± 4.8 a	5.8 c	1.3 c	4.5 a	0.7 c
5	47.8 ± 3.3 a	16.3 ± 2.6 b	64.1 ± 4.0 b	12.8 b	9.6 b	3.3 b	8.5 b
1	19.0 ± 2.1 b	1.4 c	20.4 ± 2.4 c	20.4 a	19.0 a	1.4 c	17.7 a

[1]Means ± SD followed by same letter within a column not significantly different at 5% level (Tukey's studentized test)
[2]Sum of parasitized and desiccated nymphs. Desiccated host nymphs corrected by control treatment (3.8 ± 0.9 in control).
[3]Hosts killed per female calculated by multiplying number of host nymphs (100 third instars) by proportion of total mortality, divided by number of parasitoid females used in each treatment; hosts parasitized calculated by multiplying numbers of host nymphs by proportion of parasitized nymphs, divided by number of parasitoid females used in each treatment; hosts desiccated calculated by multiplying number of host nymphs by proportion of desiccated nymphs, divided by number of parasitoid females used in each treatment; parasitoid progeny: no. nymphs x proportion parasitized nymphs x proportion emerged parasitoids/ parasitoid females used in each treatment.

Table 2. Effects of parasitoid densities key biological parameter of *E. pergandiella*[1].

Parasitoid density	% emergence	Development time (d)	Longevity (d)	Female size (mm)
15	53.1 ± 10.5 b	11.6 ± 0.6 a	10.4 ± 3.2 a	0.457 ± 0.07 b
5	88.6 ± 2.0 a	11.3 ± 0.6 b	10.7 ± 3.8 a	0.485 ± 0.07 a
1	93.2 ± 3.7 a	11.1 ± 0.5 b	10.8 ± 4.2 a	0.491 ± 0.07 a

[1]Means ± SD followed by the same letter within column are not significantly different at 5% level (Tukey's studentized range test).

Table 3. Host density effects on mortality and parasitoid progeny emergence[1].

Host density	% parasitized nymphs	% desiccated nymphs[2]	% total mortality	% parasitoids emergence
5	26.7 ± 20.6 c	64.6 ± 27.2 a	91.3 ± 9.6 a	33.3 ± 44.1 b
25	53.1 ± 7.5 ab	28.5 ± 8.3 b	81.6 ± 3.7 a	53.4 ± 8.5 b
50	62.0 ± 7.8 a	8.8 ± 5.3 b	70.8 ± 6.1 b	88.9 ± 1.5 a
100	47.8 ± 3.3 b	10.9 ± 2.9 b	58.7 ± 4.2 b	88.6 ± 2.0 a
250	19.1 ± 1.3 c	2.4 ± 0.5 c	21.5 ± 1.4 c	88.4 ± 1.1 a

[1]Means±SD followed by the same letter within column are not significantly different at 5% level (Tukey's studentized test).
[2]Host mortality after correction with control treatments (10.2 ± 1.8 in control).

Table 4. Effects of parasitoid-host on the main biological parameter of *E. pergandiella*[1].

Parasitoid-host ratio	Development time (days)	Longevity (days)	Length of progeny (mm)
1 : 1	13.0 ± 0.9 a	7.3 ± 2.2 a	0.419 ± 0.021 d
5	12.8 ± 0.8 a	7.9 ± 3.1 a	0.422 ± 0.029 d
25	12.3 ± 0.4 b	8.1 ± 5.3 a	0.446 ± 0.034 c
50	12.4 ± 0.5 b	8.5 ± 4.0 a	0.472 ± 0.061 b
100	12.3 ± 0.5 b	8.8 ± 3.4 a	0.486 ± 0.051 a

[1]Means ± SD followed by the same letter within column are not significantly different at 5% level (Tukey's studentized range test).

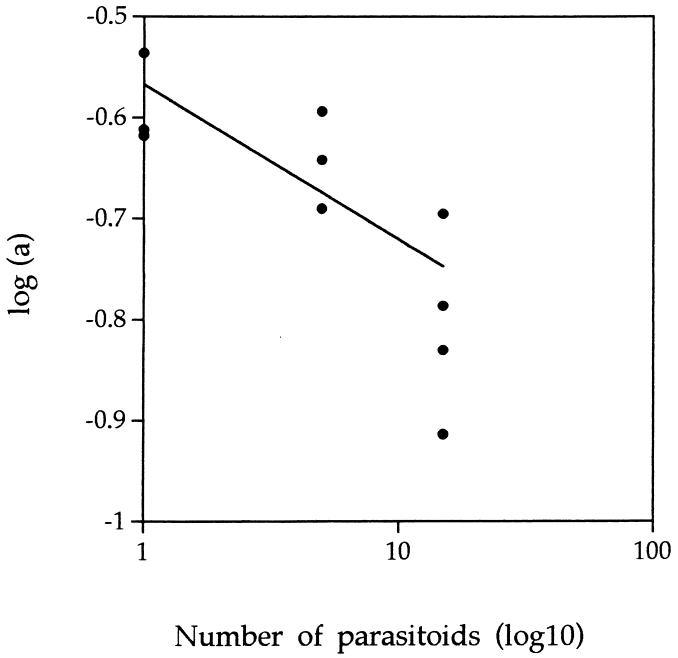

Fig. 1. Mutual interference of *E. pergandiella* at varying parasitoid densities.

this study were originally reared from *B. argentifolii* collected on berlandier fiddlewood, *Citharexylum berlandieri* Robinson (Verbenaceae), in Weslaco, Texas, and identified by M. Rose (Department of Entomology, Montana State University). The parasitoid culture was reared on *B. argentifolii* maintained on sweet potato, *Ipomoea batatas* (L.) Lam.

The *B. argentifolii* was originally collected from cabbage in Hidalgo Co., Texas in 1994, and maintained in a greenhouse, primarily on tomato, *Lycopersicum esculentum* Miller. Sweet potato was the host plant used in these tests. Leaves were detached from plants and each petiole was placed in a floral aquapic filled with a hydroponic solution (Aqua-Ponics International, Los Angeles, CA). Excised sweet potato leaves were found to readily root and not deteriorate under the fluorescent lighting (20 watt, Vita-Lite©, Duro-Test Lighting, Elk Grove, IL 60007) within an incubator. We have observed that when adult whiteflies are transferred from one plant species to another, there is a period of adjustment before they will readily oviposit. Thus, adult whiteflies from greenhouse tomato leaves were first transferred to sweet potato leaves for 24 h before being transferred to the designated test leaves. About 50 adult whiteflies were transferred to test leaves after chilling for several minutes in a plastic vial placed in a refrigerator. Whiteflies were confined within a 4.5-cm diameter clip cage to the underside of each excised test leaf and allowed to oviposit for 0.5 to 5 h depending on host density needed. Each rooted leaf with eggs was then placed in a 120 x 25 mm polystyrene tissue culture dish (Corning Inc., Corning, NY). The top of each dish was replaced with polyester organdy for ventilation. Dishes were kept in an environmental chamber at 26 ± 2ºC, 55 ± 5% RH, a photoperiod of 16 : 8 (L:D) h, at 1400 - 1725 lux. All experiments were conducted under the conditions described above.

Constant hosts, varying parasitoid densities. Third instars of *B. argentifolii* were used, because they are the most suitable host stage (Jones and Greenberg, 1999). The number of third instars of *B. argentifolii* was held constant and the number of *E. pergandiella* females was varied. When the third instar was reached, all but 100 nymphs were carefully removed with an insect pin. Subsequently, 1, 5, or 15 mated parasitoid females (<2 d old) were confined with the nymphs in a clip cage. After 24 h, the parasitoids were removed, and leaves with nymphs were replaced in a culture dish and returned to an environmental chamber.

We analyzed the effects of increasing parasitoid density on searching efficiency using the Hassell and Varley (1969) mutual interference equation: $\log a = \log Q - m \log P$ or $a = QP^{-m}$. The attack rate a is calculated as: $a = 1 / P \ln (N / N_s)$, where the slope m is the mutual interference constant; $\log Q$ the intercept is the value of $\log a$ when the log density of parasitoids is zero (number of parasitoids = 1), P is number of parasitoids; N is total number of hosts, and N_s is number of hosts surviving attack.

Constant parasitoids, varying host densities. The same exposure techniques were used as described above, except the number of host nymphs varied while the number of parasitoids was held constant. Each treatment contained 5 mated parasitoid females and 5, 25, 50, 100, or 250 whitefly nymphs. Control treatments for each host density were held without parasitoids to determine mortality in the absence of parasitoids. There were three replicates per treatment.

The data were fitted to a Type II functional response (Holling, 1959), using the equation: $N_a = a'NT / 1 + a'T_hN$, where N_a is number of hosts attacked, N is total number of host nymphs available, T is total time available for attack (=1.0 for 1 d), T_h is handling time, and a' is the instantaneous attack rate (Hassell, 1976). We calculated N_a by adding the total number of hosts parasitized, with those that were desiccated and

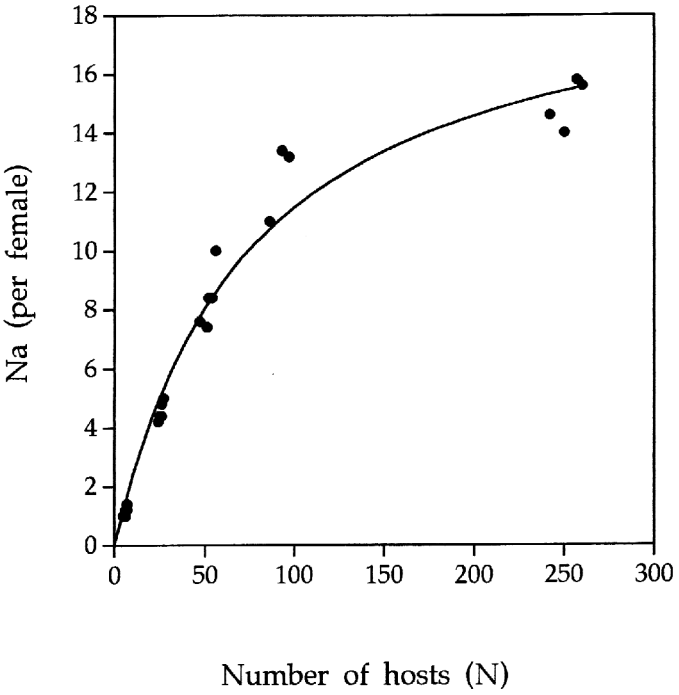

Fig. 2. Functional response *E. pergandiella.*

presumably attacked by host feeding. Because 5 females were used at each host density, we divided numbers attacked by 5 to obtain a mean attack rate per female. Estimates for *a'* and T_h were obtained by nonlinear regression (Quasi-Newton estimation method) using the Systat statistical package (Wilkinson et al., 1992). In our analyses, we set $T = T_s = 1.0$ because the hosts were exposed to the parasitoids for 24 h.

Experimental indices and their assessment. Following an initial 10 d incubation period, exposed test leaves in each treatment were subsequently examined daily for parasitoid development and emergence. The elapsed time from first to last individual to emerge was recorded. The body sizes of 50 parasitoid females were determined from frozen specimens of each treatment by measuring body length from the frons to the tip of the abdomen. Longevity was measured for honey-fed adult progeny emerging from each treatment. Mortality was checked daily at 1100 h.

In all treatments, whitefly mortality in the control treatment was used to correct the percentage of parasitoid-induced host mortality (Abbott, 1925). Percentage progeny emergence was calculated as the percentage of nymphs that yielded parasitoid progeny, under the assumption that only one parasitoid emerged per nymph. Desiccated host (residual mortality) was defined as host mortality due either to host-feeding or to unsuccessful parasitism, and was calculated as the difference between the corrected percentages of whitefly mortality and parasitized nymphs. Since the number of hosts killed by host-feeding was not observable, we were unable to partition out this factor. The number of female progeny produced per parasitoid female, and the number of host nymphs killed per parasitoid female were also recorded.

Statistical analyses. Statistical analyses were conducted using analysis of variance (ANOVA), and means were separated using Tukey's studentized range test (Wilkinson *et al.,* 1992). The data of percentage parasitism and emergence were transformed using the square root- arcsine method (Sokal and Rohlf, 1981) prior to statistical analysis, but results are presented using nontransformed means.

RESULTS AND DISCUSSION

Constant hosts, varying parasitoid densities. The percentage of total host mortality significantly increased with increasing parasitoid density (Table 1). When parasitoid densities increased from 1 to 15 females per 100 host nymphs, the number of host nymphs killed (parasitized + desiccated) per female decreased from 20.4 to 5.8 ($P < 0.001$) and female parasitoid progeny per female decreased from 17.6 to 0.7 ($P < 0.001$). The number of desiccated nymphs (after correction with the control group) per parasitoid female increased from 0.3 to 4.5 ($P < 0.001$). Percentage residual mortality significantly increased as parasitoid densities increased. Mutual interference between female parasitoids may have resulted in a reduction in individual searching efficiency.

Parasitoid density affected progeny biology (Table 2). Successful emergence was significantly lower after 15 females had been confined together for 24 h with 100 hosts, compared with 1 or 5 females. Also, development time to emergence was significantly longer, and the resulting progeny were significantly smaller in the highest density treatment.

The mutual interference (slope of the relationships) analysis resulted in a significant linear regression equation: $Y = -0.56677 - 0.1836 \log P$. Therefore, the mutual interference parameter $m = 0.184$ ($F = 14.0$; df = 1, 8; $P = 0.01$; $R^2 = 0.64$). These results demonstrate that searching efficiency decreased as parasitoid density increased from 1 to 15 (Fig.1). Hassell (1971) investigated some features of the behavior of *Nemeritis* sp. when attacking its host *Ephestia cautella* (Hübner). He found that when two searching parasitoids met, one or both of them tended to leave the area where the encounter took place. Some values for the interference constant *m* obtained from other laboratory studies of parasitic Hymenoptera were 0.18 for *Anagyrus pseudococci* (Girault), 0.38 for *E. formosa* Gahan, 0.44 for *Bracon hebetor* (Say), 0.96 for *Apanteles fumiferanae* Viereck (Hassell, 1978). This interference between parasitoids, which detracts from their searching efficiency, should increase as parasitoid density increases.

Constant parasitoid: varying host densities. Percentage nymphal mortality was inversely proportional to host density, ranging from 91.3 dead hosts at the 1 : 1 (parasitoid : host ratio), to 21.5 dead hosts at 1 : 50 ($F = 40.4$; df = 4, 21; $P < 0.001$) (Table 3). The percentage of desiccated nymphs at the lowest host density (64.6%) was significantly greater than at all other densities ($F = 16.8$; df = 4, 21; $P < 0.001$). At the highest host density (250) the percentage of dead nymphs not attributable to parasitism ("desiccated") equaled that recorded in the control treatment (no parasitoids). The percentage of parasitism at the lowest host density (26.7%) was significantly lower ($F = 5.6$; df = 4, 21; $P = 0.003$) than at other densities, except at the highest density (19.1%). Emergence of *E. pergandiella* at the three lowest parasitoid-host ratios was significantly greater than in the two highest ratios used ($F = 3.6$; df = 4, 21; $P = 0.02$).

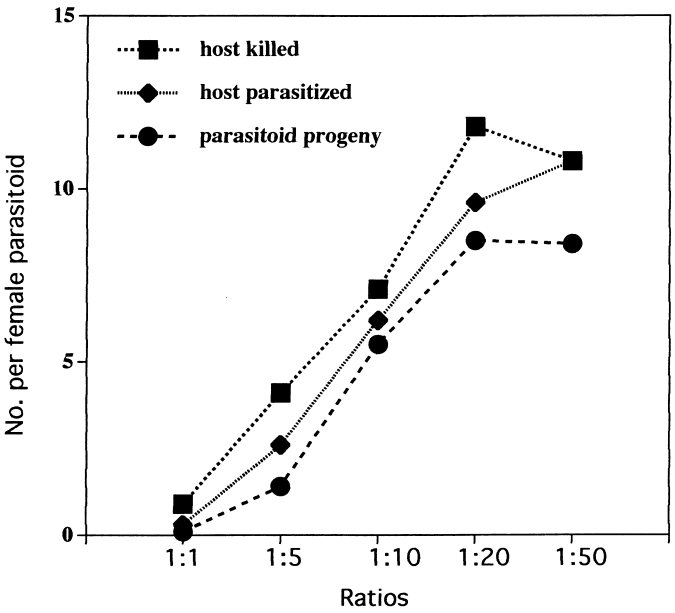

Fig. 3. Effects of parasitoid-host ratios on parasitoid progeny.

The nonlinear regression yielded a highly significant equation (F = 1288.9; df = 2, 24; $P < 0.01$; $R^2 = 0.99$), with an instantaneous rate of encountering hosts (coefficient of attack, a') estimated at 0.27 per day. The interval between a parasitoid first encountering a host and search being resumed (handling time) was 72 min. The theoretical maximum number of hosts attacked (T / T_h= 1 d/0.05 d) is 20 hosts per day. Evidently, as host density increased, the parasitoids spent an increasing proportion of total time not searching. The data can be described using a Type II functional response curve (Fig. 2), in which the attack rate rises at a constantly decreasing rate towards a maximum value, i.e., the response is curvilinear up to the asymptote.

When host density increased from 1 to 50 nymphs per parasitoid female, development time of *E. pergandiella* decreased significantly from 13.0 to 12.3 d (F = 6.6; df = 4, 262; $P < 0.01$) (Table 4). Mean progeny longevity was not statistically significant among treatments (F = 0.7; df = 4, 423; P = 0.578). Progeny size increased with increasing host density. Body length of progeny from parasitoid-host ratios of 1 : 1 to 1 : 50 ranged from 0.419 to 0.486 mm (F = 10.3; df = 4, 192; $P < 0.01$). When host density was increased from 1 to 50 per parasitoid, mean progeny and total number parasitized nymphs per female increased from 0.1 to 8.5, and from 0.3 to 10.8, respectively (Fig. 3).

To summarize and compare the total effects of parasitoid - host ratios, we propose a generalized index of efficacy (GIE). The GIE is derived from the general reproductive index (GRI) method described by Greenberg et al. (1995). It is calculated by multiplying the proportion of parasitized nymphs, by the proportion of emerged parasitoids, by the numbers of female progeny, and then by the number of host killed per parasitoid female. We assume that all factors have equal weight and a high GIE is a desirable parasitoid characteristic. This index showed that the most efficient parasitoid-host ratio was 1 : 20 (a GIE of 42.5). The highest GIE (67.9) was obtained with a density of one parasitoid female per 100 hosts. GIEs of 0.4 and 39.0 were obtained with densities of 15 and 5 females per 100 hosts, respectively.

According to Hassell (1978), the factors affecting host abundance may be thought of in terms of the number of hosts killed by parasitoids as affected by host density, and the size of the regulating parasitoid population as influenced by host availability. Assuming that successful development from egg to adult is not directly density dependent, at low host densities (where competition for hosts is high), changes in percentage residual mortality reflect changes in ovipositional restraint. There was a significant increase in the percentage residual mortality at the parasitoid - host ratio of 1 : 1 compared to other ratios, suggesting a breakdown in ovipositional restraint. The GIE represents our attempt to quantify the various parameters of parasitoid performance into a single value, allowing objective comparisons of the results of different host: parasitoid ratios.

Our results are similar to other studies of density-dependence of host mortality and parasitoid progeny in parasitoids attacking whiteflies. The functional response of *E. formosa* on *Trialeurodes ricini* Misra was density dependent and corresponded to Holling's Type II response curve (Shishehbor and Brennan, 1996). Burnett (1958) observed that *E. formosa* females tended to increase parasitism at higher host densities; when varying numbers of parasitoids searched for a constant number of hosts, *E. formosa* females tended to find hosts in proportion to the natural logarithm of parasitoid density. Fransen and Montfort (1987) also reported the effect of host density on parasitism in the *E. formosa* - *T. vaporariorum* relationship. They found that when each host instar was offered to *E. formosa* separately at different densities and for a fixed time period, a Type II functional response was obtained for each instar. Sengonca et al. (1994) observed that the highest rate of parasitism by *Eretmocerus debachi* Rose and Rosen females was at a density of 150 *Parabemisia myricae* (Kuwana).

The effect of intraspecific competition is a measurable density-dependent process. Development time, size and longevity of progeny are variable species characteristics, influenced by a range of physical and biotic factors. The success of parasitoid development may depend on factors such as the nutritional adequacy of the host (Jervis and Kidd, 1996). Active alteration of host physiology by the parasitizing female has been referred to by Vinson and Iwantsch (1980) as host regulation. Our results of longer development time, smaller size of parasitoids, and shorter progeny longevity at higher parasitoid densities have also been observed in several other parasitoid-host systems. High parasitoid densities or low parasitoid-host ratios result in longer development time and smaller parasitoids. Such observations may be due to possible differences in nutritional quantity. These resulted in a reduction of food for the developing parasitoid. Simmonds (1943) and Wylie (1983) reported that *Venturia canescens* (Gravenhorst.) (Ichneumonidae) and *Microctonus vittatae* Muesebeck (Braconidae) larvae take longer to develop in superparasitized hosts than in singly-parasitized hosts. Similarly, Vinson and Sroka (1978) showed that the development time of the solitary parasitoid *Cardiochiles nigriceps* Viereck was longest when the degree of superparasitism of its host *Helicoverpa virescens* (F.) was highest. A positive correlation between body size and progeny longevity has been shown for the adults of several parasitoid species, for example, *V. canescens* (Harvey et al., 1994), *Lariophagus distinguendus* (Forster) (Bellows, 1985), *Pediobius foveolatus* (Crawford) (Hooker et al., 1987), *Trichogramma evanescens* Westwood (Waage and Ng, 1984), and Trichogramma spp. (Salt, 1937).

The results of these studies increase our knowledge on an important parasitoid of one of the worlds most important pests. They also serve to provide information for long term studies on comparing the relative efficiencies in a series of similar studies on other candidate species of parasitoids for possible mass production for augmentation against *B. argentifolii*.

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