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The effect of varying *Bemisia argentifolii* and *Eretmocerus mundus* ratios on parasitism *

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Abstract. We investigated the effects of different host: parasitoid ratios on the efficacy of the parasitoid *Eretmocerus mundus* attacking the silverleaf whitefly, *Bemisia argentifolii*. When host density was held constant (100 second instars) and parasitoid density was decreased from 15 to 1 females, the percentage of total host mortality was significantly lower at low parasitoid densities. The number of host nymphs killed, and the number of female parasitoid progeny per female, increased 3.6 and 20.4 times, respectively. The emergence rate, sex ratio, longevity, and body lengths of progeny were significantly larger at the lowest parasitoid density while developmental time was significantly shorter. When the number of hosts was increased from 5 to 250 and parasitoid density was held constant (5 females), the percentage of nymphal mortality decreased 1.6 times. The percentage of desiccated nymphs was significantly highest (65.7%) at the lowest host density, while percentage parasitism (34.3%) was significantly lowest at the lowest host density. The data could be described using a Type I functional response curve. We propose a generalized index of efficacy (GIE) to summarize and compare the total effects of parasitoid–host ratios. This index showed that the most efficient ratio was one parasitoid female per ten second instar host nymphs.

Key words: biological parameters, functional response, host-parasitoid ratios, mutual interference

Introduction

The silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring (Homoptera: Aleyrodidae) [= sweetpotato whitefly, *Bemisia tabaci* (Gennadius), Biotype B], is a polyphagous pest species in the tropics and subtropics on all continents (Brown et al., 1995). It causes economic losses through direct feeding damage, excretion of honeydew, and plant virus transmission. Between 1987 and 1994, annual losses in the USA had exceeded $US 200 million, with an

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additional annual loss of 3000–6000 jobs (De Barro, 1995). Whitefly management programs are now being encouraged to integrate cultural and biological methods. Parasitic wasp species within the genus *Eretmocerus* (Aphelinidae) are considered to be among the most important natural enemies of whiteflies. All known *Eretmocerus* species are primary, solitary, ecto-endoparasitoids of whitefly nymphs (Rose et al., 1995). Most are arrhenotokous, but some thelytokous species have been recorded (Gerling, 1966; McAuslane and Nguyen, 1996; Rose and Zolnerowich, 1997). Eggs are deposited underneath whitefly nymphs, and the first instar larva penetrates the host from underneath (Clausen and Berry, 1932; Foltyn and Gerling, 1985).

Any method targeted at enhancing the impact of parasitoids will depend on our knowledge of many factors, including interactions between parasitoid–host. However, quantitative data on host-parasitoid interactions for *Eretmocerus* are limited. The level of mortality inflicted on a host population is determined primarily 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 whiteflies and to obtain a better understanding of host-parasitoid interactions, detailed laboratory studies are necessary. Goolsby et al. (1998), in a series of laboratory and field tests, identified *Eretmocerus mundus* Mercet (Hymenoptera: Aphelinidae) from Spain as one of the most promising species among a variety of parasitoids imported for release against *B. argentifolii* in the USA. The objectives of this study were to measure the response of *E. mundus* to varying *B. argentifolii* densities, and the effects of parasitoid density on progeny production and sex ratio.

Materials and methods

Parasitoid and host cultures

Eretmocerus mundus used in this study was originally collected from near Murcia, Spain in November 1991, from *B. tabaci* in cotton by personnel and cooperators associated with the USDA, ARS, European Biological Control Laboratory, Montpellier, France, and identified by M. Rose (Department of Entomology, Montana State University). Parasitoids were provided by USDA, APHIS, Mission Plant Protection Center (MPPC), Mission, Texas (MPPC culture No. M92014). Specimens of *E. mundus* were vouchered at the Systematic Entomology Laboratory, U.S. National Museum, Washington, DC. Original parental material was also sent to Texas A&M University and vouchered at the MPPC Genetic Diagnostic Laboratory.

The *B. argentifolii* culture was originally started from individuals collected from cabbage (*Brassica oleracea capitata* L.) in Hidalgo County, Texas in 1994, and maintained in a greenhouse, primarily on tomato, *Lycopersicon esculentum* Miller. Sweet potato, *Ipomoea batatas* (L.) Lam., was the host plant used in these tests. Test leaves were excised and each leaf 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) 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 transferred to sweet potato leaves for 25 h before being transferred to the designated test leaves for oviposition. Adult whiteflies were transferred to test leaves after chilling for several minutes in a plastic vial placed in a refrigerator. About 50 adults 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 the host density desired. Each rooted leaf with eggs was then placed in a 120 $\times$ 25 mm polystyrene tissue culture dish (Corning Inc., Corning, NY). The top of each dish was replaced with polyester organdy of ventilation. Dishes were kept in an environmental chamber at 26 $\pm$ 2 °C, 55 $\pm$ 5% RH, and a photoperiod 16:8 h (L:D), at 1400–1725 lux. All experiments were conducted under the conditions described above. Host nymphs were allowed to develop to the second instar before exposure to parasitoid females. The second instar was used because this instar was previously shown to be a suitable instar for *E. mundus* (Jones and Greenberg, 1998).

Constant host density with varying parasitoid densities

The number of 2nd instar *B. argentifolii* was held constant while the number of *E. mundus* females was varied. When the host 2nd instar was reached, all but 100 nymphs were carefully removed with an insect pin. Subsequently, 1, 5, or 15 mated parasitoid females (< 2 days old) were released and confined with the nymphs in a clip cage. After 24 h, the parasitoids were removed, and the leaf with nymphs was returned to an environmental chamber for whitefly and parasitoid development. A control treatment was held without exposure to parasitoids. There were three replicates for each treatment.

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: $a = (1/PT) \ln(N/N_s)$, where the 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; N_s is number of host surviving attack [i.e. total number of hosts − (parasitized hosts + desiccated hosts)]; and T is the duration of the experiment (set to 1.0 for 1 day).

Constant parasitoid density with varying host densities

The same exposure techniques were used as described above, except the number of host nymphs was varied, with the number of parasitoids 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 obtain an index of natural host mortality. There were three replicates for each treatment.

We can calculate numbers of hosts attacked using the equation: $N_a = a'T_sN$, where N_a is number of hosts attacked, N is total number of host nymphs available, T_s is searching time available for the parasitoid, and a' is the instantaneous attack rate (Hassell, 1978). We calculated N_a by adding the total number of hosts parasitized with those that were desiccated and presumably killed by host feeding or unsuccessful parasitism. Because 5 females were used at each host density, we divided numbers attacked by 5 to obtain attack rate per female. Estimates for a' and T_s were obtained by linear regression 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 1 day.

Experimental indices and their assessment

Following an initial 10 d incubation period, test leaves in each treatment were subsequently examined daily for parasitoid development and emergence. Time to emergence was recorded for each individual. Sex of the adult progeny was determined by examining the antennae which are sexually dimorphic. The body sizes of approximately 50 female progeny from each treatment were determined by measuring body length of frozen specimens from the frons to the tip of the abdomen. Longevity was measured for adult parasitoid progeny emerging from each treatment; these were held as honey-fed individuals in 1 cm × 3 cm glass vials. Mortality was checked daily at 1100 h.

In all treatments, whitefly mortality in the control treatment was used to correct the percent parasitoid-induced nymphal mortality (Abbott, 1925). Percentage progeny emergence was calculated as the percentage of exposed nymphs which yielded parasitoid progeny, under the assumption that only one parasitoid emerged per host. The category of desiccated hosts was defined as nymphal mortality due to host-feeding or unsuccessful parasitism and was

calculated as the difference between the corrected percentage of total whitefly mortality and percentage of 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 parasitoid progeny produced per female, and the total number of nymphs killed per parasitoid female, were also calculated. To summarize and compare the total effects of parasitoid–host ratios, we propose a generalized index of efficacy (GIE), calculated by multiplying the proportions of parasitized nymphs, emergence of parasitoids, and the number of female progeny from each parasitoid–host treatment. We assume that all factors have equal weights. The GIE is derived from the general reproductive index (GRI) method described by Greenberg et al. (1995). The GIE is intended to be an indication of reproductive potential under different host-parasitoid densities. Therefore, the calculation of those factors we deemed most likely to be contributing factors in parasitoid reproduction, were included, while excluding progeny longevity, size and developmental time.

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). Percentage data were transformed using the arcsine-square root method before statistical analysis, but results presented are nontransformed means (Sokal and Rohlf, 1981).

Results

Constant host density with varying parasitoid densities

Nymphal mortality decreased from 78.3% to 18.8% with increasing parasitoid densities of from 1 to 15 per 100 host nymphs ($F = 176.3$; df = 2, 7; $p = 0.01$) (Table 1). Conversely, the numbers of host nymphs killed and female parasitoid progeny per female decreased from 18.8 to 5.2 ($p = 0.02$) and from 14.3 to 0.7 ($p = 0.012$), respectively. The number of desiccated nymphs per female (after correction with the control group) increased from 0 to 2.6 ($p = 0.014$). The emergence rate, sex ratio, longevity, and body lengths of progeny were significantly larger at the lowest parasitoid density, while developmental time was significantly shorter (Table 2).

The linear regression in the mutual interference analysis resulted in significant equation: $Y = -0.5125 - 0.2830 \log p$ ($F = 8.76$; df = 1, 7; $p = 0.021$; $R^2 = 0.56$). The mutual interference (slope of the relationships) parameter

Table 1. Effects of parasitoid densities on host mortality and parasitoid progeny[a]

Parasitoid density, females/ 100 nymphs	Percentage of host nymphs			No. per parasitoid female[d]		
	Parasitized	Desiccated[b]	Total mortality[c]	Host nymphs killed	Host nymphs desiccated	Parasitoid female progeny
15	39.3 ± 20.2 a	39.0 ± 18.2 a	78.3 ± 6.3 a	5.2	2.6	0.7
5	58.8 ± 5.5 ab	10.1 ± 5.3 b	68.9 ± 2.3 a	13.8	2.0	5.0
1	18.8 ± 3.8 a	0.0	18.8 ± 3.8 b	18.8	0	14.3

[a] Mean ± SD followed by the same letter within a column are not significantly different at the 5% level, as determined by Tukey's studentized range set.
[b] Desiccated nymphs with correction on control group (mean control mortality was 6.4%).
[c] Sum of parasitized and desiccated nymphs.
[d] Calculated as: (a) host nymphs killed per female – by multiplying the proportion of total host mortality by 100 and dividing by no. of parasitoid females used; (b) female progeny per female – by multiplying proportion of parasitized nymphs, proportion of emerged parasitoids, and the proportion of female progeny by 100, and dividing by no. of parasitoid females used.

m = 0.283. The values calculated for a and the regression line are illustrated in Figure 1 using logarithmic axes, as in Hassell (1978). These results show that searching efficiency decreases with increasing parasitoid density. The stability of co-existence between host and parasitoid increased with an increase in mutual interference.

Constant parasitoid density with varying host densities

As the number of hosts exposed to a constant number of parasitoids increased from 5 to 250, the percentage of total nymphs dying (parasitized + desiccated after correction with the control groups) decreased from 95.6% to 58.9% (F = 32.3; df = 4, 10; p = 0.001) (Figure 2). The percentage of desiccated nymphs at the lowest host density (65.7%) was significantly higher than at all other densities (F = 24.5; df = 4, 10; p = 0.001). The percentage of parasitism at the lowest host density (34.3%) was significantly lower (F = 16.6; df = 4, 10; p = 0.001). Mean mortality of whitefly nymphs in the unparasitized control treatments ranged from 6.4–9.0.

A linear regression, fitting a Type I functional response curve, yielded a highly significant equation (F = 1520.3; df = 1, 14; $p < 0.01$; R^2 = 0.99), with a' estimated at 0.128 per day (SE = 0.003). The data, together with the functional response curve, are illustrated in Figure 3. The host densities used in the experiment were such that numbers attacked were described accurately by a linear response. Host densities higher than 250 will be needed to

Table 2. Effects of parasitoid densities on the main biological parameters of *E. mundus*[a]

Parasitoid density, females/ 100 nymphs	% Emergence	% Female progeny	Development time (d)		Longevity (d)		Female size (mm)
			Males	Females	Males	Females	
15	73.0 ± 9.5 a	37.0 ± 27.6 a	14.2 ± 1.5 a	14.1 ± 1.5 a	8.1 ± 3.6 a	9.3 ± 4.4 b	0.648 ± 0.112 a
5	83.8 ± 3.5 a	51.4 ± 24.5 b	13.6 ± 1.3 b	13.8 ± 1.0 a	8.2 ± 3.2 a	9.1 ± 5.6 b	0.649 ± 0.088 a
1	98.1 ± 3.2 b	74.6 ± 29.7 b	12.3 ± 0.5 c	13.1 ± 0.7 b	9.3 ± 3.1 b	10.7 ± 5.8 a	0.698 ± 0.076 b

[a] Means ± SD followed by the same letter within a column are not significantly different at the 5% level, as determined by Tukey's studentized range test.

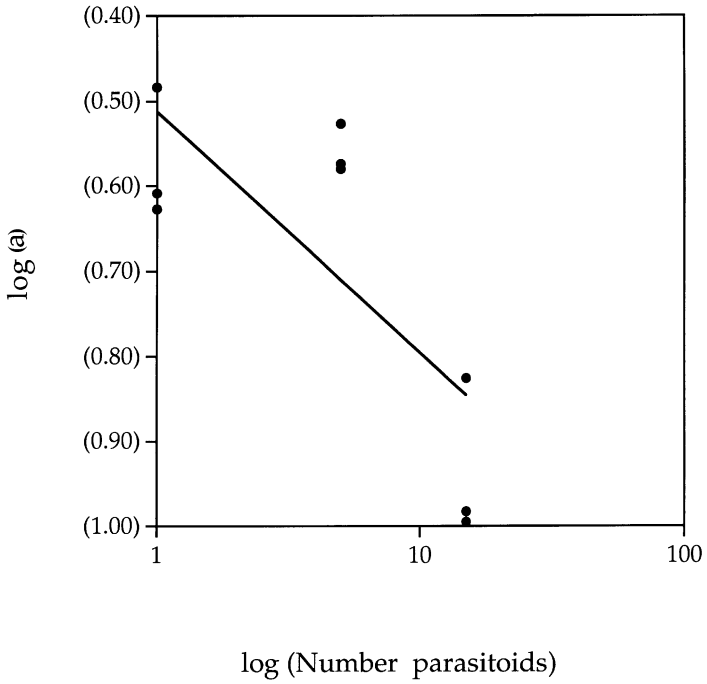

Figure 1. Mutual interference of *E. mundus*.

determine the threshold attack rate of a Type I response, or more likely, the upper asymptote of a Type II response.

Successful emergence of *E. mundus* was not significantly different at the different parasitoid–host ratios (F = 1.97; df = 4, 10; p = 0.175) (Figure 4). Percentage of progeny that were female ranged between 59.4 and 61.5% at ratios of 10–50 host nymphs per parasitoid female, compared with 33.3 to 43.5% female progeny at ratios of 1 to 5 nymphs per female (Table 3). Development time differed significantly among treatment densities, decreasing from 15.3 to 13.1 d for males (F = 10.7; df = 4, 207; p = 0.001), and from 16.2 to 13.8 d for females (F = 12.6; df = 4, 241; p = 0.002). Progeny longevity significantly increased from 4.1 to 5.3 d for males (F = 5.5; df = 4, 555; p = 0.003) and 4.8 to 6.8 d for females (F = 8.1; df = 4, 508; p = 0.001) when host density increased from 1 to 50 nymphs per parasitoid female.

The range of body length of female parasitoid progeny at parasitoid–host ratios of from 1:1 to 1:50 was from 0.568 to 0.676 mm (F = 3.4; df = 4, 140; p = 0.011) (Table 3). When host density was increased from 1 to 50 nymphs per parasitoid female, the number of female parasitoid progeny produced per female, and the number of parasitized nymphs per female, increased from 0.102 to 16.054 and from 0.34 to 28.3, respectively (Figure 5).

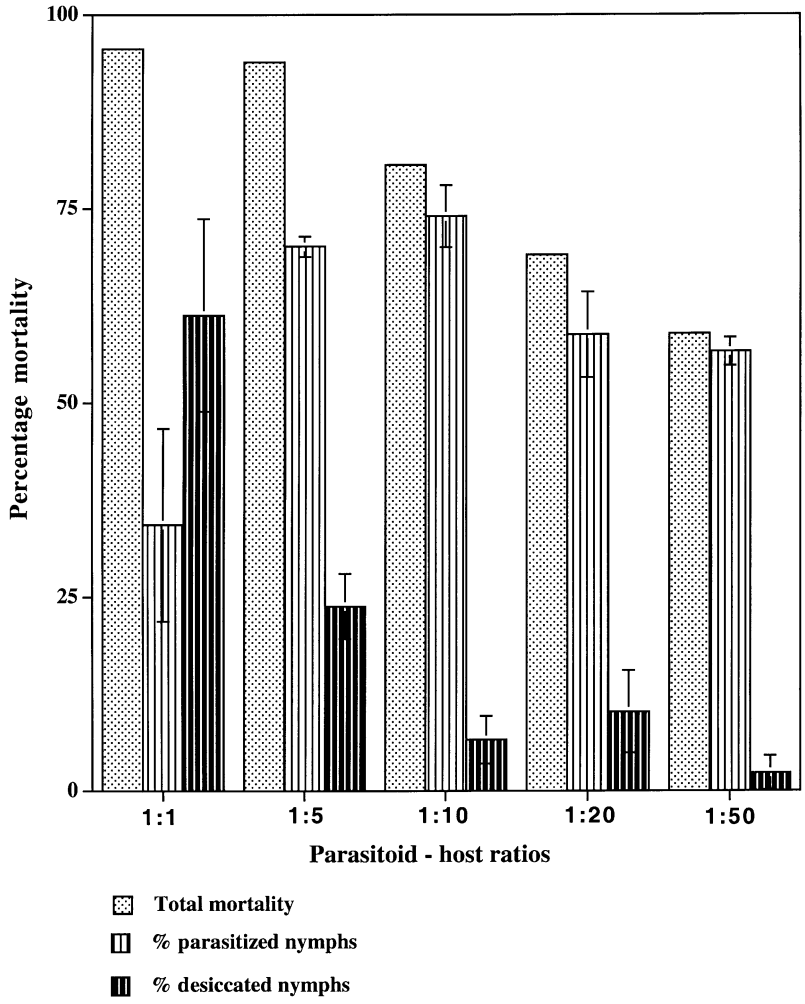

Figure 2. Effects of parasitoid–host ratios on host mortality.

The GIE calculations showed that the most efficient parasitoid–host ratio was 1:10 (Figure 6). The highest GIE (0.253) was obtained when the density was 5 parasitoid females per 100 hosts compared with GIEs of 0.106 and 0.138 when the densities were 15 or 1 females per 100 hosts, respectively.

Discussion

One of the factors affecting host abundance is the number of hosts killed by parasitoids, which is affected by host density and the size of the regulating

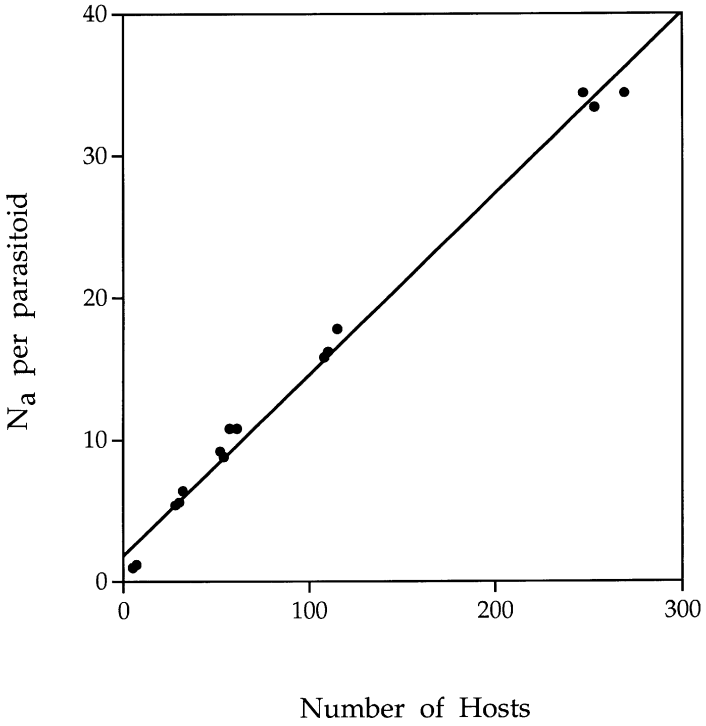

Figure 3. Functional response of *E. mundus*.

parasitoid population, which, in turn, is influenced by the host availability (Hassell, 1978). 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 of mortality reflect changes in ovipositional restraint. There was a significant increase in the percentage of desiccated nymphs at the parasitoid–host ratio of 1:1 compared to other ratios, suggesting a breakdown in ovipositional restraint at the lower host densities. We believe the observed increase in host mortality was due to excessive superparasitism.

In our experiments using varying densities of parasitoids, the percentage of host mortality due to parasitism, and the number of nymphs killed per parasitoid, were comparable to values in the second set of experiments where host density was varied. Percentage of desiccated nymphs increased with parasitoid density. Increased parasitoid densities resulted in consistent decreases in the number of nymphs killed per parasitoid, as well as reduced progeny per parasitoid. The calculation of GIE values is an attempt to quantify the various

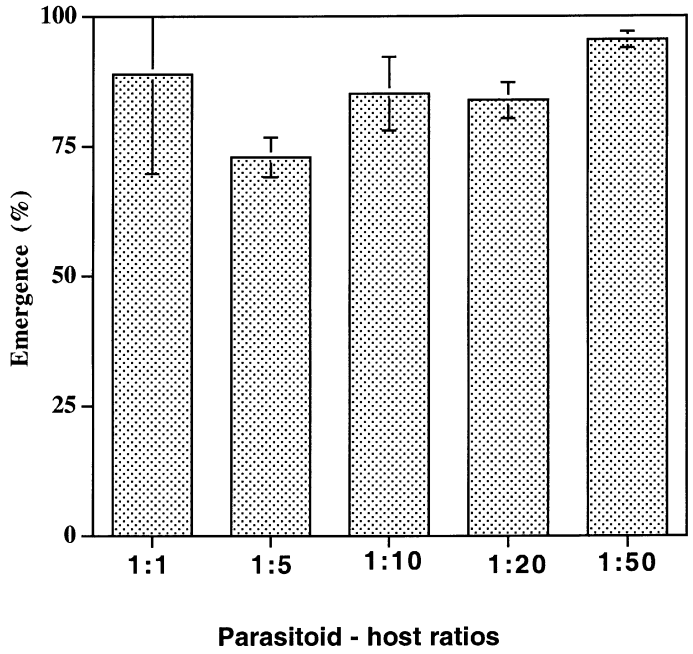

Figure 4. Effects of parasitoid–host ratios on parasitoid emergence.

parameters of parasitoid performance into a single value, allowing objective comparisons of the results of different host:parasitoid ratios.

Our results are similar to those of other authors who studied density-dependence of host mortality and parasitoid progeny in species related to *E. mundus*. The functional and numerical responses of *Eretmocerus debachi* Rose and Rosen to different densities of *Parabemisia myricae* (Kuwana) with one parasitoid female for 24 and 72 h were studied by Sengonca et al. (1994). The highest number of parasitized host nymphs per *E. debachi* female was observed at the highest host density (150), averaging 45.3 (24 h) and 52.8 (72 h). Hoddle et al. (1998) found that *Eretmocerus eremicus* Rose and Zolnerowich exhibited a Type I functional response in small and large canopies while *E. formosa* showed a Type II functional response in small canopies and a weak linear response in large canopies.

The effect of intraspecific competition is a measurable density-dependent process. The development time of parasitoids, and the size and longevity of adult 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

Table 3. Effects of parasitoid–host ratios on the main biological parameters of *E. mundus*[a]

Parasitoid–host ratios	% Female progeny	Development time (d)		Longevity (d)		Female size (mm)
		Male	Female	Male	Female	
1:1	33.3 ± 28.9 a	15.3 ± 0.6 a	16.2 ± 1.0 a	4.1 ± 1.3 a	4.8 ± 0.9 a	0.568 ± 0.05 a
1:5	43.5 ± 11.4 a	14.9 ± 0.8 a	14.9 ± 0.9 ab	4.2 ± 1.1 a	4.7 ± 1.1 a	0.0642 ± 0.06 ab
1:10	61.5 ± 2.4 b	14.3 ± 1.1 a	14.6 ± 0.9 b	5.0 ± 1.5 b	5.2 ± 1.4 a	0.637 ± 0.08 ab
1:20	61.5 ± 6.4 b	13.8 ± 1.0 b	13.6 ± 1.3 c	5.3 ± 1.8 b	6.6 ± 2.2 b	0.676 ± 0.07 b
1:50	59.4 ± 5.6 b	13.1 ± 1.5 b	13.8 ± 1.2 c	5.0 ± 0.9 b	6.8 ± 1.8 b	0.660 ± 0.07 b

[a] Means ± SD followed by the same letter within a column are not significantly different at the 5% level, as determined by Tukey's studentized range test.

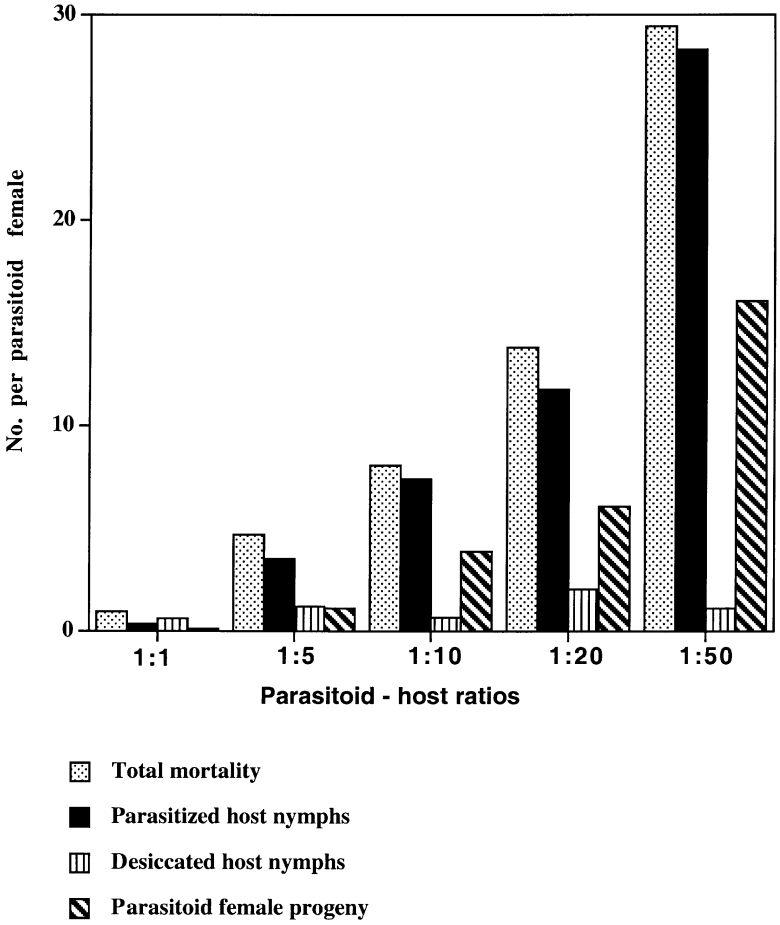

Figure 5. Host mortality and female parasitoid progeny produced per *E. mundas* female.

has been referred to by Vinson and Iwantsch (1980) as host regulation. High parasitoid densities or low parasitoid–host ratios may result in longer development time and smaller size of parasitoid progeny, due to possible differences in nutritional quantity as a consequence of host-feeding or superparasitism, resulting in exhaustion of food for developing parasitoids. As parasitoid–host ratios increase, it is possible, that parasitoids are able to 'select' more suitable hosts, with the result that, on average, the progeny are larger, live longer, and develop more rapidly. Simmonds (1943) and Wylie (1983) reported that parasitoid 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 *Cardi-*

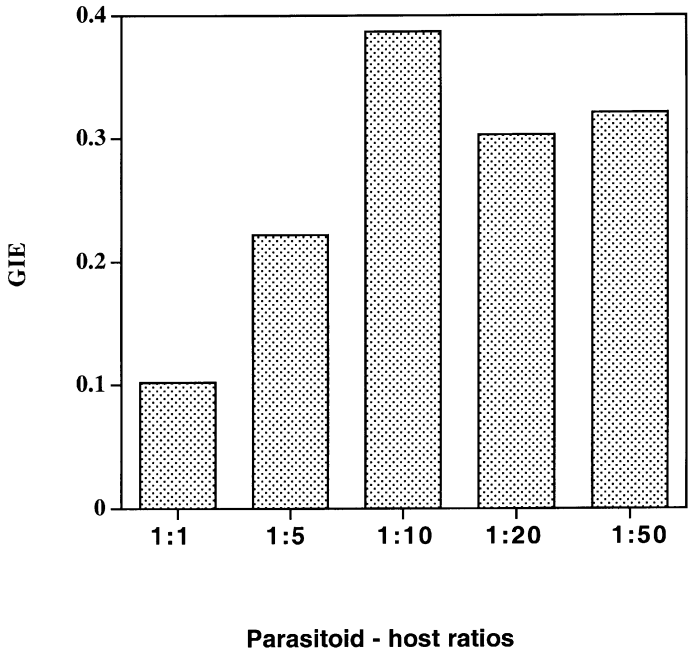

Figure 6. Generalized index of efficacy of parasitoid females.

ochiles nigriceps Viereck was longest when the degree of superparasitism of *Helicoverpa virescens* (F.) was highest. A positive correlation between body size and progeny longevity has been shown for the adults of several parasitoid species, e.g. *V. canescens* (Harvey et al., 1994), *Lariophagus distinguendus* (Förster) (Bellows, 1985), *Pediobius foveolatus* (Crawford) (Hooker et al., 1987), *Trichogramma evanescens* Westwood (Waage and Ng, 1984), and *Trichogramma* spp. (Salt, 1937). High parasitoid density yielded a higher proportion of male progeny, probably because females tended to oviposit unfertilized eggs. In addition, males can attain maturity on less food than females in some species studied (Flanders, 1968; Waage and Lane, 1984; Hohmann et al., 1988; Greenberg et al., 1995).

The results of the present study serve to increase our knowledge of an important parasitoid of one of the world's 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 propagation for augmentation against *B. argentifolii*.

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