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The parasite-host relationship between *Encarsia formosa* (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) XXXV. Life-history parameters of the greenhouse whitefly parasitoid *Encarsia formosa* as a function of host stage and temperature.

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Contents

Abstract

Life-history parameters of *Encarsia formosa*, parasitoid of the greenhouse whitefly are reviewed. The relationship immature development rate, immature mortality, sex ratio, longevity, pre-oviposition period, fecundity, oviposition frequency and temperature have been assessed by non-linear regression. Five mathematical models were fitted, the best being selected on the basis of comparison of coefficients of determination (r^2) and of curves by eye. Coefficients to describe life-history parameters and coefficients of variation (*cv*) among individuals of each life-history parameter are summarized. These will be used as inputs into a simulation model of the population dynamics of the parasitoid.

1. Introduction

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae) is an important pest on many crops. One of its natural enemies, the parasitoid *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) was used in biological control programs in the 1920s in England (Speyer, 1927) and subsequently populations were shipped to Australia, New Zealand, Canada and other countries (Tonnoir, 1937). The use of the parasitoid was discontinued in the fourties and fifties when chemical pesticides were used extensively. In the seventies when the first problems with pesticide resistance occurred, interest in the parasitoid increased again and introduction schemes were developed. *Encarsia formosa* is now used commercially in 90% of the tomato growing areas in the Netherlands and in many other countries (van Lenteren & Woets, 1988). As yet there is no explanation as to why the parasitoid cannot be applied successfully on some other crops.

A simulation model based on behavioural aspects of individuals in relation to host plant, pest insect and environment is being developed to find out more about the tritrophic system 'host plant-greenhouse whitefly-parasitoid'. One of the submodels simulates the population dynamics of *Encarsia formosa*. Inputs in this model are life-history parameters such as immature development, immature mortality, sex ratio, adult longevity, fecundity, oviposition frequency and pre-oviposition period.

Life-history parameters of *Encarsia formosa* and other whitefly parasitoids have been reviewed to some extent by Vet et al. (1980), Vet & van Lenteren (1981), van Lenteren & Hulspas-Jordaan (1983) and Artigues et al. (1987). *E. formosa* behaviour has been reviewed by Noldus & van Lenteren (1990). In this article a more comprehensive review has been given and the relationship between life-history parameters and temperature has been estimated by non-linear regression.

2. Material & Methods

Many studies have been done on *Encarsia formosa* as parasitoid of the greenhouse whitefly, *Trialeurodes vaporariorum*. In some experiments the cotton whitefly, *Bemisia tabaci*, was used as host (Lopez Avila, 1988). Life-history parameters of *Encarsia formosa* included in these studies were development rate of immature stages, percentage mortality of the immature stages, sex ratio, longevity, pre-oviposition period, fecundity and oviposition frequency. All collected data are given in Appendices A-F, in which the number of decimals have been copied from the original study. Most experiments have focused on the effect of temperature on these parameters with little attention to other environmental factors such as humidity and light. Host feeding of the parasitoid (hosts killed by predation) is not included in this study, because host feeding is not a life-history parameter.

Host and temperature are the most important factors influencing life-history parameters for many insect species. The relationship between life-history parameters and temperature was estimated by non-linear regression based on a least squares method of Marquard (Statgraphics User's Manual, version 4.0, 1989). For each parameter, several equations were used to describe the relationship to temperature. The best fitted curve was selected on the basis of the coefficient of determination (r^2, based on the corrected total sum of squares) and on visual comparison of the curves, which was necessary to check whether a curve was biologically realistic, particularly the tails.

Five mathematical equations were used, in which Y is the life-history parameter and X is the temperature (°C):

1) Linear: $Y = a + b*X$

2) Exponential: $Y = \exp(a + b*X)$

3) Third degree polynomial: $Y = a + b*X + c*X^2 + d*X^3$

4) Logan (et al., 1976): $Y = a * \{\exp(b*(X\text{-}d)) - \exp(b*(e\text{-}d)\text{-}(e\text{-}X)/c)\}$

5) Weibull (1951, in Campbell & Madden, 1990):
$$Y = c/b * ((X\text{-}a)/b)^{c-1} * \exp(-((X\text{-}a)/b)^c) * d$$

These models are described in van Roermund & van Lenteren (1992).

As four of these models descibe a non-linear relation, only life-history parameters measured at a constant temperature were used in the regression procedure. Experiments done at fluctuating temperature can only be used to validate the models in case hourly temperature data are available.

3. Results

3.1 Life-history parameters

Encarsia formosa females are black in colour with a yellow abdomen, and males are completely black. They feed on honey or honeydew, as well as on smaller whitefly larvae (host feeding). Like the whitefly, the adult is the only stage that can migrate to other leaves or plants. Females lay one egg per host preferably in the third, fourth and prepupal stages of the greenhouse whitefly (Nell et al., 1976). For terminology of whitefly stages (L1, L2, L3, L4, PP, PU), see van Roermund & van Lenteren (1992). The egg stage of the parasitoid lasts four days at 25 °C (Hooy, 1984; also Fransen, 1987), after which there are three larval stages. The immature whitefly is translucent and parasitization can only be observed after dissection. The *Encarsia* larva can pupate only when the immature whitefly reaches the fourth instar (Nechols & Tauber, 1977). After pupation of the parasitoid larva, the immature whitefly turns black and parasitism can easily be seen from the outward appearance of the whitefly. Most studies only distinguished two immature 'stages' of *Encarsia*. In this article these are referred to as the 'white' and 'black' stage.

3.1.1 Immature development rate

The development rate of each immature stage was calculated as the reciprocal of its duration. Only experiments done at a constant temperature were included. Linear regression of the development rate of the white and black stage yielded lower temperature thresholds of 10.7 and 10.2 °C respectively ($n = 53$ and 54 respectively, data not shown). Therefore, a mean value of 10.5 °C was taken as lower temperature threshold.

Osborne (1982) calculated a lower temperature threshold of 12.7 °C, based only on data from Burnett (1949). Madueke & Coaker (1984) using their own data ($n = 3$) calculated a lower temperature threshold of 13.0 °C. As data at super-optimal temperatures are lacking, the Logan model was used to estimate an upper lethal temperature. Gerling et al. (1986) showed for the cotton whitefly that this model estimated realistic tails at super-optimal temperatures. An upper lethal temperature of 38.3 °C for the total immature stage was estimated (with 10.5 °C as lower temperature threshold, $n = 80$). Therefore, 38 °C was taken for all stages, as was done for greenhouse whitefly immatures (Van Roermund & van Lenteren, 1992).

The Logan model resulted in slightly higher coefficients of determination (r^2) than the linear model. Regressions in which whitefly stages were separated yielded higher r^2, showing a difference in development rate of *E. formosa* depending on whitefly stage being parasitized. Similar findings were also obtained by Madueke (1979), Eijsackers (1969), Nechols & Tauber (1977), Arakawa (1982) and Di Pietro (1977).

Differences between development rate on whitefly L4 and prepupa as host were not clear, and because there were few experiments on these host stages, the two stages were combined. The relationships between development rate of white stage, black stage and total immature stage of *E. formosa* and temperature are shown in Tables 1 to 3 and in Figures 1 to 13.

Host plant effects on development rate of *E. formosa* cannot be examined, because of the shortage of data points at different host plants. The high r^2 in Tables 1-3 indicates that host plant effect can be disregarded. Jansen (1974) could not show a difference in development rate among host plants.

Data points of Eijsackers (1969) on L1 and L2 whitefly at 20°C were excluded from the regression because they differed greatly from other studies.

Table 1. Relationship between the development rate of *E. formosa* white stage in *T. vaporariorum* and temperature based on the Logan model where *a*, *b* and *c* are coefficients, *d* and *e* are the lower threshold and upper lethal temperature of 10.5 and 38 °C respectively, r^2 is the coefficient of determination, n_i and n_e are the number of data points included and excluded respectively.

Host stage	*a*	*b*	*c*	r^2	n_i	n_e
L1	0.0326	0.115	6.19	0.867	4	1
L2	0.0305	0.152	5.21	0.848	7	1
L3	0.0705	0.160	5.73	0.914	16	0
L4 + Prepupa	0.0571	0.142	6.01	0.943	11	0
Pupa	0.0249	0.164	4.77	0.976	4	0
All stages	0.0393	0.135	5.61	0.715	53	0

Table 2. Relationship between the development rate of *E. formosa* black stage in *T. vaporariorum* and temperature based on the Logan model where *a*, *b* and *c* are coefficients, *d* and *e* are the lower threshold and upper lethal temperature of 10.5 and 38 °C respectively, r^2 is the coefficient of determination, n_i and n_e are the number of data points included and excluded respectively.

Host stage	*a*	*b*	*c*	r^2	n_i	n_e
L1	0.0291	0.187	4.76	0.887	4	1
L2	0.0339	0.152	5.25	0.921	7	1
L3	0.0687	0.118	6.97	0.756	16	0
L4 + Prepupa	0.0643	0.133	6.35	0.869	11	0
Pupa	0.0346	0.153	5.33	0.894	4	0
All stages	0.0526	0.133	6.15	0.798	54	0

Table 3. Relationship between total immature development rate of *E. formosa* in *T. vaporariorum* and temperature based on the Logan model where *a*, *b* and *c* are coefficients, *d* and *e* are the lower threshold and upper lethal temperature of 10.5 and 38 °C respectively, r^2 is the coefficient of determination, n_i and n_e are the number of data points included and excluded respectively.

Host stage	*a*	*b*	*c*	r^2	n_i	n_e
L1	0.0222	0.157	5.69	0.977	5	1
L2	0.0230	0.159	5.52	0.960	8	1
L3	0.0302	0.135	6.28	0.896	17	0
L4 + Prepupa	0.0314	0.138	6.19	0.918	13	0
Pupa	0.0247	0.166	5.39	0.927	5	0
All stages	0.0188	0.133	5.56	0.809	80	0

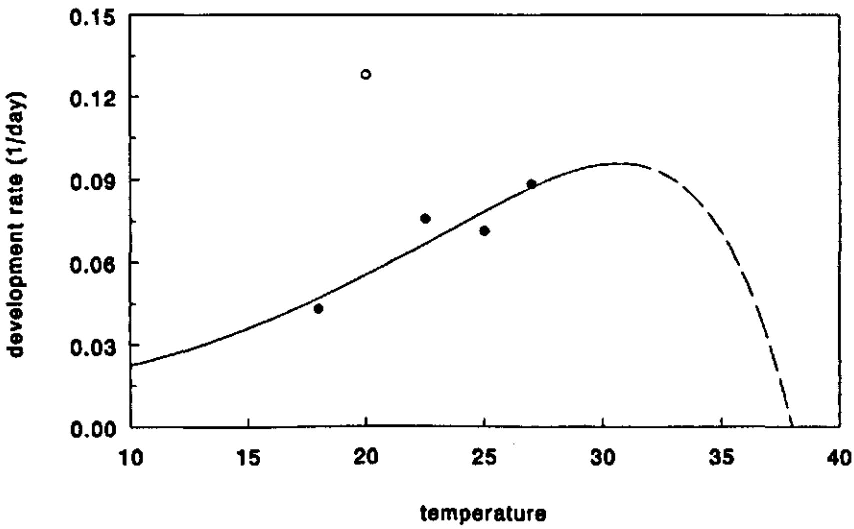

Fig. 1. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the first larval stage of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

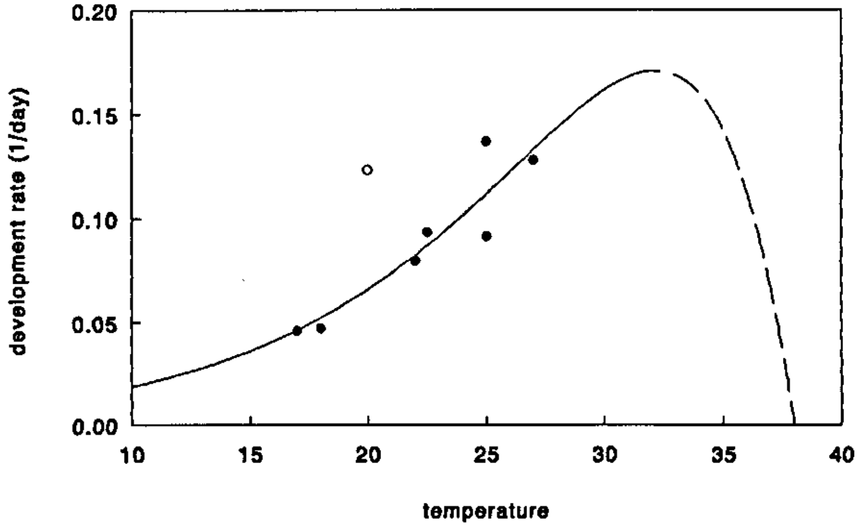

Fig. 2. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the second larval stage of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

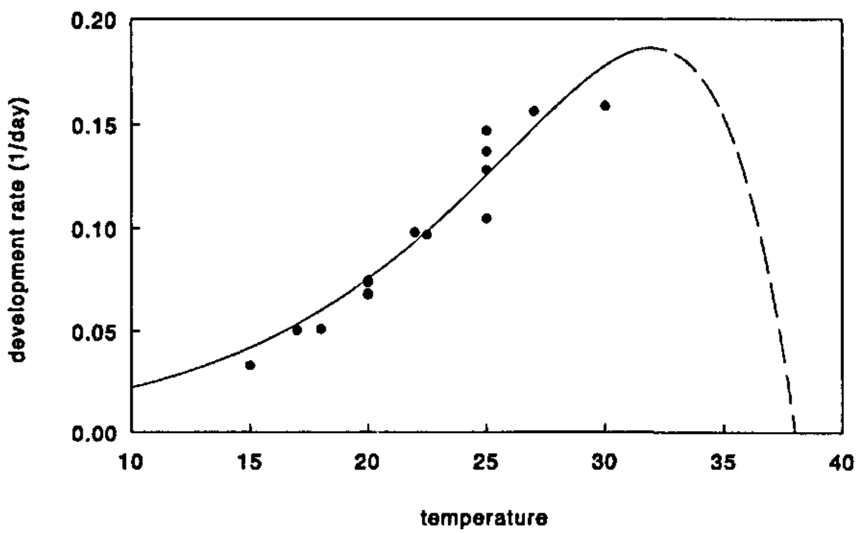

Fig. 3. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the third larval stage of the greenhouse whitefly and temperature.

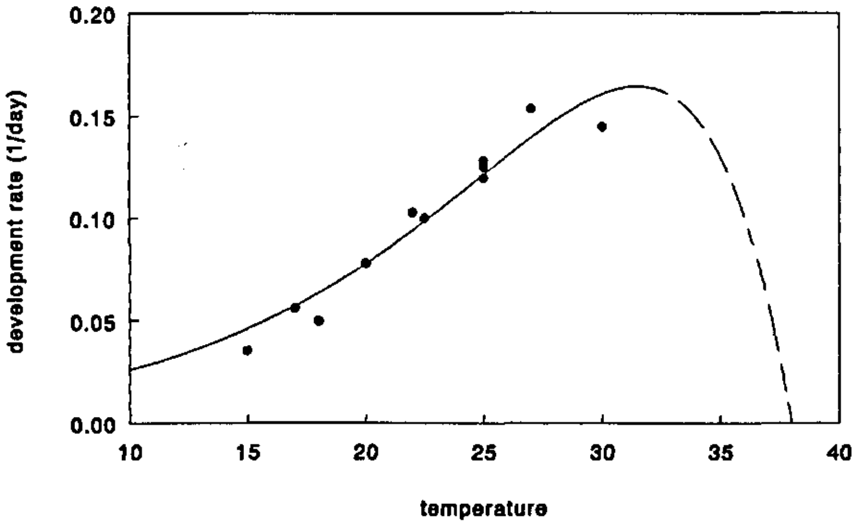

Fig. 4. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the fourth larval stage and prepupa of the greenhouse whitefly and temperature.

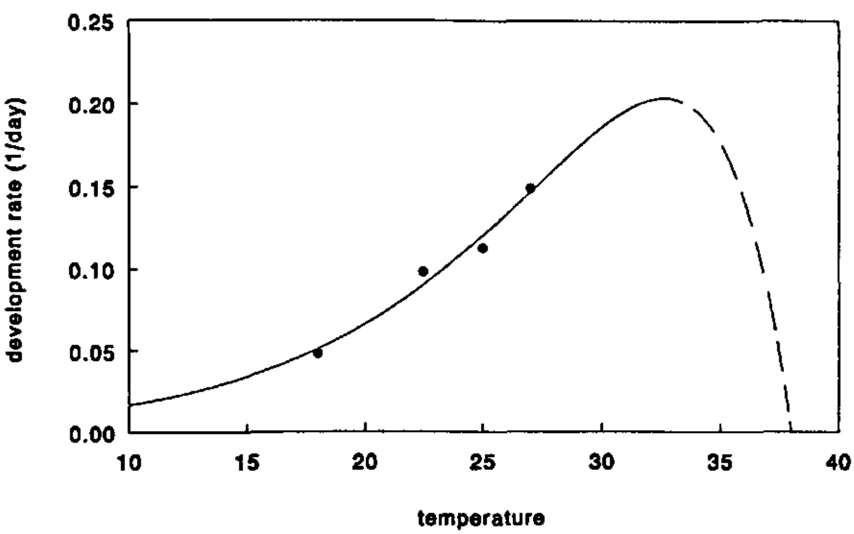

Fig. 5. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the pupa of the greenhouse whitefly and temperature.

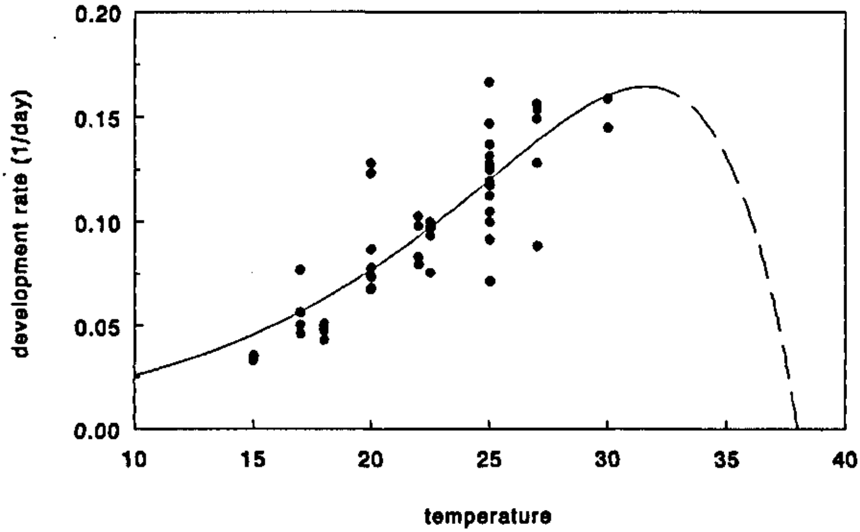

Fig. 6. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in all immature stages of the greenhouse whitefly and temperature.

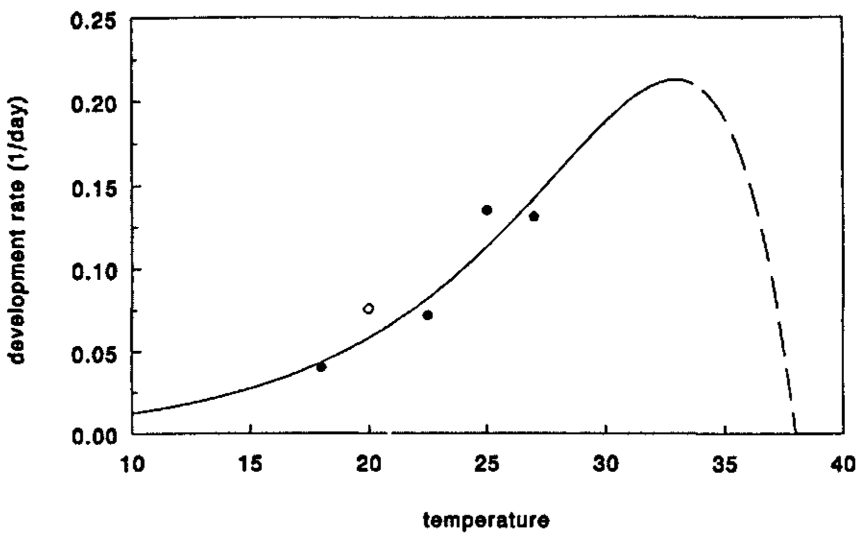

Fig. 7. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the first larval stage of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

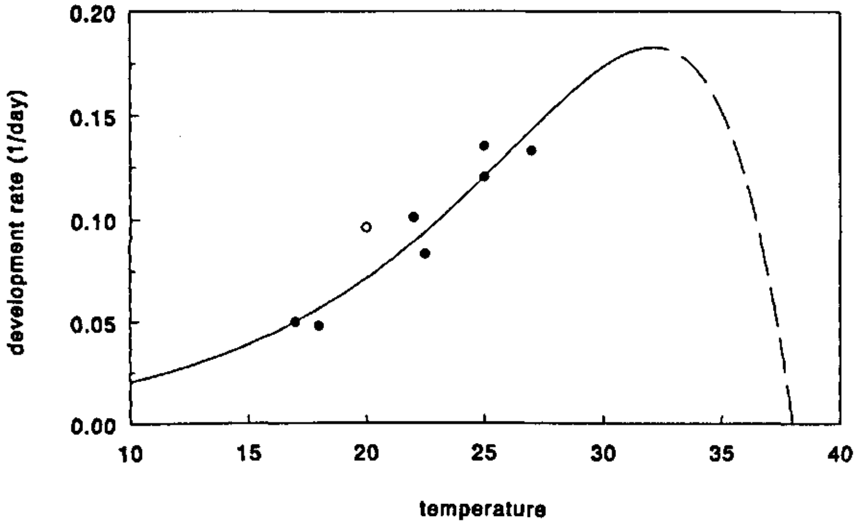

Fig. 8. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the second larval stage of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

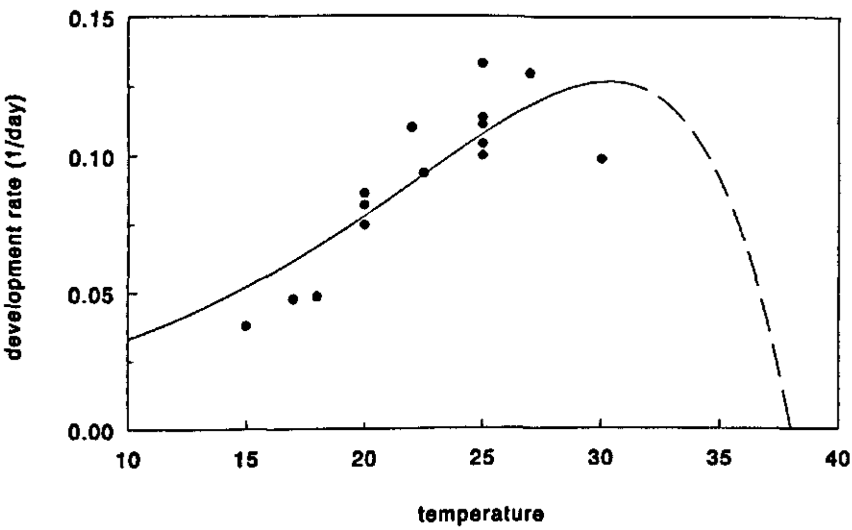

Fig. 9. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the third larval stage of the greenhouse whitefly and temperature.

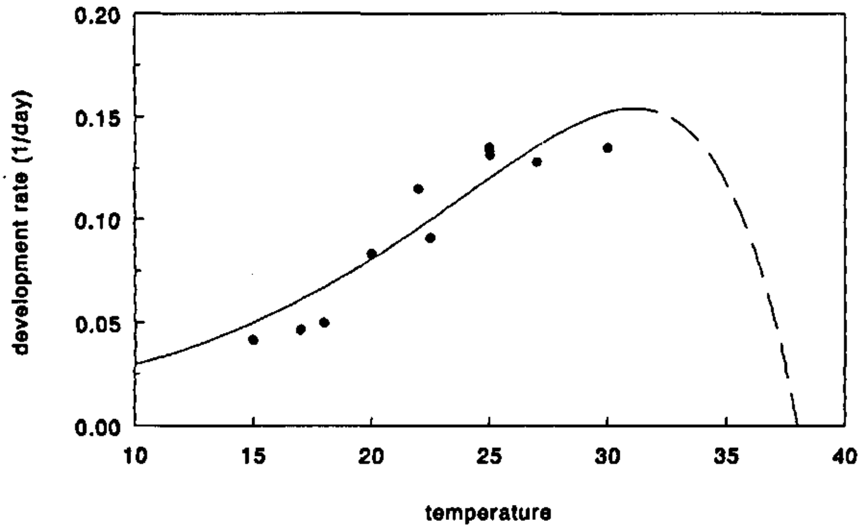

Fig. 10. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the fourth larval stage and prepupa of the greenhouse whitefly and temperature.

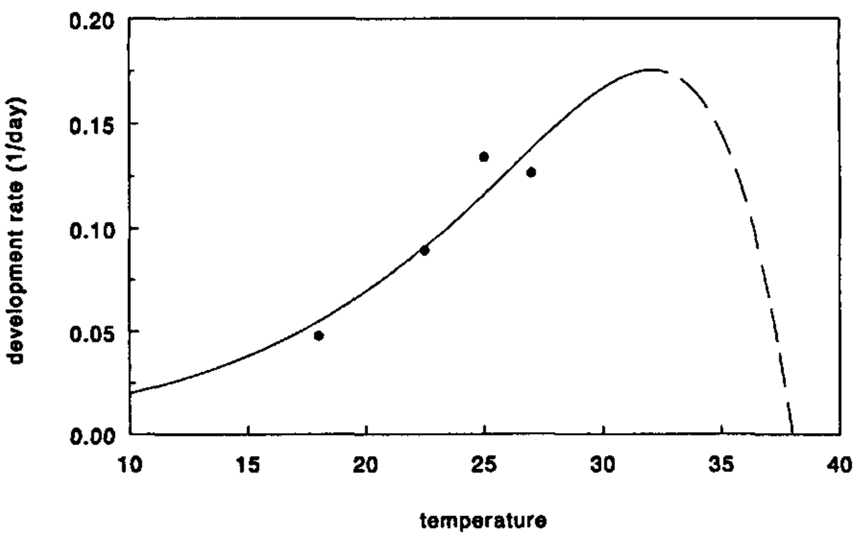

Fig. 11. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the pupa of the greenhouse whitefly and temperature.

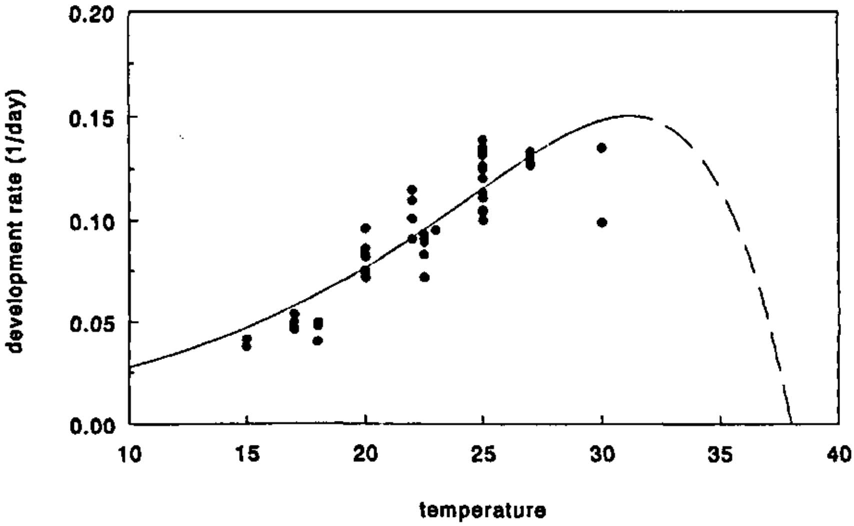

Fig. 12. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in all immature stages of the greenhouse whitefly and temperature.

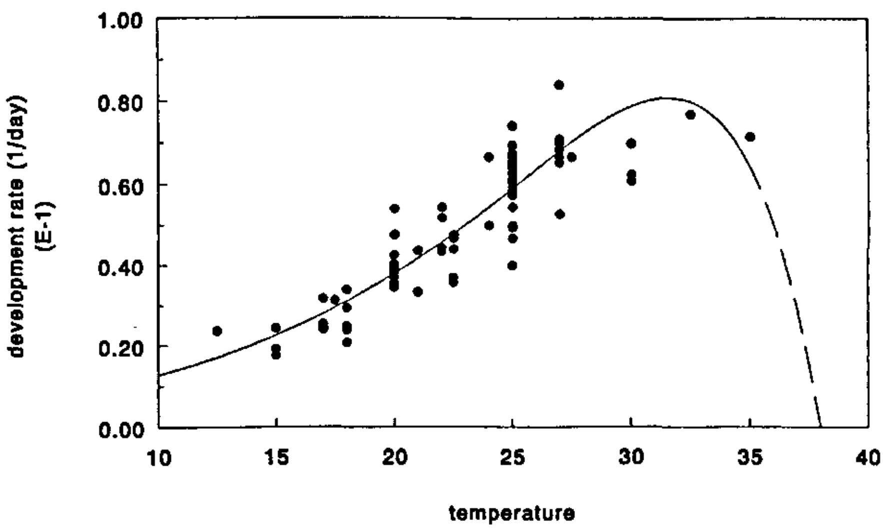

Fig. 13. Relationship between the development rate (1/day) of the total immature stage of *Encarsia formosa* in all immature stages of the greenhouse whitefly and temperature.

3.1.2 Immature mortality

Immature mortality was expressed as a percentage of the number of individuals entering a particular stage. It was only measured in experiments for the black stage and for the total immature stage. Mortality during the white or total immature stage is difficult to measure because it is not possible to see whether an egg has been laid from an intact whitefly larva. *E. formosa* does not always lay an egg during an oviposition posture, as was shown by Hulspas-Jordaan (1978) who found that 93% of the oviposition postures in unparasitized L3/L4 larvae led to the deposition of an egg. The 7% difference cannot be ascribed to mortality. In most studies the experimental set up to measure mortality during the white stage or total immature stage was not clearly described. However, Nechols & Tauber (1977) did explain how they derived mortality during the white stage from total mortality and mortality during black stage.

The relationship between percentage mortality and temperature was studied for the black stage and total immature stage of *E. formosa* on each whitefly stage separately and for all whitefly stages together. From visual inspection of the data, it was conluded that only the linear model should be tested. Eight regressions were possible, but none showed a significant relationship (data not shown). Therefore, it was concluded that percentage mortality was not related to temperature. Thus experiments conducted at fluctuating temperature could be used in the analysis.

Tables 4 and 5 give the mean percentage mortality during the black stage and during the total immature stage for each whitefly stage parasitized. Percentage mortality during the white stage derived from the total immature mortality and mortality during the black stage is presented in Table 6.

Table 4. Mean mortality during the black stage of *E. formosa* on *T. vaporariorum*, expressed as the percentage of the number entering the stage, *cv* is the coefficient of variation and n_i and n_e are the number of data points included and excluded respectively.

Host stage	Mean	*cv*	n_i	n_e
L1	7.4	0.137	3	0
L2	2.9	0.796	6	0
L3	3.3	0.672	5	0
L4	1.3	1.416	2	0
Prepupa	–	–	0	0
L2+L3+L4+Prepupa	3.4	0.737	19	4
Pupa	10.6	0.240	3	0
All stages	5.6	0.673	26	4

Table 5. Mean total immature mortality of *E. formosa* on *T. vaporariorum* expressed as percentage of number entering the egg stage, *cv* is the coefficient of variation and n_i and n_e are number of data points included and excluded respectively.

Host stage	Mean	*cv*	n_i	n_e
L1	41.9	1.154	2	0
L2	25.0	–	1	0
L3	11.8	0.151	2	0
L4	11.1	0.134	2	0
Prepupa	9.1	0.320	2	0
L3+L4+Prepupa	10.6	0.196	6	0
Pupa	26.5	0.134	2	0
All stages	21.7	0.895	12	0

Table 6. Calculated mean mortality during the white stage of *E. formosa* on *T. vaporariorum* expressed as percentage of the number entering the stage.

Host stage	Mean
L1	37.2
L2	22.3
L3+L4+Prepupa	7.5
Pupa	17.8
All stages	17.0

3.1.3 Sex ratio

Males are seldom observed. Females produce daughters parthenogenetically. Thus the sex ratio, expressed as the proportion of females of total offspring, is almost 1. As with the females, males are produced after oviposition in unparasitized hosts, unlike many other Aphelinidae, were it is thought that males are produced by parasitization of female parasitoid larvae (hyper-parasitization).

3.1.4 Longevity

Only experiments conducted at a constant temperature were used in examining the relationship between longevity and temperature. Female longevity has been studied at temperatures between 12 and 40°C. In most cases, hosts were offered during longevity tests. The exponential model yields the highest r^2 (Table 7). Extrapolation to lower temperatures with this model is unreliable; the best estimate of longevity is at 12°C. A higher longevity was observed in the absence of whitefly larvae and in the presence of honey or honeydew. Similar findings were also observed by Vet & van Lenteren (1981) and Gast & Kortenhoff (1983; also in van Lenteren et al., 1987). Results are given in Table 7 and Figures 14 and 15.

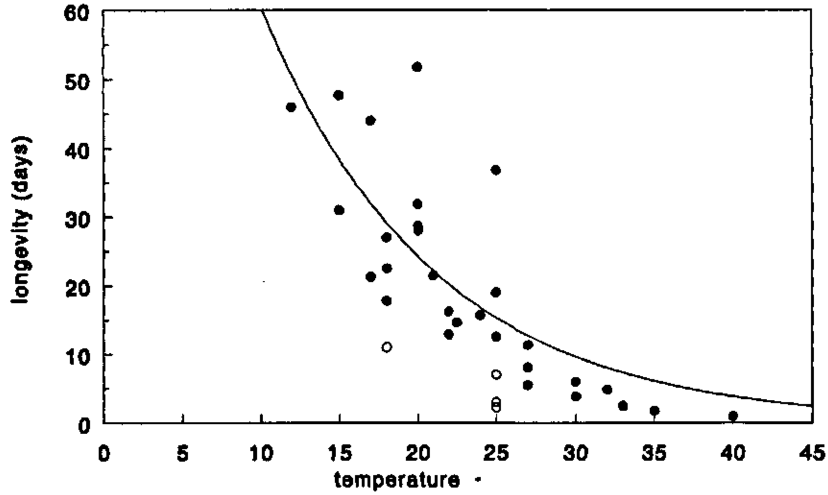

Fig. 14. Relationship between the longevity (day) of *Encarsia formosa* and temperature in the presence of greenhouse whitefly immatures. Open dots represent data points excluded from the regression.

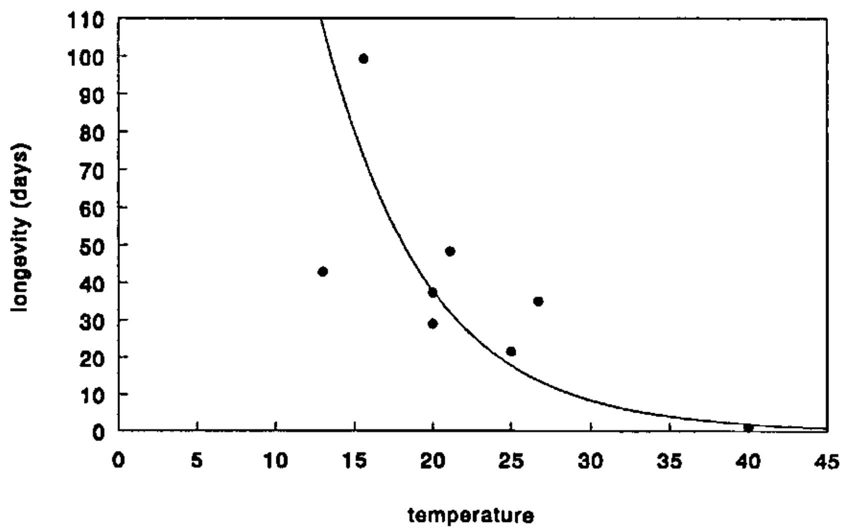

Fig. 15. Relationship between the longevity (day) of *Encarsia formosa* and temperature in the absence of greenhouse whitefly immatures and in the presence of honey or honeydew.

Table 7. Relationship between female longevity and temperature based on the exponential model where a and b are coefficients, r^2 is the coefficient of determination and n_i and n_e are number of data points included and excluded respectively.

Host	Honey/honeydew	a	b	r^2	n_i	n_e
Present	Present	5.03	-0.0921	0.635	29	5
Absent	Present	6.63	-0.150	0.813	8	0

Extreme situations were excluded from the regression, for example non-preferred whitefly stages (L2) offered (Di Pietro, 1977; Burnett, 1949) and at very low or high humidity (three times, Kajita, 1979). A longevity of 1 day at 40 °C when whitefly larvae were present (Kajita, 1979) was assumed also to be valid when whitefly larvae were absent.

There are few reports on male longevity. Gast & Kortenhoff (1983; also in van Lenteren et al., 1987) found an average male longevity at 13 °C of 53 days ($n=15$), which was 68% of female longevity.

The survival pattern of adults in relation to age has been studied by Burggraaf-van Nierop & van der Laan (1983; also in van der Laan et al., 1982) and Kajita (1989). Both studies report a linear decline in number during ageing, starting immediately at low temperatures (daily temperature range 18 to 7 °C) according to Burggraaf-van Nierop & van der Laan (1983) and starting after 20 days at 20 °C according to Kajita (1989). The survival can be reproduced by a (cumulative) normal distribution, because in both cases the mean longevity is halfway the decline.

3.1.5 Pre-oviposition period

Few data have been published on the pre-oviposition period of *E. formosa*. Only data between 18 and 30 °C (Burnett, 1949) were found. The exponential model described the best relation with temperature (Table 8 and Figure 16), but extrapolation of the pre-oviposition period to temperatures below 18 °C is unreliable. The most reliable estimate at low temperatures is the value calculated at 18 °C.

Table 8. Relationship between pre-oviposition period and temperature based on the exponential model where a and b are coefficients, r^2 is the coefficient of determination and n_i and n_e are the number of data points included and excluded respectively.

Host	a	b	r^2	n_i	n_e
All stages	5.56	-0.290	0.859	4	0

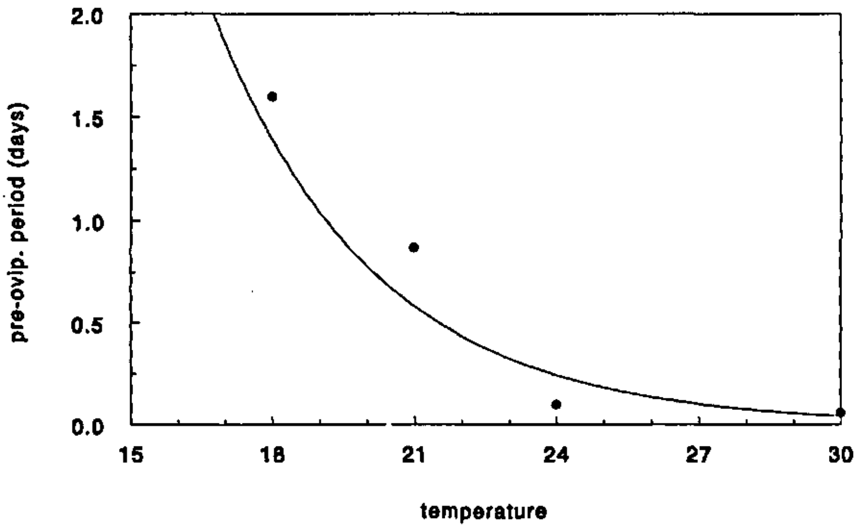

Fig. 16. Relationship between the pre-oviposition period (day) of *Encarsia formosa* and temperature in the presence of greenhouse whitefly immatures on tomato.

3.1.6 Fecundity

Data on total number of eggs laid by a female vary greatly. Data from experiments in which preferred whitefly stages were offered at a constant temperature were included. Data from less preferred whitefly L2 or L2/L3 larvae were excluded in order not to underestimate the fecundity. In most experiments, a mixture of all whitefly immature stages was offered, but numbers of preferred immatures per *E. formosa* female were not given. Direct observations indicated that about 10 eggs per day could be laid by a female if the whitefly number was not a limiting factor (Hulspas-Jordaan, 1978; Gast & Kortenhoff, 1983). Host feeding was not obligatory to maintain or enhance egg production or to promote longevity, as long as honey or honeydew was available (Gast & Kortenhoff, 1983; also in van Lenteren et al., 1987). Under these conditions the ratio between parasitization and host feeding was 5:1 (Arakawa, 1982; Gast & Kortenhoff, 1983; also in van Lenteren et al, 1987).

The lower threshold temperature for egg laying was 11.4°C (van der Schaal, 1980; also in van Lenteren & van der Schaal, 1981). Only from the experimental set up of Burnett (1949), was it clear that the numbers of available whitefly larvae were not sufficient (5 larvae per female per day), which resulted in underestimation of fecundity. Low fecundity was also reported by Woets (1972), Madueke (1977), Ibrahim (1975), Di Pietro (1977), Kajita (1979) and Kajita (1989). Kajita (1979) did experiments at a low (31 and 55%) and high (100%) relative humidity. The reasons for the low fecundity data could not be ascertained from the other studies.

The Weibull model gave the highest coefficient of determination and a biologically realistic description of the curve tails (Table 9 and Figure 17). The r^2 was very low when all data were used. A reliable curve of maximum fecundity could only be obtained when 30 of the total 38 data points from the studies were omitted. Data were included were data from Biggerstaf (in Parr et al., 1976), Arakawa (1982), van der Schaal (1980; also in van Lenteren & van der Schaal, 1981), Christochowitz & van der Fluit (1981; also in Christochowitz et al, 1981), Vet & van Lenteren (1981) and Gast & Kortenhoff (1983; also in van Lenteren et al, 1987). Data on fecundity at 35 and 40°C (at 70% RH) from Kajita (1979) were also included, because host density is unlikely to be a limiting factor at extreme temperatures. The low fecundities obtained in many experiments may be explained by the fact that it is difficult to handle the minute, delicate *E. formosa* females. Only with the utmost care do females survive daily transfer from one patch to another. We are confident that the fecundity data on which the fitted curve presented in Figure 17 do not overestimate egg production of *E. formosa*.

Table 9. Relationship between fecundity and temperature based on the Weibull model where *b*, *c* and *d* are coefficients, *a* is the lower threshold temperature of 11.4°C, r^2 is the coefficient of determination and n_i and n_e are the number of data points included and excluded respectively.

Host	*b*	*c*	*d*	r^2	n_i	n_e
L1-Pupa or L3-L4	12.9	2.48	1510	0.135	38	0
L1-Pupa or L3-L4	14.1	3.03	4780	0.963	8	30

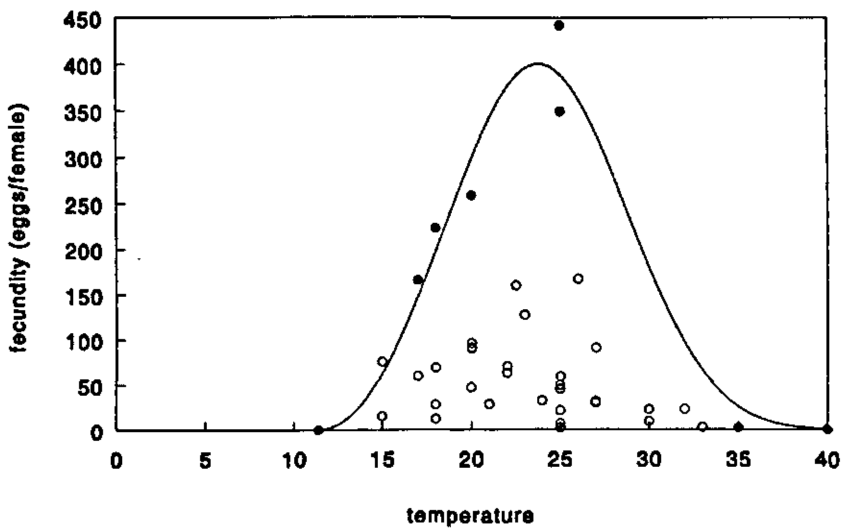

Fig. 17. Relationship between the fecundity (egg/female) of *Encarsia formosa* in greenhouse whitefly immatures of third larval stage or up and temperature. Open dots represent data points excluded from the regression.

3.1.7 Oviposition frequency

Data on the number of eggs laid per female per day vary greatly. The oviposition frequency measured over a few days only did not differ from the average oviposition frequency during a lifetime. The coefficient of determination (r^2) was the same (data not shown). Two reasons are given for this. Firstly, the observed wide variation in oviposition frequency among the various studies might have obscured differences. Secondly, oviposition frequency may change little with ageing. Our experience supports the second proposition. Thus data on oviposition frequency based on only a few days were not excluded.

Low oviposition frequencies were observed by Burnett (1949), Woets (1972b), Madueke (1977), Di Pietro (1977), Kajita (1979, 1983, 1989), Kajita & van Lenteren (1982). Burnett (1949) used too few whitefly. Hulspas-Jordaan (1978) found a low oviposition frequency when leaves were covered with large amounts of honeydew, hampering the parasitoid during searching. A reliable curve of maximum oviposition frequency was fitted when 26 of a total of 36 data points were omitted. Data points were included from Arakawa (1982), van der Schaal (1980; also in van Lenteren & van der Schaal, 1981), Christochowitz & van der Fluit (1981; also in Christochowitz et al., 1981), Vet & van Lenteren (1981) and Gast & Kortenhoff (1983; also in van Lenteren et al., 1987), Pravisani (1981), Hulspas-Jordaan (1978) and Fransen & van Montfort (1987). Data at 35 and 40°C (at 70% RH) from Kajita (1979) were included, because host density is unlikely to be a limiting factor at extreme temperatures. The Weibull model yielded the best fit; results are shown in Table 10 and Figure 18.

Table 10. Relationship between mean oviposition frequency and temperature based on the Weibull model where *b*, *c* and *d* are coefficients, *a* is the lower threshold temperature of 11.4°C, r^2 is the coefficient of determination and n_i and n_e are the number of data points included and excluded respectively.

Host	*b*	*c*	*d*	r^2	n_i	n_e
All stages	15.8	2.92	101	0.300	36	0
All stages	15.8	3.12	201	0.825	10	26

3.1.8 Change in oviposition frequency during ageing

Direct observation studies have shown that immediately after a pre-oviposition period, young *E. formosa* females can lay up to 10 eggs per day (Hulspas-Jordaan, 1978; Gast & Kortenhoff, 1983). This does not change over the subsequent few days, thus *E. formosa* has a very short maturation period in which the egg laying capacity increases, if at all.

Burggraaf-van Nierop & van der Laan (1983; also in van der Laan et al., 1982) have shown that oviposition frequency remains constant until the maximum longevity is reached. Arakawa (1982) and Kajita (1989) demonstrated a

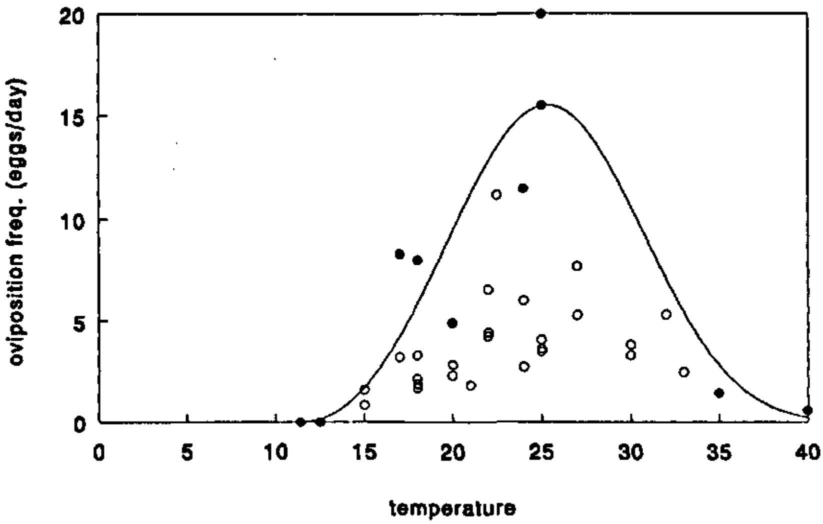

Fig. 18. Relationship between the oviposition frequency (egg/female/day) of *Encarsia formosa* in all immature stages of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

linear decline after about 20 days at 20-25 °C, but did not specify whether oviposition frequency was calculated per still living female or per introduced female. Comparison of data on longevity and oviposition frequency of Kajita (1989) suggest that oviposition frequency was calculated per introduced female, indicating that the decline is probably due to adult mortality instead of a reduction in oviposition frequency.

3.2 Variation among individuals

In the non-linear regression only mean values of the life-history parameters were taken from each study in order to estimate the coefficients to describe the relationship with temperature. As a measure of variation among individuals, the coefficient of variation (*cv*) can be calculated as the population standard deviation divided by the mean ($cv = sd_{n-1}$ /mean). These *cv* values (or relative dispersion) should be used as input parameters in simulation models when stochasticity is desired and normality can be assumed, as for developmental dispersion (Goudriaan & van Roermund, 1989; Schaub & Baumgärtner, 1989).

Mean *cv* values were calculated and are presented in Tables 11-13. Data were not included when the number of replicates was lower than the total number of parasitoids used in the experiments, if the observation had been excluded from the regression analysis or if the *cv* value was exceptional because it was measured at an extreme temperature. The latter two categories are given as the number of data points excluded (n_e).

Only experiments done at a constant temperature were included. If the relationship between *cv* value and temperature was not significant, then *cv* values obtained at fluctuating temperature were also used to calculate the mean *cv* value when all data were combined.

3.2.1 Immature development duration

cv values of immature development duration (which are almost equal to the *cv* values of the development rate) obtained at a constant temperature were analysed to assess a possible host stage effect. A Kruskall-Wallis test ($\alpha = 0.05$) did not show a host stage effect (data not shown). These data were then combined to study the relationship between *cv* and temperature. After visual inspection of the data, it was concluded that only the linear model should be tested. A significant linear relationship between *cv* of the white stage and temperature was found ($\alpha = 0.05$, $n = 28$), but the r^2 was very low (0.245). The relationship was not significant for the black stage and was just significant ($\alpha = 0.05$, $n = 56$) for the total immature stage, but the r^2 was very low (0.071).

In spite of a significant linear relationship, only 25 and 7% respectively of the variation in *cv* value can be explained by differences in temperature. Thus *cv* values were assumed not to relate to temperature. Therefore, data points measured at fluctuating temperature could also be included in the calculation of the mean *cv* value. Table 11 shows the mean *cv*s of the development duration of *E. formosa* in each whitefly stage and number of observations included (n_i). No observations were excluded ($n_e = 0$). No significant effect of host stage could be found (Kruskall-Wallis, $\alpha = 0.05$); the *cv* values are relatively low.

Table 11. Mean coefficient of variation (*cv*) of the immature development duration of *E. formosa* on each whitefly larval stage.

	White stage		Black stage		Total stage	
Host stage	*cv*	n_i	*cv*	n_i	*cv*	n_i
L1	0.10	4	0.19	1	0.083	6
L2	0.071	6	0.29	1	0.073	9
L3	0.077	6	0.10	1	0.10	11
L4+Prepupa	0.11	7	0.26	2	0.074	12
Pupa	0.070	4	0.06	1	0.058	5
All stages	0.084	30	0.17	7	0.083	60
Kruskall-Wallis	$p = 0.953$, $n = 27$		$p = 0.446$, $n = 6$		$p = 0.973$, $n = 43$	

Sequential dependence of development duration of individuals during successive stages, that is individuals developing slowly during one stage and compensating for this by developing faster in the next stage, can be studied if development duration of each individual is known. This was not done for *E. formosa*. If sequential dependence occurs, then the observed variance (sd^2) of the total immature development duration will be lower than when calculated from the variances of the separate stages. When data of Nechols & Tauber (1977a) were used to compare the observed variance of the total immature development duration to the calculated variance, no significant difference was found (Wilcoxon signed rank test, $p=0.402$, $n=6$ pairs). Thus sequential dependence appears to be absent.

3.2.2 Longevity and pre-oviposition period

Only data obtained when whitefly larvae were available for parasitization were used in asssessing the relationship between *cv* of longevity and temperature. After visual inspection of the data, it was concluded that the linear model only should be tested. No significant linear regression was found ($\alpha=0.05$, $n=18$). The mean *cv* values of longevity with and without the presence of whitefly larvae and honeydew are given in Table 12. No significant differences were found (Kruskall-Wallis, $\alpha=0.05$, $n=24$). Data on *cv* of pre-oviposition period have not been published.

Table 12. Mean coefficient of variation (*cv*) of longevity with and without the presence of whitefly larvae and honeydew and number of data points included (n_i) and excluded (n_e).

Host stage	*cv*	n_i	n_e
Larvae present, honeydew present	0.40	21	5
Larvae absent, honeydew present	0.37	3	0
Larvae absent, honeydew absent	0.30	1	0
All data	0.39	25	5
Kruskall-Wallis	$p=0.798$, $n=25$		

3.2.3 Fecundity and oviposition frequency

After visual inspection of the *cv* values, it was concluded that only the linear model should be tested. The regressions of *cv* of fecundity ($n=29$) and of oviposition frequency ($n=23$) on temperature were not significant ($\alpha=0.05$) when data at temperatures below 35 °C were included ($\alpha=0.05$, $n=29$ resp. 23). Only when data obtained at 35 and 40 °C were added (Kajita, 1979), the relationship between *cv* of fecundity and temperature was significant ($\alpha=0.05$, $n=31$), but r^2 was still very low (0.408). Thus it was concluded that *cv* of fecundity and oviposition frequency are not related to temperature under 'normal' circumstances.

Table 13 presents data on *cv* in two ways. Firstly, data used for the non-linear regression in Sections 3.1.6 and 3.1.7 were included except those of Kajita (1979) obtained at 35 and 40 °C. Secondly, data not used in the regression were included

Table 13. Mean coefficient of variation (*cv*) of fecundity and oviposition frequency based on (*n*) data included or excluded in the non-linear regression of Sections 3.1.6 and 3.1.7.

	Fecundity		Oviposition frequency	
Non-linear regression	*cv*	*n*	*cv*	*n*
Only included data	0.29	6	0.35	8
Only excluded data	0.45	25	0.39	19
All data	0.42	31	0.38	27
Kruskall-Wallis	p = 0.0643, $n = 31$		p = 0.490, $n = 27$	

except those of Kajita (1979) at low or high humidity. The majority of data points was excluded from the regression because they were low. Since both sets of data were not significantly different (Kruskall-Wallis test, $\alpha = 0.05$), the mean *cv* can be calculated from all the data.

4. Discussion

Most studies on the life-history parameters of *Encarsia formosa* have focused on their relationship to temperature and have given little attention to other environmental factors. Relative humidity and light intensity have in most case not been quantified accurately. Milliron (1940) found the highest percentage parasitation at 50-70% RH; Burnett (1948) noted that *E. formosa* avoids higher humidities; and Ekbom (1977) reported that biological control failed more often when *E. formosa* was released at high humidities. Kajita (1979) concluded that longevity and fecundity were reduced to about 14, 37 and 8% at a constant RH of 31, 51 and 100% respectively at 25 °C compared to the value of 19 days and 59.5 eggs at 74% RH.

McDevitt (1973, also in Scopes, 1973) observed maximum oviposition at light intensity above 7300 lux over a 16-hour period, and observed no oviposition at 4200 lux. However, we have frequently observed oviposition at about 100 lux. Van Alphen (1972) found no oviposition in the dark. Scopes (1973) reported a reduction in longevity at light intensities of 4200 lux over a 16-hour period, but did not give mean values. Hussey et al. (1976) did not obtain differences in percentage parasitation between shaded and unshaded plants. Burnett (1948) noted a higher dispersion in light.

As discussed for the greenhouse whitefly (van Roermund & van Lenteren, 1992), the method used to calculate the average value of each life-history parameter is not always clearly explained. It was not always clear whether longevity and development rate were calculated as mean or 50% point. Three calculation methods were used for oviposition frequency. Where ageing effects were studied, it was not always clear whether oviposition was expressed per still living female or per introduced female.

Immature mortality of *E. formosa* during the white stage and during the total immature development is difficult to quantify. Oviposition behaviour has firstly to be observed and then the number of observed oviposition postures corrected for postures not resulting in oviposition. This means that at first an experiment should be carried out to measure number of oviposition 'failures'. Hulspas-Jordaan (1978) measured 7% oviposition 'failures' when unparasitized L3 larvae were offered. In many of the studies on mortality, the procedure followed has not been specified.

The whitefly density was often not specified in studies on fecundity and oviposition frequency. Mean values differed greatly, as expressed by the low r^2 values in Tables 9 and 10. Oviposition frequency of the parasitoid does not depend on temperature alone, but also on the total number of encounters which is related to whitefly larval density and the searching capacity of the parasitoid. Direct observations of parasitization behaviour and checking for parasitoid eggs at the end of the experiment gives the most reliable assessment.

The coefficients which describe the life-history parameters in relation to temperature and sometimes host stage will be used as inputs in a simulation model of the population dynamics of the parasitoid *E. formosa* in a single whitefly colony. Population dynamics will be explained from integration of individual life-history parameters and their separate effects studied. A different approach will be followed for oviposition frequency, because it does not depend on temperature alone. Whitefly larval density, host plant effects and parasitoid behaviour have also to be taken into account. Thus the coefficients of Tables 9 and 10 will not be used in the simulation model.

The relationship between oviposition frequency (or number of hosts parasitized) and whitefly density is expressed by the functional response, which can be obtained empirically (e.g., Yano, 1987), but experiments often result in estimates for specific situations in which the parasitoid cannot always leave the colony freely. Thus generalizations cannot be made about large whitefly densities under natural conditions. Therefore, in our simulation model of the population dynamics of *E. formosa*, a functional response curve will be used as simulated by a separate model of the parasitization behaviour and not by using measured oviposition frequencies. This model also simulates the number of hosts killed by host feeding (van Roermund, in prep.).

The model of population dynamics of the parasitoid will be used as a submodel in a simulation model of the tritrophic interaction between host plant, greenhouse whitefly and parasitoid (van Roermund & van Lenteren, 1990). Knowledge of such complicated tritrophic systems is important in understanding whether biological control is feasible. It is essential to be able to predict under which conditions biological control will be successful, particularly when new crops and other environmental factors are involved.

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Appendix A1. Development duration (days) of the white stage of *E. formosa* in *T. vaporariorum*. *cv*, coefficient of variation; *n*, number of replicates; *n*(ef), total number of *Encarsia*'s (ef).

Host stage	Host plant	Cultivar	Temp. (°C)		Duration				Remarks	Reference
			Mean	Range	Mean	cv(%)	n	n(ef)		
L1	Bean	'Canadian Wonder'	18.0		23.2	1.6	40	40		Madueke, 1979
L1	Bean	'Canadian Wonder'	22.5		13.2	3.2	36	36		Madueke, 1979
L1	Bean	'Canadian Wonder'	27.0		11.3	13.5	32	32		Madueke, 1979
L1	Tomato	'Moneydor'	20.0		7.8	-	-	-		Eysackers, 1969
L1	Tobacco	'N.C.2326'	25.0		13.97	22.6	6	6		Nechols & Tauber, 1977a
L2	Bean	'Canadian Wonder'	18.0		21.1	1.3	31	31		Madueke, 1979
L2	Bean	'Canadian Wonder'	22.5		10.7	2.4	41	41		Madueke, 1979
L2	Bean	'Canadian Wonder'	27.0		7.8	5.2	34	34		Madueke, 1979
L2	Bean	-	17.0		21.66	6.2	92	92		Di Pietro, 1977
L2	Bean	-	22.0		12.54	2.7	197	197		Di Pietro, 1977
L2	Tomato	'Moneydor'	20.0		8.1	-	-	-		Eysackers, 1969
L2	Tomato	'Moneydor'	25.0		7.3	-	-	-		Eysackers, 1969
L2	Tobacco	'N.C.2326'	25.0		10.92	24.9	8	8		Nechols & Tauber, 1977a
L3	Bean	'Canadian Wonder'	18.0		19.6	2.4	45	45		Madueke, 1979
L3	Bean	'Canadian Wonder'	22.5		10.3	4.4	41	41		Madueke, 1979
L3	Bean	'Canadian Wonder'	27.0		6.4	7.9	40	40		Madueke, 1979
L3	Bean	-	17.0		19.80	3.8	125	125		Di Pietro, 1977
L3	Bean	-	22.0		10.18	2.6	152	152		Di Pietro, 1977
L3	Tomato	'Moneydor'	20.0		14.8	-	-	28	50%-point	Jansen, 1974
L3	Cucumber	'IVT 71-240'	20.0		14.6	-	-	76	50%-point	Jansen, 1974
L3	Sweet pepper	-	20.0		13.6	-	-	18	50%-point	Jansen, 1974
L3	Tomato	'Moneydor'	25.0		6.8	-	-	21	50%-point	Jansen, 1974
L3	Cucumber	'IVT 71-240'	25.0		6.8	-	-	6	50%-point	Jansen, 1974
L3	Sweet pepper	-	25.0		7.8	-	-	9	50%-point	Jansen, 1974
L3	Tomato	'Moneydor'	15.0		30.1	-	-	-		Eysackers, 1969
L3	Tomato	'Moneydor'	20.0		13.4	-	-	-		Eysackers, 1969
L3	Tomato	'Moneydor'	25.0		7.3	-	-	-		Eysackers, 1969
L3	Tomato	'Moneydor'	30.0		6.3	-	-	-		Eysackers, 1969
L3	Tobacco	'N.C.2326'	25.0		9.53	24.9	6	6		Nechols & Tauber, 1977a
L4	Bean	-	17.0		17.77	4.4	128	128		Di Pietro, 1977
L4	Bean	-	22.0		9.73	2.3	241	241		Di Pietro, 1977
L4	Tobacco	'N.C.2326'	25.0		8.01	31.8	8	8		Nechols & Tauber, 1977a
PP	Tobacco	'N.C.2326'	25.0		8.36	20.6	7	7		Nechols & Tauber, 1977a
PU	Bean	'Canadian Wonder'	18.0		20.8	2.0	35	35		Madueke, 1979
PU	Bean	'Canadian Wonder'	22.5		10.2	17.0	41	41		Madueke, 1979
PU	Bean	'Canadian Wonder'	27.0		6.7	6.4	37	37		Madueke, 1979
PU	Tobacco	'N.C.2326'	25.0		8.88	2.9	2	2		Nechols & Tauber, 1977a
L3+L4	Cucumber	'Gele Tros'	25.0		8.5	-	-	-	egg stage: 4.5 day	Hooy, 1984
L4+PP	Bean	'Canadian Wonder'	18.0		20.0	1.4	50	50		Madueke, 1979 Madueke & Coaker, 1984
L4+PP	Bean	'Canadian Wonder'	22.5		10.0	7.6	40	40		Madueke, 1979 Madueke & Coaker, 1984
L4+PP	Bean	'Canadian Wonder'	27.0		6.5	7.6	38	38		Madueke, 1979 Madueke & Coaker, 1984
L4+PP	Tomato	'Moneydor'	15.0		28.0	-	-	-		Eysackers, 1969
L4+PP	Tomato	'Moneydor'	20.0		12.8	-	-	-		Eysackers, 1969
L4+PP	Tomato	'Moneydor'	25.0		7.8	-	-	-		Eysackers, 1969

Appendix A1 (continued). Development duration (days) of the white stage of *E. formosa* in *T. vaporariorum*.

Host stage	Host plant	Cultivar	Temp. (°C)		Duration				Remarks	Reference
			Mean	Range	Mean	cv(%)	*n*	*n*(ef)		
L4+PP	Tomato	'Moneydor'	30.0		6.9	-	-	-		Eysackers, 1969
L3-PP	Sweet pepper	'Marike'	25.0		7.6	9.6	8	-	50%-point	van Bruggen, 1975
L3-PP	Tomato	'Moneydor'	25.0		7.9	12.6	8	-	50%-point	van Bruggen, 1975
L3-PP	Eggplant	'Claresse'	25.0		6	8.9	8	-	50%-point	van Bruggen, 1975
L3-PP	Cucumber	'IVT 71-240'	25.0		7.8	6.0	8	-	50%-point	van Bruggen, 1975
L3-PU	Bean	'Sarka'	20.0		11.5	7.0	66	66		Laska et al., 1980
L3-PU	Tree tobacco	-	17.0		13.0	-	-	-		Vet & van Lenteren, 1981
L1-PU	-	-	25.0		10	-	-	-		Woets, 1972b
L1-PU	Tree tobacco	-	22.0		12	-	-	-		Delorme et al., 1985
L3	Tomato	'Moneydor'	23.1	25/20	12.8	-	-	50	50%-point	Jansen, 1974
L3	Cucumber	'IVT 71-240'	23.1	25/20	11.7	-	-	43	50%-point	Jansen, 1974
L3	Sweet pepper	-	23.1	25/20	14.0	-	-	3	50%-point	Jansen, 1974
L3+L4	Tomato	'Tropic'	24.0	34/14	7.7	7.0	480	480	temp.sum measured	Osborne, 1982
L3+L4	Tomato	'Moneydor'	11.4	18/7	17.2	4.4	21	21		Christochowitz & van der Fluit, 1981
										Christochowitz et al., 1981
L2	Tomato	-	26.7	30/20	11.5	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	9.7	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	17.9	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	9.7	-	-	-	ef density medium	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	10.1	-	-	-	ef density high	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	16.9	-	-	-	ef density medium	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	17.6	-	-	-	ef density high	Yano, 1988
PP+PU	Tomato	-	26.7	30/20	9.7	-	-	-	ef density low	Yano, 1988
-	-	-	22.5	24/21	9	-	-	-		Agekyan, 1981
-	-	-	-		11	-	-	-		Milliron, 1940
-	Tomato	-	-		16.5	-	-	-		Speyer, 1927

Appendix A2. Development duration (days) of the black stage of *E. formosa* in *T. vaporariorum*. *cv*, coefficient of variation; *n*, number of replicates; *n*(ef), total number of *Encarsia*'s (ef).

Host stage	Host plant	Cultivar	Temp. (°C)		Duration				Remarks	Reference
			Mean	Range	Mean	cv(%)	n	n(ef)		
L1	Bean	'Canadian Wonder'	18.0		24.7	-	-	-		Madueke, 1979
L1	Bean	'Canadian Wonder'	22.5		13.9	-	-	-		Madueke, 1979
L1	Bean	'Canadian Wonder'	27.0		7.6	-	-	-		Madueke, 1979
L1	Tomato	'Moneydor'	20.0		13.2	-	-	-		Eysackers, 1969
L1	Tobacco	'N.C.2326'	25.0		7.38	19.3	6	6		Nechols & Tauber, 1977a
L2	Bean	'Canadian Wonder'	18.0		20.8	-	-	-		Madueke, 1979
L2	Bean	'Canadian Wonder'	22.5		12.0	-	-	-		Madueke, 1979
L2	Bean	'Canadian Wonder'	27.0		7.5	-	-	-		Madueke, 1979
L2	Bean	-	17.0		20.0	-	-	-		Di Pietro, 1977
L2	Bean	-	22.0		9.9	-	-	-		Di Pietro, 1977
L2	Tomato	'Moneydor'	20.0		10.4	-	-	-		Eysackers, 1969
L2	Tomato	'Moneydor'	25.0		8.3	-	-	-		Eysackers, 1969
L2	Tobacco	'N.C.2326'	25.0		7.39	28.7	8	8		Nechols & Tauber, 1977a
L3	Bean	'Canadian Wonder'	18.0		20.6	-	-	-		Madueke, 1979
L3	Bean	'Canadian Wonder'	22.5		10.7	-	-	-		Madueke, 1979
L3	Bean	'Canadian Wonder'	27.0		7.7	-	-	-		Madueke, 1979
L3	Bean	-	17.0		21.0	-	-	-		Di Pietro, 1977
L3	Bean	-	22.0		9.1	-	-	-		Di Pietro, 1977
L3	Tomato	'Moneydor'	20.0		13.4	-	-	28	50%-point	Jansen, 1974
L3	Cucumber	'IVT 71-240'	20.0		11.6	-	-	76	50%-point	Jansen, 1974
L3	Sweet pepper	-	20.0		13.4	-	-	18	50%-point	Jansen, 1974
L3	Tomato	'Moneydor'	25.0		8.8	-	-	21	50%-point	Jansen, 1974
L3	Cucumber	'IVT 71-240'	25.0		9.6	-	-	6	50%-point	Jansen, 1974
L3	Sweet pepper	-	25.0		9.0	-	-	9	50%-point	Jansen, 1974
L3	Tomato	'Moneydor'	15.0		26.3	-	-	-		Eysackers, 1969
L3	Tomato	'Moneydor'	20.0		12.2	-	-	-		Eysackers, 1969
L3	Tomato	'Moneydor'	25.0		10.0	-	-	-		Eysackers, 1969
L3	Tomato	'Moneydor'	30.0		10.1	-	-	-		Eysackers, 1969
L3	Tobacco	'N.C.2326'	25.0		7.51	9.5	6	6		Nechols & Tauber, 1977a
L4	Bean	-	17.0		21.5	-	-	-		Di Pietro, 1977
L4	Bean	-	22.0		8.7	-	-	-		Di Pietro, 1977
L4	Tobacco	'N.C.2326'	25.0		7.48	33.3	8	8		Nechols & Tauber, 1977a
PP	Tobacco	'N.C.2326'	25.0		7.60	18.1	7	7		Nechols & Tauber, 1977a
PU	Bean	'Canadian Wonder'	18.0		20.8	-	-	-		Madueke, 1979
PU	Bean	'Canadian Wonder'	22.5		11.2	-	-	-		Madueke, 1979
PU	Bean	'Canadian Wonder'	27.0		7.9	-	-	-		Madueke, 1979
PU	Tobacco	'N.C.2326'	25.0		7.46	5.7	2	2		Nechols & Tauber, 1977a
L3+L4	Cucumber	'Gele Tros'	25.0		8.0	-	-	-		Hooy, 1984
L4+PP	Bean	'Canadian Wonder'	18.0		20.1	-	-	-		Madueke, 1979 Madueke & Coaker, 1984
L4+PP	Bean	'Canadian Wonder'	22.5		11.0	-	-	-		Madueke, 1979 Madueke & Coaker, 1984
L4+PP	Bean	'Canadian Wonder'	27.0		7.8	-	-	-		Madueke, 1979 Madueke & Coaker, 1984
L4+PP	Tomato	'Moneydor'	15.0		24.0	-	-	-		Eysackers, 1969
L4+PP	Tomato	'Moneydor'	20.0		12.0	-	-	-		Eysackers, 1969
L4+PP	Tomato	'Moneydor'	25.0		7.4	-	-	-		Eysackers, 1969

Appendix A2 (continued). Development duration (days) of the black stage of *E. formosa* in *T. vaporariorum*.

Host stage	Host plant	Cultivar	Temp. (°C)		Duration				Remarks	Reference
			Mean	Range	Mean	cv(%)	n	n(ef)		
L4+PP	Tomato	'Moneydor'	30.0		7.4	-	-	-		Eysackers, 1969
L3-PP	Sweet pepper	'Marike'	25.0		7.2	-	8	57	50%-point	van Bruggen, 1975
L3-PP	Tomato	'Moneydor'	25.0		7.9	-	8	837	50%-point	van Bruggen, 1975
L3-PP	Eggplant	'Claresse'	25.0		9.5	-	8	1691	50%-point	van Bruggen, 1975
L3-PP	Cucumber	'IVT 71-240'	25.0		7.6	-	8	1436	50%-point	van Bruggen, 1975
L3-PU	Bean	'Sarka'	20.0		13.9	-	-	-		Laska et al., 1980
L3-PU	Tree tobacco	-	17.0		18.6	-	-	-		Vet & van Lenteren, 1981
L1-PU	-	-	25.0		10	-	-	-		Woets, 1972b
L1-PU	Tree tobacco	-	22.0		11	-	-	-		Delorme et al., 1985
-	Tomato	-	23.0		10.5	-	-	-		Keymeulen & Degheele, 1977
L3	Tomato	'Moneydor'	23.1	25/20	11.6	-	-	50	50%-point	Jansen, 1974
L3	Cucumber	'IVT 71-240'	23.1	25/20	8.9	-	-	43	50%-point	Jansen, 1974
L3	Sweet pepper	-	23.1	25/20	11.0	-	-	3	50%-point	Jansen, 1974
L3+L4	Tomato	'Tropic'	24.0	28/22	9.0	3.9	70	70	temp.sum measured	Osborne, 1982
L3+L4	Tomato	'Moneydor'	11.4	18/7	22.3	-	-	-		Christochowitz & van der Fluit, 1981
										Christochowitz et al., 1981
L2	Tomato	-	26.7	30/20	7.5	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	8.9	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	17.1	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	8.9	-	-	-	ef density medium	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	9.7	-	-	-	ef density high	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	19.1	-	-	-	ef density medium	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	20.6	-	-	-	ef density high	Yano, 1988
PP+PU	Tomato	-	26.7	30/20	10.3	-	-	-	ef density low	Yano, 1988
-	-	-	22.5	24/21	8.5	-	-	-		Agekyan, 1981
-	Tomato	-	16.0	19/13	19.5	-	-	-		Keymeulen & Degheele, 1977
-	-	-	-		17	-	-	-		Milliron, 1940

Appendix A3. Total immature development duration (days) of *E. formosa* in *T. vaporariorum*. *cv*, coefficient of variation; *n*, number of replicates; *n*(ef), total number of *Encarsia*'s (ef).

Host stage	Host plant	Cultivar	Temp. (°C) Mean	Temp. (°C) Range	Duration Mean	Duration cv(%)	Duration n	Duration n(ef)	Remarks	Reference
L1	Bean	'Canadian Wonder'	18.0		47.9	2.4	37	37		Madueke, 1979
L1	Bean	'Canadian Wonder'	22.5		27.1	6.6	33	33		Madueke, 1979
L1	Bean	'Canadian Wonder'	27.0		18.9	8.4	30	30		Madueke, 1979
L1	Tomato	'Moneydor'	20.0		21.0	3.4	-	-		Eysackers, 1969
L1	Tobacco	'N.C.2326'	25.0		21.35	18.6	6	6		Nechols & Tauber, 1977a
L1	Tobacco	-	25.0		20.2	10.3	12	12		Arakawa, 1982
L2	Bean	'Canadian Wonder'	18.0		41.9	1.4	30	30		Madueke, 1979
L2	Bean	'Canadian Wonder'	22.5		22.7	5.0	39	39		Madueke, 1979
L2	Bean	'Canadian Wonder'	27.0		15.3	5.6	32	32		Madueke, 1979
L2	Bean	-	17.0		41.63	3.8	92	92		Di Pietro, 1977
L2	Bean	-	22.0		22.49	3.2	195	195		Di Pietro, 1977
L2	Tomato	'Moneydor'	20.0		18.5	7.2	-	-		Eysackers, 1969
L2	Tomato	'Moneydor'	25.0		15.6	5.5	-	-		Eysackers, 1969
L2	Tobacco	'N.C.2326'	25.0		18.31	20.7	8	8		Nechols & Tauber, 1977a
L2	Tobacco	-	25.0		17.4	13.4	15	15		Arakawa, 1982
L3	Bean	'Canadian Wonder'	18.0		40.2	2.9	43	43		Madueke, 1979
L3	Bean	'Canadian Wonder'	22.5		21.0	6.2	39	39		Madueke, 1979
L3	Bean	'Canadian Wonder'	27.0		14.1	2.2	38	38		Madueke, 1979
L3	Bean	-	17.0		40.8	3.8	125	125		Di Pietro, 1977
L3	Bean	-	22.0		19.28	3.0	149	149		Di Pietro, 1977
L3	Tomato	'Moneydor'	20.0		28.2	-	-	28	50%-point	Jansen, 1974
L3	Cucumber	'IVT 71-240'	20.0		26.2	-	-	76	50%-point	Jansen, 1974
L3	Sweet pepper	-	20.0		27.0	-	-	18	50%-point	Jansen, 1974
L3	Tomato	'Moneydor'	25.0		15.6	-	-	21	50%-point	Jansen, 1974
L3	Cucumber	'IVT 71-240'	25.0		16.4	-	-	6	50%-point	Jansen, 1974
L3	Sweet pepper	-	25.0		16.8	-	-	9	50%-point	Jansen, 1974
L3	Tomato	'Moneydor'	15.0		56.4	5.0	-	-		Eysackers, 1969
L3	Tomato	'Moneydor'	20.0		25.6	34.6	-	-		Eysackers, 1969
L3	Tomato	'Moneydor'	25.0		17.3	7.5	-	-		Eysackers, 1969
L3	Tomato	'Moneydor'	30.0		16.4	17.3	-	-		Eysackers, 1969
L3	Tobacco	'N.C.2326'	25.0		17.04	17.1	6	6		Nechols & Tauber, 1977a
L3	Tobacco	-	25.0		15.9	11.0	34	34		Arakawa, 1982
L4	Bean	-	17.0		39.31	2.7	128	128		Di Pietro, 1977
L4	Bean	-	22.0		18.38	2.2	235	235		Di Pietro, 1977
L4	Tobacco	'N.C.2326'	25.0		15.49	11.0	8	8		Nechols & Tauber, 1977a
L4	Tobacco	-	25.0		15.0	10.2	58	58		Arakawa, 1982
PP	Tobacco	'N.C.2326'	25.0		15.96	14.8	7	7		Nechols & Tauber, 1977a
PP	Tobacco	-	25.0		15.0	7.5	32	32		Arakawa, 1982
PU	Bean	'Canadian Wonder'	18.0		41.6	3.0	32	32		Madueke, 1979
PU	Bean	'Canadian Wonder'	22.5		21.4	6.5	37	37		Madueke, 1979
PU	Bean	'Canadian Wonder'	27.0		14.6	7.0	32	32		Madueke, 1979
PU	Tobacco	'N.C.2326'	25.0		16.30	3.6	2	2		Nechols & Tauber, 1977a
PU	Tobacco	-	25.0		14.4	9.1	19	19		Arakawa, 1982
L2+L3	Tomato	'Selandia'	18.0		34	14.7	-	-		Stenseth, 1975 Stenseth, 1976 Stenseth, 1977
L2+L3	Tomato	'Selandia'	21.0		30	16.7	-	-		Stenseth, 1975

Appendix A3 (continued). Total immature development duration (days) of *E. formosa* in *T. vaporariorum*.

Host stage	Host plant	Cultivar	Temp. (°C) Mean	Temp. (°C) Range	Duration Mean	Duration cv(%)	Duration n	Duration n(ef)	Remarks	Reference
										Stenseth, 1976
										Stenseth, 1977
L2+L3	Tomato	'Selandia'	24.0		20	20.0	-	-		Stenseth, 1975
										Stenseth, 1976
										Stenseth, 1977
L2+L3	Tomato	'Selandia'	27.0		15	13.3	-	-		Stenseth, 1975
										Stenseth, 1976
										Stenseth, 1977
L3+L4	Tomato	'Bonnie Best'	18.0		29.5	3.1	70	70		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	21.0		22.9	5.8	177	177		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	24.0		15	9.4	69	69		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	27.0		11.9	4.9	134	134		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	30.0		10	11.2	35	35		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	12.7		>>	-	-	-	from Burnett, 1949	Osborne, 1982
L3+L4	Cucumber	'Gele Tros'	25.0		16.5	-	-	-	egg stage: 4.5 day	Hooy, 1984
L4+PP	Bean	'Canadian Wonder'	18.0		40.1	5.4	46	46		Madueke, 1979
										Madueke & Coaker, 1984
L4+PP	Bean	'Canadian Wonder'	22.5		21.0	7.2	37	37		Madueke, 1979
										Madueke & Coaker, 1984
L4+PP	Bean	'Canadian Wonder'	27.0		14.3	3.3	35	35		Madueke, 1979
										Madueke & Coaker, 1984
L4+PP	Tomato	'Moneydor'	15.0		52.0	-	-	-		Eysackers, 1969
L4+PP	Tomato	'Moneydor'	20.0		24.8	5.3	-	-		Eysackers, 1969
L4+PP	Tomato	'Moneydor'	25.0		15.2	14.1	-	-		Eysackers, 1969
L4+PP	Tomato	'Moneydor'	30.0		14.3	5.2	-	-		Eysackers, 1969
PP+PU	Bean	-	20.0		23.5	3.4	15	15		Kajita, unpubl.
PP+PU	Bean	-	25.0		13.5	2.6	15	15		Kajita, unpubl.
L3-PP	Sweet pepper	'Marike'	25.0		14.8	2.5	8	57	50%-point	van Bruggen, 1975
L3-PP	Tomato	'Moneydor'	25.0		15.8	6.1	8	837	50%-point	van Bruggen, 1975
L3-PP	Eggplant	'Claresse'	25.0		15.5	3.5	8	1691	50%-point	van Bruggen, 1975
L3-PP	Cucumber	'IVT 71-240'	25.0		15.4	2.1	8	1436	50%-point	van Bruggen, 1975
L3-PU	Bean	'Sarka'	20.0		25.4	6.7	66	66		Laska et al., 1980
L3-PU	Tree tobacco	-	17.0		31.6	5.7	786	786		Vet & van Lenteren, 1981
L2-PU	Bean	-	12.5		42.3	-	3	-		Pravisani, 1981
L2-PU	Bean	-	15.0		41	-	3	-		Pravisani, 1981
L2-PU	Bean	-	17.5		32	-	1	-		Pravisani, 1981
L2-PU	Bean	-	20.0		29	-	2	-		Pravisani, 1981
L2-PU	Bean	-	22.5		28	-	2	-		Pravisani, 1981
L2-PU	Bean	-	25.0		25	-	3	-		Pravisani, 1981
L2-PU	Bean	-	27.5		15	-	3	-		Pravisani, 1981
L2-PU	Bean	-	30.0		16	-	3	-		Pravisani, 1981
L2-PU	Bean	-	32.5		13	-	2	-		Pravisani, 1981
L2-PU	Bean	-	35.0		14	-	3	-		Pravisani, 1981
L1-PU	-	-	25.0		20	-	-	-		Woets, 1972b
L1-PU	Tree tobacco	-	22.0		23	-	-	-		Delorme et al., 1985
L2+L3	Tomato	'Selandia'	22.0	24/18	26	15.4	-	-		Stenseth, 1975
										Stenseth, 1976

Appendix A3 (continued). Total immature development duration (days) of *E. formosa* in *T. vaporariorum*.

Host stage	Host plant	Cultivar	Temp. (°C)		Duration				Remarks	Reference
			Mean	Range	Mean	cv(%)	*n*	*n*(ef)		
										Stenseth, 1977
L2+L3	Tomato	'Selandia'	25.0	27/21	17	11.8	-	-		Stenseth, 1975
										Stenseth, 1976
										Stenseth, 1977
L3	Tomato	'Moneydor'	23.1	25/20	24.4	-	-	50	50%-point	Jansen, 1974
L3	Cucumber	'IVT 71-240'	23.1	25/20	20.6	-	-	43	50%-point	Jansen, 1974
L3	Sweet pepper	-	23.1	25/20	25.0	-	-	3	50%-point	Jansen, 1974
L3+L4	Tomato	'Tropic'	24.0	34/14	16.7	5.8	239	239	temp.sum measured	Osborne, 1982
L3+L4	Tomato	'Moneydor'	11.4	18/7	39.5	1.7	21	21		Christochowitz & van der Fluit, 1981
										Christochowitz et al., 1981
L2	Tomato	-	26.7	30/20	19.0	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	18.6	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	35.0	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	18.6	-	-	-	ef density medium	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	19.8	-	-	-	ef density high	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	36.0	-	-	-	ef density medium	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	38.2	-	-	-	ef density high	Yano, 1988
PP+PU	Tomato	-	26.7	30/20	20.0	-	-	-	ef density low	Yano, 1988
-	-	-	22.5	24/21	17.5	-	-	-		Agekyan, 1981
-	-	-	-		28	-	-	-		Milliron, 1940
-	Tomato	-	-		>28	-	-	-		Speyer, 1927
-	-	-	-		20	-	-	-		Tonnoir, 1937

Appendix B1. Mortality of the black stage (% of individuals entering the stage) of *E. formosa* in *T. vaporariorum*. *cv*, coefficient of variation; *n*, number of replicates; *n*(ef), total number of *Encarsia*'s (ef).

Host stage	Host plant	Cultivar	Temp. (°C)		Mortality				Remarks	Reference
			Mean	Range	mean	cv(%)	n	n(ef)		
L1	Bean	'Canadian Wonder'	18.0		7.5	-	40	40		Madueke, 1979
L1	Bean	'Canadian Wonder'	22.5		8.3	-	36	36		Madueke, 1979
L1	Bean	'Canadian Wonder'	27.0		6.3	-	32	32		Madueke, 1979
L2	Bean	'Canadian Wonder'	18.0		3.2	-	31	31		Madueke, 1979
L2	Bean	'Canadian Wonder'	22.5		4.9	-	41	41		Madueke, 1979
L2	Bean	'Canadian Wonder'	27.0		5.9	-	34	34		Madueke, 1979
L2	Bean	-	17.0		0.0	-	92	92		Di Pietro, 1977
L2	Bean	-	22.0		1.0	-	197	197		Di Pietro, 1977
L3	Bean	'Canadian Wonder'	18.0		4.4	-	45	45		Madueke, 1979
L3	Bean	'Canadian Wonder'	22.5		4.9	-	41	41		Madueke, 1979
L3	Bean	'Canadian Wonder'	27.0		5.0	-	40	40		Madueke, 1979
L3	Bean	-	17.0		0.0	-	125	125		Di Pietro, 1977
L3	Bean	-	22.0		2.0	-	152	152		Di Pietro, 1977
L4	Bean	-	17.0		0.0	-	128	128		Di Pietro, 1977
L4	Bean	-	22.0		2.5	-	241	241		Di Pietro, 1977
L4+PP	Bean	'Canadian Wonder'	18.0		8.0	-	50	50		Madueke, 1979
L4+PP	Bean	'Canadian Wonder'	22.5		7.5	-	40	40		Madueke, 1979
L4+PP	Bean	'Canadian Wonder'	27.0		7.9	-	38	38		Madueke, 1979
PU	Bean	'Canadian Wonder'	18.0		8.6	-	35	35		Madueke, 1979
PU	Bean	'Canadian Wonder'	22.5		9.8	-	41	41		Madueke, 1979
PU	Bean	'Canadian Wonder'	27.0		13.5	-	37	37		Madueke, 1979
L3-PU	Tree tobacco	-	17.0		7.7	-	795	795		Vet & van Lenteren, 1981
L2	Tomato	-	26.7	30/20	2.1	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	3.5	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	5.8	-	-	-	ef density medium	Yano, 1988
L3+L4	Tomato	-	26.7	30/20	20.1	-	-	-	ef density high	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	7.6	-	-	-	ef density low	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	12.4	-	-	-	ef density medium	Yano, 1988
L3+L4	Tomato	-	20.0	25/10	18.4	-	-	-	ef density high	Yano, 1988
PP+PU	Tomato	-	26.7	30/20	14.0	-	-	-	ef density low	Yano, 1988

Appendix B2. Total immature mortality (% of individuals entering the egg stage) of *E. formosa* in *T. vaporariorum*. *cv*, coefficient of variation; *n*, number of replicates; *n*(ef), total number of *Encarsia*'s (ef).

Host stage	Host plant	Cultivar	Temp. (°C)		Mortality				Remarks	Reference
			Mean	Range	Mean	cv(%)	n	n(ef)		
L1	Tobacco	'N.C.2326'	25.0		76	-	-	-	calculated	Nechols & Tauber, 1977a
L1	Tobacco	-	25.0		7.7	-	13	13		Arakawa, 1982
L2	Tobacco	-	25.0		25.0	-	20	20		Arakawa, 1982
L3	Tobacco	'N.C.2326'	25.0		13	-	-	-	calculated	Nechols & Tauber, 1977a
L3	Tobacco	-	25.0		10.5	-	38	38		Arakawa, 1982
L4	Tobacco	'N.C.2326'	25.0		10	-	-	-	calculated	Nechols & Tauber, 1977a
L4	Tobacco	-	25.0		12.1	-	66	66		Arakawa, 1982
PP	Tobacco	'N.C.2326'	25.0		7	-	-	-	calculated	Nechols & Tauber, 1977a
PP	Tobacco	-	25.0		11.1	-	36	36		Arakawa, 1982
PU	Tobacco	'N.C.2326'	25.0		29	-	-	-	calculated	Nechols & Tauber, 1977a
PU	Tobacco	-	25.0		24.0	-	25	25		Arakawa, 1982
-	-	-	22.5	24/21	34.5	-	-	-		Agekyan, 1981

Appendix C. Longevity (days) of *E. formosa*. *cv*, coefficient of variation; *n*, number of replicates; *n*(ef), total number of *Encarsia*'s.

Host stage	Host plant	Cultivar	Temp. (°C) Mean	Temp. (°C) Range	Longevity Mean	Longevity cv(%)	Longevity n	Longevity n(ef)	Remarks	Reference
L3	Bean	-	22.0		16.20	40.6	15	15		Di Pietro, 1977
L3+L4	Bean	-	18.0		22.5	43.3	18	18	host during 30 days	Christochowitz & van der Fluit, 1981 Christochowitz et al., 1981
L4	glass	-	25.0		36.8	18.6	6	6		Arakawa, 1982
L4	Tomato	'Bonnie Best'	12.0		46.0	-	32	32		Burnett, 1949
L4	Tomato	'Bonnie Best'	15.0		31.0	-	31	31		Burnett, 1949
L4	Tomato	'Bonnie Best'	18.0		27.0	-	30	30		Burnett, 1949
L4	Tomato	'Bonnie Best'	21.0		21.5	-	30	30		Burnett, 1949
L4	Tomato	'Bonnie Best'	24.0		15.7	-	30	30		Burnett, 1949
L4	Tomato	'Bonnie Best'	27.0		8.1	-	34	34		Burnett, 1949
L4	Tomato	'Bonnie Best'	30.0		3.9	-	34	34		Burnett, 1949
L4	Tomato	'Bonnie Best'	33.0		2.5	-	32	32		Burnett, 1949
L4	Bean	'Canadian Wonder'	18.0		17.8	52.3	13	13		Madueke, 1979
L4	Bean	'Canadian Wonder'	22.5		14.6	33.8	13	13		Madueke, 1979
L4	Bean	'Canadian Wonder'	27.0		11.4	56.5	14	14		Madueke, 1979
L4	Bean	-	17.0		21.29	53.4	31	31		Di Pietro, 1977
L4	Bean	-	22.0		12.84	54.1	31	31		Di Pietro, 1977
L4	Bean	-	27.0		5.55	32.9	31	31		Di Pietro, 1977
L4	Bean	-	32.0		4.89	42.6	27	27		Di Pietro, 1977
L4-PU	Tobacco	'Bright Yellow'	15.0		47.7	19.9	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	20.0		31.9	19.7	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		12.5	32.7	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	30.0		6.0	23.6	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	35.0		1.8	43.7	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	40.0		1.0	0.0	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	20.0		28.0	23.4	10	10		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		3.0	23.3	10	10	31% RH	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		7.0	43.9	10	10	55% RH	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		19.0	44.9	10	10	74% RH	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		2.2	139.8	10	10	100% RH	Kajita, 1979
PP+PU	Tomato	'Kyoryoku-beiju'	20.0		28.7	23.7	-	-		Kajita, 1989
L1-PU	Bean	-	20.0		51.8	42.4	18	18		Gast & Kortenhoff, 1983 van Lenteren et al., 1987
L3-PP	Tree tobacco	-	17.0		44.0	-	7	7	host during 20 days	Vet & van Lenteren, 1981
L2	Bean	-	22.0		12.95	50.4	18	18		Di Pietro, 1977
L2+L3	Tomato	'Bonnie Best'	18.0		11.0	-	64	64		Burnett, 1949
L3+L4	Bean	-	11.6	18/7	32.6	62.8	17	17	host during 30 days	Christochowitz & van der Fluit, 1981 Christochowitz et al., 1981
L3+L4	Tomato	'Moneydor'	11.6	18/7	24.7	73.3	15	15		Burggraaf & van der Laan, 1983 van der Laan et al., 1982
-	-	-	-		28	-	-	-		Milliron, 1940
No host	Bean	-	25.0		21.6	23.1	216	216	with honeydew	Lopez Avila, 1988
No host	glass	-	15.6		99.3	-	24	24	with honeydew	Vet & van Lenteren, 1981
No host	glass	-	21.1		48.4	-	28	28	with honeydew	Vet & van Lenteren, 1981
No host	glass	-	26.7		35.2	-	20	20	with honeydew	Vet & van Lenteren, 1981
No host	glass	-	13.0		42.9	60.3	30	30	with honeydew	van Vianen & van Lenteren, 1982 van Lenteren et al., 1987

Appendix C (continued). Longevity (days) of *E. formosa*.

Host stage	Host plant	Cultivar	Temp. (°C)		Longevity				Remarks	Reference
			Mean	Range	Mean	cv(%)	*n*	*n*(ef)		
No host	glass	-	13.0		9.9	30.3	21	21	no food	van Vianen & van Lenteren, 1982 van Lenteren et al., 1987
No host	Tomato	'Bonnie Best'	18.0		5.8	-	50	50	no food	Burnett, 1949
No host	Tomato	'Moneydor'	11.6	18/7	57.6	28.4	13	13	with honeydew	Christochowitz & van der Fluit, 1981
No host	glass	-	20.0		3.2	-	62	62	no food	Gast & Kortenhoff, 1983 van Lenteren et al., 1987
No host	glass	-	20.0		3.4	-	59	59	with water	Gast & Kortenhoff, 1983 van Lenteren et al., 1987
No host	glass	-	20.0		29.1	-	31	31	with honeydew	Gast & Kortenhoff, 1983 van Lenteren et al., 1987
No host	glass	-	20.0		37.4	-	27	27	with honey	Gast & Kortenhoff, 1983 van Lenteren et al., 1987
No host	-	-	22.5	24/21	22.5	-	-	-		Agekyan, 1981
No host	Tomato	-	26.7	30/20	1.5	-	-	-	with water	Yano, 1988
No host	Tomato	-	20.0	25/10	2.5	-	-	-	with water	Yano, 1988

Appendix D. Pre-oviposition period (days) of *E.formosa*. *cv*, coefficient of variation; *n*, number of replicates; *n*(ef), total number of *Encarsia*'s.

Host stage	Host plant	Cultivar	Temp. (°C)		Pre-oviposition period				Remarks	Reference
			Mean	Range	Mean	cv(%)	*n*	*n*(ef)		
L3+L4	Tomato	'Bonnie Best'	18.0		1.60	-	70	70		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	21.0		0.87	-	177	177		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	24.0		0.10	-	69	69		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	30.0		0.06	-	35	35		Burnett, 1949

Appendix E. Fecundity (eggs per female per lifetime) of *E. formosa*. *cv*, coefficient of variation; *n*, number of replicates; *n*(ef), total number of *Encarsia*'s.

Host stage	Host plant	Cultivar	Temp. (°C) Mean	Temp. (°C) Range	Fecundity Mean	Fecundity cv(%)	Fecundity *n*	Fecundity *n*(ef)	Remarks	Reference
L3	Bean	-	22.0		63.13	52.3	15	15		Di Pietro, 1977
L4	Bean	-	17.0		59.59	54.7	31	31		Di Pietro, 1977
L4	Bean	-	22.0		70.45	53.5	31	31		Di Pietro, 1977
L4	Bean	-	27.0		32.13	31.6	31	31		Di Pietro, 1977
L4	Bean	-	32.0		23.15	47.3	27	27		Di Pietro, 1977
L4	glass	-	25.0		442.2	12.1	6	6		Arakawa, 1982
L3+L4	Tomato	'Moneydor'	11.4		0	-	10	10		van der Schaal, 1980
										van Lenteren & van der Schaal, 1981
L3+L4	Bean	-	18.0		223	10.7	30	30		Christochowitz & van der Fluit, 1981
L4+PP	Bean	'Canadian Wonder'	18.0		69.0	69.4	13	13		Madueke, 1979
L4+PP	Bean	'Canadian Wonder'	22.5		160.2	38.5	13	13		Madueke, 1979
L4+PP	Bean	'Canadian Wonder'	27.0		91.1	64.9	14	14		Madueke, 1979
L4-PU	Tobacco	'Bright Yellow'	15.0		75.8	19.9	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	20.0		90.3	25.3	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		45.5	41.2	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	30.0		23.0	37.6	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	35.0		2.6	90.8	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	40.0		0.6	209.9	12	12		Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	20.0		91.5	26.0	10	10	74% RH	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		7.3	51.7	10	10	31% RH	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		21.8	48.7	10	10	55% RH	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		59.5	50.5	10	10	74% RH	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		2.7	134.6	10	10	100% RH	Kajita, 1979
PP+PU	Tomato	'kyoryoku-beiju'	20.0		96.0	26.4	10	10		Kajita, 1989
L3-PU	Tree tobacco	-	17.0		165.6	19.8	9	9		Vet & van Lenteren, 1981
L1-PU	Bean	-	20.0		259	42.5	18	18		Gast & Kortenhoff, 1983
L1-PU	-	-	25.0		50	-	-	-		Woets, 1972b
-	-	-	25.0		350	-	-	-		Biggerstaff in Parr et al., 1976
-	-	-	20.0		47.3	-	-	-		Ibrahim, 1975
										Madueke, 1979
-	-	-	23.0		127.6	-	-	-		Ibrahim, 1975
										Madueke, 1979
-	-	-	26.0		167.6	-	-	-		Ibrahim, 1975
										Madueke, 1979
-	-	-	-		100	-	-	-		Tonnoir, 1937
-	-	-	-		50	-	-	-		Speyer, 1927
-	-	-	-		135.5	-	-	-		Scheeuwe (pers.comm.)
										Vet et al., 1980
-	-	-	-		50	-	-	-		Milliron, 1940
-	-	-	22.5	24/21	85	-	-	-	between 50-120	Agekyan, 1981
L2	Bean	-	22.0		47.78	66.9	18	18		Di Pietro, 1977
L3+L4	Bean	-	11.6	18/7	99	11.3	24	24		Christochowitz & van der Fluit, 1981
L3+L4	Tomato	'Moneydor'	11.6	18/7	76.7	79.4	15	15	70.8 in publ.	Burggraaf & van der Laan, 1983
										van der Laan et al., 1982
L2	Tomato	'Bonnie Best'	18.0		13.00	53.1	32	32		Burnett, 1949
L3	Tomato	'Bonnie Best'	18.0		12.38	33.2	32	32		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	15.0		15.58	37.7	31	31		Burnett, 1949

Appendix E (continued). Fecundity (eggs per female per lifetime) of *E. formosa*.

Host stage	Host plant	Cultivar	Temp. (°C)		Fecundity				Remarks	Reference
			Mean	Range	Mean	cv(%)	*n*	*n*(ef)		
L3+L4	Tomato	'Bonnie Best'	18.0		28.20	47.2	30	30		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	21.0		28.77	37.2	30	30		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	24.0		32.67	36.7	30	30		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	27.0		30.50	35.4	34	34		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	30.0		9.86	61.4	32	32		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	33.0		2.89	70.6	18	18		Burnett, 1949

Appendix F. Oviposition frequency (eggs per (still living) female per day) of *E. formosa*. *cv*, coefficient of variation; *n*, number of replicates; *n*(ef), total number of *Encarsia*'s.

Host stage	Host plant	Cultivar	Temp. (°C)		Oviposition frequency				Remarks	Reference
			Mean	Range	Mean	*cv*(%)	*n*	*n*(ef)		
L2	Bean	-	22.0		4.45	43.7	18	18		Di Pietro, 1977
L3	Bean	-	22.0		4.25	31.3	15	15		Di Pietro, 1977
L3+L4	Bean	-	18.0		8.0	50.2	30	30		Christochowitz & van der Fluit, 1981 Christochowitz et al., 1981
L4	Bean	-	17.0		3.21	28.1	31	31		Di Pietro, 1977
L4	Bean	-	22.0		6.55	22.9	31	31		Di Pietro, 1977
L4	Bean	-	27.0		7.70	27.6	31	31		Di Pietro, 1977
L4	Bean	-	32.0		5.32	33.4	27	27		Di Pietro, 1977
L4	Glass	-	25.0		20	-	6	6	during 15 days	Arakawa, 1982
L4+PP	Bean	'Canadian Wonder'	18.0		3.3	-	13	13		Madueke, 1979
L4+PP	Bean	'Canadian Wonder'	22.5		11.2	-	13	13		Madueke, 1979
PP+PU	Tomato	'Kyoryoku-beiju'	20.0		2.3	65.2	10	10		Kajita, 1989
L4-PU	Tobacco	'Bright Yellow'	15.0		1.59	-	10	10	fecundity/longevity	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	20.0		2.83	-	10	10	fecundity/longevity	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	25.0		3.64	-	10	10	fecundity/longevity	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	30.0		3.83	-	10	10	fecundity/longevity	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	35.0		1.44	-	10	10	fecundity/longevity	Kajita, 1979
L4-PU	Tobacco	'Bright Yellow'	40.0		0.6	-	10	10	fecundity/longevity	Kajita, 1979
L3-PU	Tree tobacco	-	17.0		8.3	12.7	9	9		Vet & van Lenteren, 1981
L2-PU	Bean	-	12.5		0	-	-	-		Pravisani, 1981
L1-PU	Bean	-	20.0		4.9	28.6	46	46		Gast & Kortenhoff, 1983
L3+L4	Tomato	-	25.0		4.1	48.2	100	100	during 2 days	Kajita & van Lenteren, 1982
L3+L4	Tomato	'kyoryoku-beiju'	25.0		4.07	48.4	120	120	during 2 days	Kajita, 1983
L3-PP	Cucumber	'IVT 71-240/ 761077Mayak'	24.0		11.5	35.7	10	10	during 3 hours	Hulspas, 1978
L3-PP	Cucumber	'IVT 71-240'	24.0		6.0	60.0	3	3	during 3 hours + honeydew	Hulspas, 1978
L3-PP	Tomato	'Moneymaker'	20.7	23/16	8.75	35.7	12	12	during 1 day	Veerkamp, 1975
L3-PP	Cucumber	'IVT 71-241'	20.7	23/16	8.68	24.1	19	19	during 1 day	Veerkamp, 1975
L1-L4	Bean	'Canadian Wonder'	25.0		15.5	-	47	47	during 1 day	Fransen & van Montfoort, 1987
L1-PU	Tomato	'Moneydor'	11.4		0	0.0	10	10	during 3 hours	van der Schaal, 1980 van Lenteren & van der Schaal, 1981
L1-PU	-	-	25.0		3.5	-	-	-		Woets, 1972b
L1-PU	Bean	-	23.5		0	-	10	10	at night	van Alphen, 1972
L1-PU	Cucumber	-	23.5		0	-	10	10	at night	van Alphen, 1972
-	-	-	-		0	-	30	30	<4200 lux, 16 hours	McDevitt, 1973 Scopes, 1973
-	-	-	-		max.	-	30	30	7300 lux, 16 hours	McDevitt, 1973 Scopes, 1973
L3+L4	Bean	-	11.6	18/7	3.5	59.9	24	24		Christochowitz & van der Fluit, 1981 Christochowitz et al., 1981
L3+L4	Bean	-	11.6	18/7	2.44	-	-	-	bad experiment	Christochowitz & van der Fluit, 1981 Christochowitz et al., 1981
L3+L4	Bean	-	11.6	18/7	2.48	-	-	-	bad experiment	Christochowitz & van der Fluit, 1981 Christochowitz et al., 1981
L3+L4	Tomato	'Moneydor'	11.6	18/7	3.2	31.8	15	15		Burggraaf & van der Laan, 1983 van der Laan et al., 1982

Appendix F (continued). Oviposition frequency (eggs per (still living) female per day) of *E. formosa*.

Host stage	Host plant	Cultivar	Temp. (°C)		Oviposition frequency				Remarks	Reference
			Mean	Range	Mean	cv(%)	*n*	*n*(ef)		
L3+L4	Tomato	'Bonnie Best'	15.0		0.85	26.2	31	31		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	18.0		1.68	45.6	30	30		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	21.0		1.81	27.2	30	30		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	24.0		2.74	36.0	30	30		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	27.0		5.30	36.3	34	34		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	30.0		3.31	47.9	32	32		Burnett, 1949
L3+L4	Tomato	'Bonnie Best'	33.0		2.47	48.1	18	18		Burnett, 1949
L2	Tomato	'Bonnie Best'	18.0		2.13	39.8	32	32		Burnett, 1949
L3	Tomato	'Bonnie Best'	18.0		1.87	30.3	32	32		Burnett, 1949