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Life-history parameters of *Encarsia formosa*, *Eretmocerus eremicus* and *E. mundus*, aphelinid parasitoids of *Bemisia argentifolii* (Hemiptera: Aleyrodidae)

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Abstract. Life-history parameters (juvenile development time, adult longevity, host instar preference and rate of parasitism) of four parasitoids of *Bemisia argentifolii* (two strains of *Encarsia formosa* (D and B), *Eretmocerus eremicus* and *Eretmocerus mundus*) were studied in the laboratory. At 15°C juvenile development time was the shortest for *E. formosa* B (48 days), longest for *E. eremicus* (79.3 days) and intermediate for *E. formosa* D (62.8 days) and *E. mundus* (64 days) at 15°C. With increase in temperature, development time decreased to around 14 days for all species/strains at 32°C. The lower developmental threshold for development was 11.5, 8.1, 13.0 and 11.5°C for *E. formosa* D, *E. formosa* B, *E. eremicus* and *E. mundus*, respectively. *E. formosa* D and B, and *E. mundus* all appeared to prefer to parasitize 3rd instar nymphs. The presence of hosts shortened adult longevity in most of the parasitoids, with the exception of *E. formosa* B, which lived longer than other species/strains irrespective of the presence of hosts. At 15°C daily parasitism was very low by all parasitoids. The two *Encarsia* strains had a constant, but low rate of reproduction during adult life, while the two *Eretmocerus* species had a very high rate of reproduction when one-day old, which then decreased very quickly. Lifetime fecundity, estimated using a non-linear model, indicated that it was higher for the two *Encarsia* strains than for the *Eretmocerus* species. Life history parameters reported in the literature for the four parasitoids are reviewed and compared with our results. Finally, the potential value for the biological control of whiteflies on greenhouse crops of parasitoids having either a high reproductive rate over a short period (*Eretmocerus* spp.) or a low rate of reproduction over a long period (*Encarsia* spp.) is discussed.

INTRODUCTION

Bemisia tabaci (Gennadius) (Hemiptera: Aleyrodidae) was first described in 1889 as a potential pest of tobacco in Greece (Gennadius, 1889). It was frequently reported as a pest of field crops, like bean and cotton (Brown et al., 1995), and causing serious damage to poinsettia in greenhouses in Florida (Price, 1987). *Bemisia* then spread all over the United States damaging a range of field crops, vegetables and ornamental plants. It was accidentally imported into Europe around 1987 (Fransen, 1994) and became a serious pest of crops in greenhouses. In the past two decades the pest has invaded all continents, which has resulted in research into ways of controlling this pest. The species was first designated as the "B" strain of *B. tabaci*, and later on identified as a new species, *B. argentifolii* (Bellows et al., 1994). However, the taxonomy of this pest remains confused and controversial (Naranjo & Ellsworth, 2001), and we refer to Perring (2001) for a recent discussion of the *Bemisia tabaci* species complex. *Bemisia* causes direct feeding damage, vectors a number of devastating plant viruses, reduces the quality of the harvested product as a result of the excretion of honeydew, and can be the source of various other problems (Drost et al., 1998).

At present, management of *B. argentifolii* depends mainly on chemical control but as this species is resistant to many insecticides, chemical control is difficult and resistance management is of high priority (Costa et al., 1993; Cahill et al., 1996; Palumbo et al., 2001). Also, chemical pesticides interfer with biological pest control, which is now the main means of pest control in modern greenhouses (van Lenteren, 2000). In addition, chemical control may create problems for human health and the environment. So there is an urgent need for more sustainable, more effective and environmentally friendlier methods of control.

During the past decades, much research was directed at finding efficient natural enemies of whiteflies, in particular of *B. argentifollii* (for overviews, see Gerling 1990; Gerling & Mayer, 1995; Gerling et al., 2001). According to Naranjo (2001) about 1500 papers on the biological control of *Bemisia* appeared between 1984 and the end of 2000. Between the end of 2000 and March 2003, we estimate that another 270 papers were published on natural enemies of whitefly. Most of the papers published since the start of 2000 concern whitefly parasitoids of the genera *Encarsia* (circa 125; e.g. DeBarro et al., 2000), *Eretmocerus* (circa 45; e.g. Drost et al., 2000) and *Amitus* (circa 15; e.g. Manzano et al., 2000; de Vis et al., 2003), about 70 on various groups of predators (e.g. Gerling et al., 2001), and several (circa 15) on entomopathogenic fungi (e.g. Faria & Wright, 2001; Meekes et al., 2002). Despite all these publications on the biological control of *Bemisia*, Naranjo & Ellsworth (2001) conclude that: "biological control of *B. tabaci* by parasitoids, predators and fungi represents a key strategy whose potential has gone largely unrealized in many affected

cropping systems throughout the world." Gerling et al. (2001) when reviewing parasitoids and predators of *Bemisia*, state: "Although certain natural enemies have proven effective components in *B. tabaci* control, there are still unexplored, potentially valuable species in many areas of the world.", and also: "The listed fauna of *B. tabaci* parasitoids is extensive, but relatively few have been studied or are intentionally used for pest control." In our view many whitefly biological control projects were opportunistic, terminated prematurely and often even without publishing the results. As such projects contribute negatively to the image of biological control, our philosophy is to do long-term, pure scientific and applied research on whiteflies (e.g. van Lenteren & Noldus, 1990) and parasitoids (e.g. van Lenteren et al., 1996).

Our research group has for the past 25 years been working on the biological control of greenhouse pests, initially mainly on parastioids of greenhouse whitefly (*Trialeurodes vaporariorum* (Westwood), van Lenteren et al., 1996) and during the past 15 years also on parasitoids of *Bemisia* (van Lenteren et al., 1997; Drost et al., 2000). For *B. tabaci*, Gerling et al. (2001) list 34 species of *Encarsia*, 12 species of *Eretmocerus*, one species of *Signiphora* and *Methycus*, and two *Amitus* species. These authors conclude that: "with the exception of *E. formosa* … and despite the frequent use of *Encarsia* species, data on their biological and taxonomic characteristics remain deficient even for commonly used species." Even less is known about other parasitoid genera, although recently the biology of *Eretmocerus* and *Amitus* have received some attention (see below).

Over the last 30 years the seasonal inoculative releases of *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) to control greenhouse whitefly, *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) in greenhouses have been commercially very successful (van Lenteren & Woets, 1988; Gerling et al., 2001). However, *B. argentifolii* is a less favourable host for the *E. formosa* strain that is mass produced in the Netherlands, and control with *E. formosa* in greenhouses is not successful at high release rates of 4–7 adult females per plant per week in North America (Hoddle & van Driesche, 1996). As a strain of *E. formosa* collected in Maryland, USA (the so called Beltsville strain) was considered to be a more promising agent for *B. argentifolii* control, according to laboratory and greenhouse evaluation (Heinz & Parrella, 1994; van Lenteren & Brasch, 1994; Hoddle et al., 1997; van Lenteren et al., 1997), it was included in the current study, together with the Dutch *E. formosa* strain for comparison. Field studies showed that in North America *Eretmocerus* species are the most abundant parasitoids (Goolsby et al., 1998) of *B. argentifoliii*. Further, inundative releases of *Eretmocerus eremicus* Rose and Zolnerowich (Hymenoptera: Aphelinidae) in greenhouses reduce *B. argentifolii* populations substantially (Hoddle et al., 1998). As in Europe *Eretmocerus mundus* often spontaneously entered greenhouses and attacked *Bemisia*, we included *E. eremicus* and *E. mundus* Mercet (Hymenoptera: Aphelinidae) in our study. We also studied the parasitoid *Amitus bennetti* Viggiani and Evans (Hymenoptera: Aphelinidae), because it has a different reproduction strategy (Drost et al.,1999). *Encarsia* and *Eretmocerus* are synovigenic and exhibit host feeding, whereas *Amitus* is proovigenic. We have recently published behavioural data on these 4 species of parasitoids (Drost et al., 1998, 1999, 2000).

Although there are plenty of published data on the life history parameters of whitefly parasitoids, few were obtained under the same experimental conditions (whitefly species, host plant species, confusion over the taxonomic status of parasitoid species and temperature etc.). Therefore it is very difficult to compare between these data. In this study we investigated the life-history parameters of four aphelinid parasitoids of *B. argentifolii* using the same experimental protocol. Analyses of the differences in parameter values can help us predict the relative capacity of these parasitoids to control *B. argentifolii* at different temperatures. In addition, the potential value for the biological control of whiteflies on greenhouse crops of parasitoids, having either a high reproductive rate over a short period (*Amitus* and *Eretmocerus* spp.) or a low rate of reproduction over a long period (*Encarsia* spp.), is discussed.

MATERIALS AND METHODS

Origin of whitefly and parasitoid species/strains

Bemisia argentifolii originated from a population that entered the Netherlands on poinsettia cuttings from California in 1989 (Fransen, 1994) and has been reared on poinsettia (cultivar Goldfinger) in the Laboratory of Entomology, Wageningen, since 1995.

Encarsia formosa D (the Dutch strain of *Encarsia formosa*) pupae were obtained from Koppert Biological Systems Inc.,The Netherlands. They have been reared on *T. vaporariorum* on tobacco for more than 20 years. Adults that emerged from the pupae were used directly in the experiments.

Encarsia formosa B (the Maryland strain of *E. formosa*) was collected from *T. vaporariorum* in Maryland, USA, and subsequently reared on *B. argentifolii* on poinsettia for more than nine years, and is referred to as the Beltsville strain (Bentz, 1996). A starting colony was received from J. P. Sanderson at Cornell University in 1995, since when it has been cultured in the Laboratory of Entomology, Wageningen.

Eretmocerus eremicus, formerly named *E.* nr. *californicus*, pupae were from Koppert Biological Systems Inc., The Netherlands. The species originated from Arizona, USA and has been reared on *T. vaporariorum* on tobacco since 1995. Adults that emerged from the pupae were used directly in the experiments.

Eretmocerus mundus pupae were obtained from Bioplanet, Cesena, Italy, where the parasitoid was reared on *B. tabaci* (unknown biotype) on courgette. *E. mundus* was reared on *B. argentifolii* on poinsettia since 1995 in the Laboratory of Entomology, Wageningen.

Rearing procedures

Colonies of *B. argentifolii* were maintained by infesting poinsettia plants with whitefly adults for three days in cages (50 cm × 50 cm × 56 cm) and subsequently keeping the infected plants, without whitefly adults, in separate cages. In this way a continuous supply of plants with the desired nymphal stages for the parasitoid cultures or for the whitefly culture was maintained. The whitefly culture was maintained in a greenhouse at 26 ±

1°C and 70% R.H. with a 16L: 8D h photoperiod. Colonies of *E. formosa* (MD) and *E. mundus* were established using poinsettia plants infested with third and/or fourth instar nymphs of *B. argentifolii*. About 150 parasitized pupae per parasitoid species were left to emerge in cages (40 cm × 40 cm × 30 cm) containing a poinsettia plant infested with whitefly nymphs. By starting every new colony with pupae and keeping cultures of different species of the same genus in different rooms, contamination of parasitoid cultures by other parasitoid species was prevented. All parasitoid cultures were kept at 25 ± 1°C and 60% R.H. with a 16L: 8D h photoperiod. Parasitized pupae were collected after 18 days.

Juvenile development time

Poinsettia plants, 25 cm heigh, were cut down to three leaves two days before infestation with whitefly. Small leaf clip cages (2 cm inside diameter), each containing 6 pairs of whitefly adults, were used to create three to four groups of third/fourth instar *B. argentifolii* on the underside of leaves. The adult whiteflies were introduced at 17:00 h and removed at 08:00 h the next day, as most eggs are laid between 6:00 am (lights on) to 8:00 am (van Lenteren & Noldus, 1990). When the nymphs reached the third/fourth instar, female parasitoids were released in each group in a large clip cage (3.5 diameter), which covered the whole group of whitefly, which was larger than during the egg stage due to the movement of crawlers. About 5–6 parasitoids were released in each leaf cage and removed after 24 h. Plants were kept in climate cabinets at 15, 20, 25 or 32°C. When parasitoids were on the verge of emerging from the pupae, daily counts were made of the number that had emerged.

The developmental times of the species/strains at different temperatures were compared using a one-way ANOVA test (SPSS for Windows, version 6). The effect of species or temperature was considered significant when $P < 0.05$ in a Least Significant Difference test.

Lower developmental threshold for development

We found that between 15°C and 25°C the relationship between temperature and development rate (the inverse of the development time) was linear with constant α and regression coefficient β (see results). Using this linear relationship, the lower developmental threshold at which the development rate is zero (T_0) was estimated as $-\alpha/\beta$, and the number of day degrees (°D) as °D = development time * ($T-T_0$).

Adult longevity

Longevity of individual parasitoid females was measured in 36ml clear-plastic cups. The lids of the cups had a hole, 3cm in diameter, which was covered with fine gauze to prevent a build up of moisture. Longevity without hosts was measured in cups containing only a few droplets of honey. Longevity with hosts was measured in cups containing a 0.5 cm layer of agar (1% solution) on which a disc of a poinsettia leaf, underside up, infested with third or fourth instar *B. argentifolii* nymphs was placed. Each leaf disc was infested with about 100 nymphs. After two to three days, the females were transferred to a new cup with hosts. Cups were kept in climate cabinets at 15, 20 or 25°C. The number of females alive was checked daily. Longevity data were analysed using the Kaplan-Meier analysis (SPSS for Windows, Version 6), which allows the inclusion of the results from all the females used in the experiment, including those females that died an unnatural death because of handling, or escaped. In other methods only those females that die a natural death can be used to estimate longevity, which was usually a small fraction of the initial number of females used.

The longevities of species/strains at different temperatures were compared using one-way ANOVA test (SPSS for Windows, version 6). The effects of species and temperature were considered significant when $P < 0.05$ using a Least Significant Difference test. The effect of host availability on longevity was tested by using a two-sample t-test.

Instar preference studies

A poinsettia plant infested with *B. argentifolii* nymphs of all stages was cut down to three leaves and each leaf was enclosed in a leaf cage. Whole-leaf cages were made by taping the open ends of two clear-plastic 500ml cups together. Both bottoms were cut out, one of which was covered with fine screening, while the other was fitted with a clear-plastic lid that covered the leaf petiole. One parasitoid female was released per leaf cage (at 25°C and 60 % R.H.). The number of whiteflies offered was in the range of 43–111, with an average of 66 per leaf. After 24 h the parasitoids were removed and the number of each instar present per leaf was counted and mapped to enable later identification of the instars that were parasitized. The plants were kept at 25°C and 60% R.H. for the duration of the development of the parasitoids.

In order to compare the distribution of parasitoid eggs over the different instars with the ratio of the instars on a leaf, a preference index was estimated for each female (see also Drost et al., 1999). This was necessary because 1) females were released onto leaves with slightly different ratios of whitefly instars, 2) it was unknown how many hosts of each instar were encountered per female, and 3) each female laid a different total number of eggs. If females are assumed to walk at a constant speed and the difference in size of the host nymphs is ignored, then the expected (expe) fraction of nymphs of instar *j* parasitized by individual *i* may be calculated by expressing the number of instar *j* as a proportion of the total number of nymphs present:

$$\text{expe}_{i,j} = \frac{\text{number of nymphs of instar } j}{\text{total number of nymphs}}$$

The observed (obs) fraction of nymphs of instar *j* parasitized by individual *i* is

$$\text{obs}_{i,j} = \frac{\text{number of parasitised nymphs of instar } j}{\text{total number of parasitised nymphs}}$$

The deviation between the observed and expected values is a measure of the preference of individual *i* for instar *j* :

$$\text{Preference}_{i,j} = \text{obs}_{i,j} - \text{expe}_{i,j}$$

The deviation will be zero when no preference occurs, positive when there is preference for a certain instar and negative when an instar is rejected. Thus, this method of analysis allows the detection of individual variation in instar preference. A one-sample t-test was performed to test whether the preference is different from zero.

Age-specific parasitism

Parasitization of whitefly was achieved using the same procedure as in the development time experiment. One parasitoid female was introduced into a large clip cage enclosing a group of whitefly for exactly 24 h at either 15, 20 or 25°C in a controlled climate cabinet. Two age groups of females were tested. In the first group females less than 24 hours old were used. In the second group three day old females of *Encarsia* strains and five day old females of *Eretmocerus* species were used. These females had been previously exposed to hosts over several days. After removal of the adult parasitoids, the plants were kept at 25°C until the parasitoids reached the pupal stage. When the parasitized nymphs changed colour from light to dark, they were counted in each infested group. In this way, the number of parasitized hosts was determined.

TABLE 1. Juvenile development time (S.E. and number of replicates) of four aphelinid parasitoids, linear regression of development rate (at < 30°C) against temperatures, estimated lower temperature thresholds (T_0) and day-degrees (°D) for juvenile development. α and β are constants, r is coefficient of linear regression.

Species	Development time: mean (S.E.; n)				α	β	r	T_0	°D
	15°C	20°C	25°C	32°C					
E. formosa D[1]	62.8(0.46;184)b[2]	29.8(0.26;75)b	15.6(0.32;24)a	13.6(0.45;24)a	–0.0505	0.004378	0.970	11.51c	228a
E. formosa B[1]	48.3(0.87;40)a	28.0(0.48;58)a	19.8(0.24;126)d	14.8(0.13;271)b	–0.0247	0.003044	0.901	8.11a	329b
E. eremicus	79.3(1.36;10)d	34.0(0.37;88)c	18.6(0.57;21)c	14.6(0.23;71)b	–0.0575	0.004409	0.928	13.04d	227a
E. mundus	64.0(0.29;146)c	29.1(0.52;39)ab	17.1(0.40;43)b	13.7(0.19;129)a	–0.0499	0.004352	0.885	11.47b	230a

[1]*E. formosa* D is the Dutch strain of *E. formosa*, *E. formosa* B the Beltsville strain.
[2]Different letters in a column indicate significant differences. One-way ANOVA with LSD ($P < 0.05$).

Estimate of total parasitism

Age-specific parasitism data were fitted to a function (1) that is composed of a linear function describing the increase of egg laying by a young adult parasitoid and an exponential function describing the decrease in egg laying by older adults (Enkegaard, 1993a). Temperature can be included in the model.

$$F_x = (\alpha + \beta T)\, x \exp\{-(\delta + \varepsilon T)x\} \quad (1)$$

F_x is the daily age-specific parasitism, T is the temperature, x is the age of the parasitoids in days and α, β, δ, ε, are constants. The least square regression method was used with the Chi-square tolerant value of 10^{-6} using SPSS for Windows, version 6. The average life time parasitism F was estimated using the model:

$$F = \int_0^y (\alpha + \beta T)\, y \exp\{-(\delta + \varepsilon T)y\}\, dy \quad (2)$$

where y is the average female longevity. The estimated total fecundity of different species/strains was compared using Chi-square tests.

RESULTS

Juvenile development time

The development time from egg to adult decreased exponentially from low to high temperatures (Table 1). At 15°C mean development time was shortest for *E. formosa* B, longest for *E. eremicus*, and intermediate for *E. formosa* D and *E. mundus*. At 20°C *E. eremicus* had a longer mean development time than the other three parasitoids, whose development times did not differ significantly. At 25°C mean development time for *E. formosa* B was longer than that of *E. eremicus*, which was longer than that for *E. mundus* and *E. formosa* D. Differences in mean development time between species/strains decreased with increase in temperature. At 32°C *E. formosa* B and *E. eremicus* had identical mean development times, and that of *E. formosa* D was similar to that of *E. mundus*. The latter two species developed faster than the former two at 32°C.

Lower developmental threshold for development

Linear regressions of the development rate against temperature were fitted for all species/strains. The α and β values as well as the lower temperature threshold for *E. formosa* D and *E. mundus* were almost identical. *E. formosa* B had the lowest and *E. eremicus* the highest lower developmental threshold. Day-degrees necessary for the juvenile development of *E. formosa* D and the two *Eretmocerus* species were similar.

Adult longevity

Adult females of strains of *Encarsia* and of species of *Eretmocerus* lived longer at low temperatures in the presence or absence of hosts (Table 2), except for *E. mundus* for which the mean longevity at 25°C in the presence of hosts was slightly higher than that at 20°C. At 25°C, adult females of *E. formosa* D and *Eretmocerus* species lived longer in the absence of hosts. For *E. formosa* B there was no difference in the longevity of adults in the presence or absence of hosts. *E. mundus* lived longer in the presence of hosts than in their absence at 25°C. *E. mundus* had the longest longevity of the four parasitoids at 15°C but the shortest at 25°C when hosts were absent. Longevity of *E. mundus* at 25°C was 89.5% shorter than that at 15°C, which indicates a high sensitivity to temperature. *E. formosa* B was the least temperature sensitive, adult female longevity was 35% shorter at 25°C than at 15°C. Adult females of this strain lived longest at 25°C. When hosts were present, *E. formosa* B had the longest longevity at all three temperatures. Contrary to the results when hosts were absent, *E. mundus* showed

TABLE 2. Mean female adult longevity (days) of four aphelinid parasitoids of *B. argentifolii* in the absence and presence of *B. argentifolii*. S.E. and number of replicates are given between brackets.

Species	Hosts absent			Hosts present		
	15°C	20°C	25°C	15°	20°	25°
E. formosa D[1]	36.9(5.9;15)a[2]	22.5(3.4;15)a	11.2(2.1;15)ab	23.0(1.2;13)b	15.8(0.9;12)a	7.8(0.9; 9)a
E. formosa B[1]	47.2(3.8;19)a	35.5(2.7;20)b	30.5(2.5;21)c	50.4(4.5;15)c	33.5(3.0;13)b	28.6(2.7;12)c
E. eremicus	38.4(3.6;21)a	33.8(1.9;22)b	18.9(1.6;19)b	24.3(1.3;13)b	16.4(0.9;12)a	9.3(0.4; 9)a
E. mundus	55.0(3.6;14)b	24.5(2.7;15)a	5.8(0.9;15)a	14.4(0.7;15)a	11.3(1.3;15)a	12.4(1.5;11)b

[1]*E. formosa* D is the Dutch strain of *E. formosa*, *E. formosa* B the Beltsville strain.
[2]Different letters in a column indicate significant differences. One-way ANOVA with LSD ($P < 0.05$).

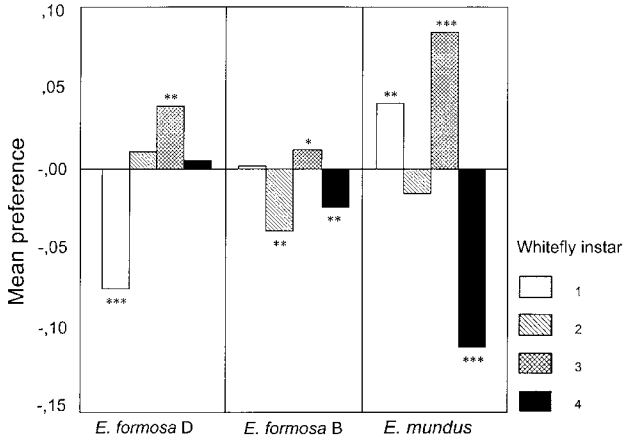

Fig. 1. Host instar preferences of three aphelinid parasitoids of *B. argentifolii*. Asterisks indicate a significant difference from zero based on t-test. *: $P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

very little sensitivity to temperature when hosts were present: longevity only decreased by 13.9% at 25°C compared to that at 15°C. Longevity does not seem to be genus or species specific. Large differences in longevity were found between the two *Eretmocerus* species and the *Encarsia* strains. Nevertheless the longevities of the adults of *E. formosa* D and *E. eremicus*, and their response to temperature and presence of hosts were analogous. These two species are normally reared on the same host, *Trialeurodes vaporariorum*.

Instar preference

The instar preferences of *E. formosa* D and B, and *E. mundus* were tested. All species/strains were offered all instars of *B. argentifolii*, but showed an obvious preference. *E. formosa* D preferred the third instar larvae of *B. argentifolii* ($t = 2.77$, df = 69, p = 0.007) compared to other instars. Significantly fewer eggs were laid in 1st instar nymphs than expected based on their abundance ($t = –4.36$, df = 101, $p < 0.0005$) (Fig. 1). *E. formosa* B also preferred 3rd instar nymphs for parasitism to the other nymphal stages ($t = 3.69$, df = 113, p = 0.01). *E. formosa* B parasitized considerably fewer fourth instar nymphs ($t = –2.67$, df = 113, p = 0.009) than expected. Third instar larvae were also the most preferred ($t = 20.05$, df = 56, $p < 0.0005$) and fourth instar nymphs the least preferred by *E. mundus* ($t = –25.2$, df = 56, $p < 0.0005$). *E. eremicus* was not tested.

Daily parasitism

At 15°C daily parasitism by both age groups was low in all species/strains. In most cases daily parasitism was not significantly different from 0 (One sample T-test, $p < 0.05$) except for *E. formosa* D of both age groups and *E. mundus* of age group 0 (Table 3). Rates of parasitism were about the same at 20 and 25°C for all species/strains, and were higher than at 15°C. On the first day, *E. mundus* had a much higher rate of parasitism at 20°C than the other parasitoid species/strains. It had a similar rate to *E. eremicus*, but higher than that of the two *Encarsia* strains at 25°C. When three or five day old, the two *Encarsia* strains had a higher rate of parasitism at 20°C than the *Eretmocerus* species, while no differences were found between the four parasitoids at 25°C. At 20 and 25°C, the two *Eretmocerus* species had a higher rate of parasitism when 1 day old, whereas the two *Encarsia* strains had a higher rate of parasitism when 5 days old.

Estimate of life-time parasitism

The relationship between age-specific fecundity and adult age is described by model (1) for the four species/strains of parasitoids (Fig. 2). In general, the daily egg laying increased with increase in temperature. Daily reproduction increased with age up to a maximum, and thereafter decreased. *Eretmocerus* spp. oviposited at a higher rate when young than *E. formosa*. The latter maintained a high rate of reproduction for longer. The relationships of age-specific parasitism to adult age, based on the age-specific parasitism data from Table 3 are described in Table 4. There was no significant difference in the daily parasitism by the two *Encarsia* strains, but *E. formosa* B had a higher estimated total fecundity than *E. formosa* D at 20°C ($\chi^2 = 7.30$, df = 1, $P < 0.01$) (Table 3). *E. mundus* had a higher life-time parasitism than *E. eremicus* at 15 ($\chi^2 = 4.43$, df = 1, $P < 0.05$) and 20°C ($\chi^2 = 9.57$, df = 1, $P < 0.005$). The two *Eretmocerus* spp. produced similar numbers of progeny at 25°C.

DISCUSSION

Juvenile development time

Juvenile development times for the four aphelinid parasitoids of *B. tabaci* reported by other authors are listed in Table 5. In the present study, the juvenile development time of *E. formosa* D at 20 (29.8) and 25°C (15.6) corresponds to those reported by Enkegaard (1993b) (25.3 at 22°C, and 14.0 at 28°C), although Enkegaard found a

TABLE 3. Mean daily parasitism by < 1 day old females and 3-day old females of *Eretmocerus* species and 5-day old females of *Encarsia* strains at different temperatures. S.E. and number of replicates are in brackets.

Species	Females of age < 1			Females of age 3 or 5		
	15°C	20°C	25°C	15°	20°C	25°C
E. formosa D[1]	4.20(0.83;15)b[2]	8.87(0.70;23)a	6.75(1.00;8)a	2.40(0.34;10)b	11.22(1.28;9)b	9.88(1.85; 8)a
E. formosa B[1]	0.83(0.46;12)a	7.04(0.68;23)a	5.25(1.33;8)a	0.90(0.41;10)ab	10.5(1.06;6)b	10.38(0.89;8)a
E. eremicus	1.50(0.85;12)a	6.69(1.01;26)a	16.00(4.57;8)ab	0.63(0.25;38)a	0.71(0.71;7)a	3.91(1.60;11)a
E. mundus	2.26(0.86;19)ab	16.33(1.28;12)b	19.81(2.15;16)b	0.56(0.41;18)a	3.58(1.18;12)a	4.00(2.04;7)a

[1]*E. formosa* D is the Dutch strain of *E. formosa*, *E. formosa* B the Beltsville strain.
[2]Different letters in a column indicate significant differences. One-way ANOVA with LSD ($P < 0.05$).

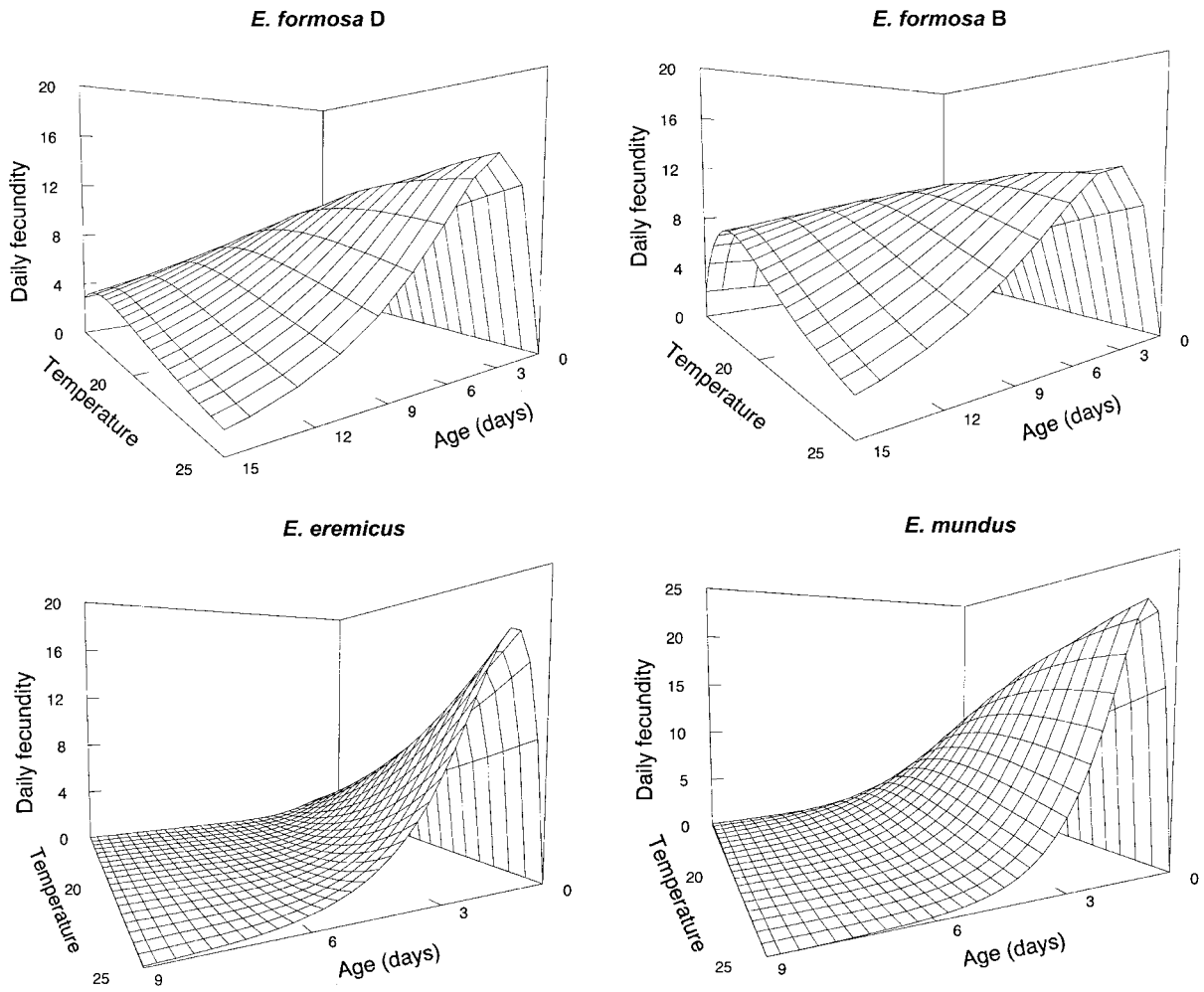

Fig. 2. Fitted curves for age-specific fecundity over a range of temperatures for four aphelinid parasitoids of *B. argentifolii*.

longer development time at 16°C (72.8) than we did at 15°C (62.8). Because of the longer development time the T0 (13.3) value cited by Enkegaard is also higher than we found (11.5). Consequently the day-degrees value (207) is lower than recorded here (228). The host plant cultivar we used (Goldfinger) is different from that by Enkegaard (Angelica), which might be the reason for the different results. Notable differences between the two *Encarsia* strains were observed in our study. The linear regressions of development rate against temperature (α and β values are different from each other) and the T_0 and °D values were different for the two strains. At temperatures below 20°C, *E. formosa* B had a higher development rate than *E. formosa* D. *E. formosa* B had a lower T_0 value (8.1) than the other parasitoids (11.5, 13.4 and 11.5). The T_0 value was also lower than that of the host, *B. argentifolii* (13.9) (Enkegaard, 1993a). The two *Eretmocerus* species and *E. formosa* D required fewer day-degrees for development than *B. tabaci* (B type) on poinsettia (327°C) (Enkegaard, 1993a); *E. formosa* B and *B. tabaci* had similar values (Enkegaard, 1993a). These values might indicate that *E. formosa* B has a better capacity to control

TABLE 4. Estimated coefficients: α, β, δ and ε, coefficient of determination r^2 of the age-specific function (1), and estimated lifetime parasitism (F_{est}) at different temperatures of four aphelinid parasitoids of *B. argentifolii*.

Species	*E. formosa* D*			*E. formosa* B*			*E. eremicus*			*E. mundus*		
α	–15.281			–13.215			–42.711			–94.701		
β	1.125			0.900			3.326			6.553		
δ	–0.155			–0.300			2.57			–0.374		
ε	0.029			0.023			–0.066			0.063		
r^2	0.710			0.887			0.998			0.976		
Temperature	15	20	25	15	20	25	15	20	25	15	20	25
F_{est}	62.5	94.5	80.9	75.8	156.6	109.6	2.3	13.2	43.6	10.7	43.4	42.5

* *E. formosa* D is the Dutch strain of *E. formosa*, *E. formosa* B the Beltsville strain.

TABLE 5. Development times of four aphelinid parasitoids on *B. tabaci* reported by various authors (Only results from laboratory experiments at constant temperatures are included).

Species	Origin	Test plant	Temp. (°C)	Development time	n	Reference
Encarsia formosa	Holland	Poinsettia/ Angelica	16	72.80 ± 0.90	115	Enkegaard, 1993b
Encarsia formosa	Holland	Poinsettia/ Angelica	22	25.30 ± 0.30	100	Enkegaard, 1993b
Encarsia formosa	Holland	Poinsettia/ Angelica	28	14.00 ± 0.20	121	Enkegaard, 1993b
Eretmocerus eremicus	Oxnard, CA	Sweet potato	15	63.3 ± 0.13	33	Greenberg et al., 2000
Eretmocerus eremicus	Oxnard, CA	Sweet potato	21	26.4 ± 0.16	69	Greenberg et al., 2000
Eretmocerus eremicus	Oxnard, CA	Sweet potato	24	21.1 ± 0.16	211	Greenberg et al., 2000
Eretmocerus eremicus	Oxnard, CA	Sweet potato	32	18.1 ± 0.16	169	Greenberg et al., 2000
Eretmocerus eremicus	Hawaii	cotton	20	33.95 ± 0.31	97	Powell & Bellows, 1992
Eretmocerus eremicus	Hawaii	cotton	29	18.76 ± 0.15	158	Powell & Bellows, 1992
Eretmocerus eremicus	Hawaii	cucumber	20	35.06 ± 0.14	345	Powell & Bellows, 1992
Eretmocerus eremicus	Hawaii	cucumber	29	16.10 ± 0.11	185	Powell & Bellows, 1992
Eretmocerus eremicus	Indio. CA	cotton	20	35.78 ± 0.46	60	Powell & Bellows, 1992
Eretmocerus eremicus	Indio. CA	cotton	29	18.31 ± 0.46	32	Powell & Bellows, 1992
Eretmocerus eremicus	Indio. CA	cucumber	20	36.39 ± 0.22	196	Powell & Bellows, 1992
Eretmocerus eremicus	Indio. CA	cucumber	29	16.29 ± 0.13	196	Powell & Bellows, 1992
Eretmocerus mundus	Israel	cotton	29.5	30.00		Gameel, 1969
Eretmocerus mundus	Spain	sweet potato	26	15.4		Jones & Greenberg, 1998
Eretmocerus mundus	Jordan	tomato	14	44.00		Sharaf & Batta, 1985
Eretmocerus mundus	Jordan	tomato	25	16.00		Sharaf & Batta, 1985
Eretmocerus mundus	Egypt	sweet potato	29.8	17.90	35	Tawfik et al., 1978

whiteflies at low temperatures. *E. formosa* D and *E. mundus* have more or less identical α, β, T_0 and °D values. Developmental times of *E. eremicus* on *B. argentifolii* recorded by Greenberg et al. (2000) were less sensitive to temperature change than we observed. The differences might be due to the different host plants used and/or the fact that the parasitoid strain used in their experiments were reared on the same host as was used in the experiments. In another study, Greenberg et al. (2002) found that *E. mundus* developed faster on *Bemisia* than on *Trialeurodes*, which is similar to what we found. Powell & Bellows (1992) tested the effect of the host plant on the development time of two strains of *E. eremicus* on *B. tabaci* at 20 and 29°C. The development time on cotton at 20°C (33.9 days) is similar to our result (34.0 days) in spite of different host plants. Similarly, the development time for *E. mundus* measured at 25°C corresponds with the result of Sharaf & Beatta (1985) (16 days) at the same temperature, and also was in the same range as the results of Jones & Greenberg (1998) at 26°C. Sharaf & Batta (1985) found a much shorter development time at 14°C (44 days) than we found at 15°C (64 days).

Adult longevity

Vet & van Lenteren (1981) and van Lenteren et al. (1987) compared the longevity of *E. formosa* at different temperatures in the presence or absence of hosts reported by different authors, and concluded that being given access to hosts shortened adult longevity in *E. formosa*, but not in *Eretmocerus* species. In the present study adult longevity was shorter in the presence than absence of hosts in *E. formosa* D and the two *Eremocerus* species. Adult female longevity is shorter in the presence of hosts in another parasitoid of *Bemisia*, *Amitus bennetti* Viggiani & Evans (Hymenoptera: Platygasteridae) (Drost et al., 1999). Shorter adult life-spans in the presence of hosts is found in other parasitoids. Takagi (1985) recorded the highest longevity in female *Pteromalus puparum* (Hymenoptera: Pteromalidae), a gregarious parasitoid of many butterfly pupae, when they are kept with honey but without hosts. Nakamura (1994) reported a negative correlation between adult female longevity in *Exorista japonica* (Diptera: Tachinidae) and frequency of oviposition, when the common armyworm *Pseudaletia separata* (Lepidoptera: Noctuidae) is used as a host. The shorter life span recorded here might be caused by transferring the parasitoids to fresh hosts every two or three days. However, life-span did not differ in *E. formosa* B in the presence or absence of hosts, and this parasitoid lived longer than *Eretmocerus* species and *E. formosa* D in both situations. It is important to realize that the two strains of *E. formosa* are normally reared on different hosts: *E. formosa* B on *B. argentifolii* and *E. formosa* D on *T. vaporariorum*. Bethke et al. (1991) report a longer adult longevity for *E. formosa* reared on *B. tabaci* (8.3 days) than when reared on *T. vaporariorum* (4.8 days) when *B. tabaci* nymphs were present.

Longevities of *E. formosa* reared on *T. vaporariorum* and tested in the presence of *B. tabaci* or *T. vaporariorum* were very different. Van Lenteren et al. (1987) studied the effect of host quality on adult longevity of *E. formosa,* and discovered a longer longevity when all instars of *T. vaporariorum* larvae were present during the test, than

TABLE 6. Adult longevities of four aphelinid parasitoids of *B. argentifolii* reported by various authors (Only results from laboratory experiments at constant temperatures are included).

Species	Origin	Temp. (°C)	Longevity	n	Hosts	Honey	Reference
Encarsia formosa	Holland	16	30.1 ± 2.5	23	yes	no	Enkegaard, 1993b
Encarsia formosa	Holland	22	15.2 ± 0.9	22	yes	no	Enkegaard, 1993b
Encarsia formosa	Holland	28	9.2 ± 0.8	28	yes	no	Enkegaard, 1993b
Encarsia formosa	Beltsville	27.6	7.7 ± 0.4	30	yes	no	Heinz & Parrella, 1994
Encarsia formosa	Canada	27.6	3.9 ± 0.2	29	yes	no	Heinz & Parrella, 1994
Eretmocerus eremicus	CA	28	5.0 ± 0.5	36	yes	no	Headrick et al., 1999
Eretmocerus eremicus	CA	1.7	8.4 ± 0.1	46	no	yes	Gerling, 1966
Eretmocerus eremicus	CA	15.5	40.5 ± 7.9	7	no	yes	Gerling, 1966
Eretmocerus eremicus	CA	26.7	8.6 ± 0.2	15	no	yes	Gerling, 1966
Eretmocerus mundus	Egypt	18	7.6	25	yes	yes	Tawfik et al., 1978
Eretmocerus mundus	Egypt	30	10.5	25	yes	yes	Tawfik et al., 1978
Eretmocerus mundus	Jordan	14	11.3	18	yes	no	Sharaf & Batta, 1985
Eretmocerus mundus	Jordan	25	9.1	17	yes	no	Sharaf & Batta, 1985
Eretmocerus mundus	Jordan	14	14.8		yes	no	Sharaf & Batta, 1985
Eretmocerus mundus	Jordan	25	9.6		yes	no	Sharaf & Batta, 1985
Eretmocerus mundus	Egypt	23	3.22	34	no	no	Tawfik et al., 1978
Eretmocerus mundus	Egypt	18	4.2	15	no	no	Tawfik et al., 1978
Eretmocerus mundus	Egypt	18	5.3	20	no	yes	Tawfik et al., 1978
Eretmocerus mundus	Egypt	10	6.1	20	no	yes	Tawfik et al., 1978
Eretmocerus mundus	Egypt	–4	0.42	10	no	no	Tawfik et al., 1978
Eretmocerus mundus	Israel	25	7.65		no	yes	El-Ghany et al., 1990

when only 1st instar larvae were present, which are not suitable for parasitism. It seems that the presence of "poor" quality hosts shortens the life-span of adult *E. formosa* although further investigation is needed. Our results showed that in the absence of hosts adult *E. formosa* B lived longer than *E. formosa* D in spite of the fact that the latter was reared on a more favourable host. This indicates an intrinsic or even heritable difference between the strains. Heritable differences have been found between these two strains in their host acceptance, host handling behaviour, immature development, immature survival and rate of parasitism (van Lenteren et al., 1997; Henter & van Lenteren, 1996; Henter et al., 1996). A large difference in the life-spans of the two *E. formosa* strains was found when hosts were present. This might be the result of the type of host present during the experiment. For *E. formosa* D, *B. argentifolii* was a strange host, whereas *E. formosa* B might have adapted to *B. argentifolii* after generations of cultivation on this host. Heinz & Parrella (1994, Table 6) record a longer longevity in *E. formosa* B (7.7 days) than in a Canadian commercial strain of *E. formosa* (3.9 days) at 27°C when reared on *B. argentifolii.* The Canadian commercial strain is supposedly *E. formosa* D.

We recorded a comparatively longer longevity for both *E. formosa* B and *E. formosa* D at 25°C. Enkegaard (1993b) records a longer longevity for *E. formosa* when hosts were present than we found for *E. formosa* D when hosts were present (Table 6). The difference might be due to different methods of offering the hosts. Longevity of *E. eremicus* at 15°C without hosts (38.4) is in the same range as Gerling's results (1966) at 15.5°C (40.5). *E. mundus* had a longer longevity at 20°C (33.8) than Tawfik et al. (1978) records at 18°C (5.3), and a slightly shorter longevity at 25°C (5.8) than El-Ghany et al. (1990) records (7.65) when hosts are absent. When hosts were present we recorded a longer life-span (12.4) for *E. mundus* at 25°C than Sharaf & Batta found (9.6) (1985).

Instar preference

The results on host-stage preference indicate that both *Encarsia* strains showed a preference for 3rd instar *Bemisia* nymphs. This does not agree with Enkegaard's (1993b) results, which indicate that 4th instar *Bemisia* nymphs are preferred. Enkegaard observed the oviposition behaviour for 1/2 to 2 1/2 hours, while in our experiment parasitoids were left to parasitize for 24 hours. This difference might account for the different results. Jones and Greenberg (1998) record that *E. mundus* laid most eggs under 2nd instar nymphs of *B. argentifolii* in a no-choice test. In *E. mundus* the strongest preference for 3rd instar nymphs was observed when all host stages were available. This result agrees with that of Foltyn & Gerling (1985) who also used a mixed-age host population. McAuslane & Nguyen (1996) report that the third instar nymphal stage of *B. argentifolii* is the most favourable host stage for an *Eretmocerus* spp.

Daily and life-time parasitism

Encarsia and *Eremocerus* species are synovigenic, which means that females mature eggs during their adult life. *Encarsia* species are anautogenous, which means that females do not have mature eggs in their ovaries at emer-

TABLE 7. Fecundities of four aphelinid parasitoids of *B. argentifolii* reported by various authors. (Only results from laboratory experiments at constant temperatures are included).

Species	Origin	Rear. host	Test plant/ cultivar	Temp. (°C)	Fecundity	S.E.	n	References
E. formosa	England	T.v.	Poinsettia/ A.H.B.D.	26.7	26.7			Bethke, et al., 1991
E. formosa	CA, USA	B.t.	Poinsettia/ A.H.B.D.	26.7	30.2			Bethke, et al., 1991
E. formosa	Holland		Poinsettia/ Angelica	16	0.8/d			Enkegaard, 1994
E. formosa	Holland		Poinsettia/ Angelica	22	5.6/d			Enkegaard, 1994
E. formosa	Holland		Poinsettia/ Angelica	28	10.4/d			Enkegaard, 1994
E. formosa	Canada	T.v.	Poinsettia/ Lilo	27.6	2.0/3d	0.3	30	Heinz & Parrella, 1994
E. formosa	Canada	T.v.	Poinsettia/ A.H.B.D.	27.6	1.9/3d	0.3	30	Heinz & Parrella, 1994
E. formosa	Beltsville	B.t.	Poinsettia/ Lilo	27.6	8.0/3d	0.6	30	Heinz & Parrella, 1994
E. formosa	Beltsville	B.t.	Poinsettia/ A.H.B.D.	27.6	6.7/3d	0.6	30	Heinz & Parrella, 1994
E. formosa	Holland	T.v.	Poinsettia	22.5	59.2			Szabo et al., 1993
E. formosa	Holland	B.t.	Poinsettia	22.5	51.3			Szabo et al., 1993
E. eremicus	CA, USA	B.a.	cotton	28	23.1	5.6		Headrick et al., 1999
E. eremicus	Hawaii	B.t.	cotton	20	23.5	13.7	6	Powell & Bellows, 1992
E. eremicus	Hawaii	B.t.	cotton	29	41.1	48	7	Powell & Bellows, 1992
E. eremicus	Hawaii	B.t.	cucumber	20	43	23.8	10	Powell & Bellows, 1992
E. eremicus	Hawaii	B.t.	cucumber	29	47	37.1	5	Powell & Bellows, 1992
E. eremicus	Indio. CA	B.t.	cotton	20	31.4	25.8	7	Powell & Bellows, 1992
E. eremicus	Indio. CA	B.t.	cotton	29	20	15.1	5	Powell & Bellows, 1992
E. eremicus	Indio. CA	B.t.	cucumber	20	27.8	15.2	10	Powell & Bellows, 1992
E. eremicus	Indio. CA	B.t.	cucumber	29	35.9	18.1	11	Powell & Bellows, 1992
E. mundus	Jodan	B.t.	tomato	14	20		8	Sharaf & Batta, 1985
E. mundus	Jodan	B.t.	tomato	25	27.4		8	Sharaf & Batta, 1985
E. mundus	Egypt	B.t.	sweet potato	18	14.5		25	Tawfik et al., 1978
E. mundus	Egypt	B.a.	sweet potato	30	48		25	Tawfik et al., 1978

gence. *Eremocerus* species are autogenous as the adults already have a number of mature eggs in their ovaries at emergence (Headrick et al., 1999). This difference in egg maturation leads to different patterns in age-specific fecundity. *Encarsia* species have a low rate of parasitism at emergence, which increases gradually to a maximum level, which is maintained for some time and then decreases to zero during the last phase of adult life. Egg laying in *Encarsia* occurs during most of adult life. In *Eretmocerus* species, however, the maximum rate of parasitism occurs shortly after emergence and then quickly decreases. Here, most eggs were deposited by young females. The daily rates of parasitism recorded for *E. formosa* D at 25°C are similar to those found at 28°C by Enkegaard (1994), but were higher at 15 and 20°C than found by Enkegaard (Table 7). Bethke et al. (1991) found a higher fecundity for an *E. formosa* strain reared for 18 generations on *B. tabaci* than a strain reared on *T. vaporariorum* (Table 7), which suggests adaptation to the rearing host. *E. formosa* B had a higher fecundity than *E. formosa* D at 20°C according to our estimate, which might also be due to host adaptation. Heinz & Parrella (1994) record a higher rate of parasitism for *E. formosa* B than a Canadian *E. formosa* strain, although the rates were quite low for both strains. The estimated fecundity for *E. eremicus* at 20°C obtained in this study was slightly lower than Powell & Bellows (1992) record. Sharaf & Batta (1985) record a slightly higher fecundity for *E. mundus* at 14°C than we estimated at 15°C, and a slightly lower fecundity (27.4) than we estimated (42.5) at 25°C.

Epilogue

Our results show that *E. formosa* B has the shortest development time, the longest life-span in the presence of hosts, and the highest fecundity at temperatures lower than 20°C, which indicates that this parasitoid is a favourable candidate for *Bemisia* control at low temperatures. At temperatures higher than 20°C, the *Eretmocerus* species perform better. In Europe, biological control of *B. tabaci* in greenhouses is currently achieved by releasing two species of parasitoids: either *E. formosa* and *E. eremicus* (both parasitoids attack *Bemisia* and *Trialeurodes*) or *E. formosa* and *E. mundus* (*Encarsia* attacks both species of whitefly, *E. mundus* only attacks *Bemisia*) (Gerling et al., 2001). The mixture of *E. formosa* and *E. eremicus* has successfully been applied on a large scale for several years, e.g. on 500 ha of tomato and 1000 ha of pepper in Spain (Gerling et al., 2001). The use of two species is based on: (1) The *Eretmocerus* species are excellent parasitoids of *B. argentifolii*, and (2) they are effective at relatively high temperatures; (3) *E. formosa* is an excellent parasitoid of *T. vaporariorum*, which often occurs together with *B. argentifolii* in Mediterranean

Europe, and (4) this species is effective at relatively low temperatures.

There might, however, be another good reason for using a mix of parasitoid species. *Eretmocerus* species and *Amitus* species even more so, mainly parasitize hosts during the first days of their adult life (*Eretmocerus eremicus* up to 62/day, Soler, 2003; *Amitus bennetti* up to 99/day, Drost et al., 1999). *Encarsia* species produce few eggs per day (up to 12/day, Vet et al., 1981). The fast reproducing species like *Amitus* and *Eretmocerus* might be best suited for reducing high density whitefly populations, while the *Encarsia* species can be used to maintain whitefly population at low densities.

That a mix of parasitoid species with very different life histories might be very effective for whitefly control is true not only for greenhouses in the Mediterranean, but also for classical biological control, where, for example, proovigenic *Amitus* species were combined with synovigenic *Encarsia* species. *Aleurocanthus woglumi*, the citrus blackfly was successfully controlled in Mexico and the USA by introducing 4 species of parasitoids: at the start of the introductions and when host density was very high, the pro-ovigenic *Amitus hesperidum* was the dominant parasitoid, and aphelinids like *Encarsia opulenta* were rarely found. When host densities become low as a result of parasitism by *A. hesperidum*, *E. opulenta* become the dominant parasitoid (Flanders, 1969; Thompson et al, 1987; Dowell et al, 1981; Nguyen & Hamon, 1994).

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