Understanding biological control of greenhouse whitefly with the parasitoid *Encarsia formosa*

From individual behaviour to population dynamics

Promotoren: dr. J.C. van Lenteren
hoogleraar in de entomologie,
in het bijzonder de oecologie der insekten

dr.ir. R. Rabbinge
hoogleraar in de produktie-ecologie,
met bijzondere aandacht voor de plantaardige produktie

Herman J.W. van Roermund

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The cover design shows a Dutch stamp with a greenhouse whitefly (right) and its natural enemy, the parasitoid *Encarsia formosa* (left). The stamp was issued by the Dutch postal services in 1993 on behalf of the 75th anniversary of the Wageningen Agricultural University.

Stellingen

1. Een hoger aantal *Encarsia formosa* sluipwespen op bladeren met witte vlieg vergeleken met dat op schoon blad is een gevolg van het langer blijven op een blad na contact met wittevlieglarven of honingdauw, en niet van het op afstand lokaliseren van besmet blad door de sluipwesp, zoals Ledieu (1976) concludeerde.
   Ledieu, M.S., 1976. IOBC/WPRS Bull. 1976/4: 121-124.
   Dit proefschrift.

2. Bij de bestrijding van kaswittevlieg met *Encarsia formosa* op tomaat kan beter gesproken worden van plaagonderdrukking door inundatieve bestrijding dan van regulatie door seizoens-inoculatieve bestrijding.
   Lenteren, J.C. van, 1986. In: Insect Parasitoids. Waage, J.K.; Greathead, D.J. (Eds.). Academic Press, London. pp 341-374.
   Dit proefschrift.

3. Een *Encarsia*-stam met meer ovariolen dan de huidige stam leidt alleen tot een betere biologische bestrijding, indien die grotere sluipwespen sneller lopen en een langere levensduur hebben. De grotere ei-voorraad zelf speelt geen rol.
   Vianen, A. van; Lenteren, J.C. van, 1986. J. appl. Ent. 101: 321-331.
   Dit proefschrift.

4. De zoekactiviteit en de gastheer-acceptatie van de sluipwesp *Encarsia formosa* worden lager naarmate haar ei-voorraad afneemt. Dit fenomeen is vergelijkbaar met de afname in zoekactiviteit en prooi-acceptatie van predatoren zoals roofmijten en loopkevers naarmate hun darm meer gevuld raakt.
   Sabelis, M.W. 1986. In: The Dynamics of Physiologically Structured Populations. Metz, J.A.J.; Diekmann, O. (Eds.). Lecture Notes in Biomathematics 68. Springer-Verlag, Berlin. pp. 298-321.
   Mols, P.J.M., 1987. Acta Phytopath. Entom. Hung. 22: 187-205.
   Dit proefschrift.

5. Het grote effect van variatie in zoektijden van *Encarsia formosa* op de bestrijding van kaswittevlieg toont aan hoe belangrijk het is om modellen van deze gastheer-parasitoid interactie te baseren op individueel gedrag.
   Dit proefschrift.

6. Eén publikatie over schadedrempels voor kaswittevlieg op tomaat in 40 jaar tegenover honderden over de biologie en het populatieverloop van wittevlieg en *E. formosa* illustreert de ondervertegenwoordiging van de produktie-ecologische benaderingswijze.

7. Omdat plaagdichtheden in het gewas op een laag niveau gehouden moeten worden, is de zoekefficiëntie van een natuurlijke vijand een beter criterium voor haar geschiktheid in biologische bestrijding dan de intrinsieke populatiegroeisnelheid (r_m).
   Dit proefschrift.

8. De grote aandacht in de literatuur voor stabiliteit in predator-prooi relaties kan niet gerechtvaardigd worden door het belang van stabiliteit voor de geslaagde toepassing van natuurlijke vijanden in de gewasbescherming.
   Murdoch, W.W.; Chesson, J.; Chesson, P.L., 1985. Am. Nat. 125: 344-366.

9. Wanneer universiteiten onbeperkt de hoogte van het collegegeld mogen vaststellen, is dat het begin van de ontwikkeling naar aparte universiteiten voor arm en rijk.

10. Het binnen 4 jaar afronden van promotie-onderzoek aan Nederlandse universiteiten blijft een illusie indien het verwachtingspatroon ten aanzien van een proefschrift niet verandert.

11. Het uitvoeren van een groot deel van het universitaire onderzoek als promotieprojekten leidt tot een voor de maatschappij veel te hoog aantal opgeleide onderzoekers.

12. Het zou auteurs veel tijd besparen indien alle wetenschappelijke tijdschriften dezelfde voorschriften zouden hanteren voor het opstellen van literatuurlijsten.

13. Het probleem van een lange rekenduur bij simulatiemodellen is slechts een kwestie van tijd.

Herman J.W. van Roermund
Understanding biological control of greenhouse whitefly with the parasitoid *Encarsia formosa*. From individual behaviour to population dynamics.
Wageningen, 18 oktober 1995.

Contents

Chapter 1

General introduction

Whitefly pests, damage and control

About 1200 whitefly species have been described, of which few are known to be pests. Only two whitefly pest species occur in protected agriculture (Byrne et al., 1990): the greenhouse whitefly, *Trialeurodes vaporariorum*, and the sweet potato whitefly, *Bemisia tabaci*. Both species are highly polyphagous pest insects, occur worldwide and lead to serious economic losses (Gerling, 1990).

Damage to crops caused by whiteflies can be grouped into three categories. First, adult and immature whiteflies are phloem feeders and can contribute to reduced productivity by directly consuming transportable carbohydrates, nitrogen and other nutrients. Secondly, they produce large amounts of honeydew on the leaf, on which occasionally sooty moulds develop, thus reducing leaf photosynthesis. Both damage components reduce crop yield, as observed for tomato by Lindquist et al. (1972). More important is the economic damage due to the residue of sticky honeydew on fruits and ornamentals. Hussey et al. (1958) measured significant yield reduction on tomato at an average pest density (between start of pest and final picking of fruits) of 22 scales/cm^2 leaf or more, and an economic damage at 6 scales/cm^2 or more. Finally, whiteflies can transmit various virus diseases. A survey of damage and pest status of whiteflies can be found in Byrne et al. (1990).

In natural ecosystems and agroecosystems where pesticides are not used, usually an array of natural enemies keeps the number of whiteflies at very low numbers: predators, parasitoids and pathogens all take their toll. Work on two cropping systems - tomatoes in the 1960s in California and cotton during the period 1925-1992 in Sudan - has shown that whiteflies can be kept under perfect *natural control* (van Lenteren et al., 1995). When pesticides are applied, natural enemies are exterminated and whiteflies attain pest status. Furthermore, changes in cropping rotation, shortening of fallow periods, and concurrent or overlapping growth of whitefly sensitive crops may result in such a high and continuous whitefly pressure that natural enemies are not capable of a sufficient reduction of whitefly numbers.

Chemical pesticides have been the main agent used for the control of insect pests since World War II. Advantages of chemical control were: adequate protection of crops, simple application methods and reliability. After the euphoria, disadvantages of solely relying on pesticides became clear: the risks for man and environment, and the development of resistance by insects against pesticides triggered research for other control methods. These problems were recognized recently at the policy level and have resulted in the Netherlands in the Multi-Year Term Plan of Crop Protection of the Ministry of Agriculture, Nature and Fisheries (MJP-G, 1991). This plan aims at a 50% reduction of the use of pesticides by the year 2000. One of the important alternatives for chemical control is biological control, where predators, parasitoids or pathogens are

released to control pest insects. As whitefly pests are now common worldwide, an intensive search for natural enemies is going on (Onillon, 1988).

History of whitefly biological control

The greenhouse whitefly, *T. vaporariorum* (Westwood) (Homoptera, Aleyrodidae) was found in 1856 in greenhouses in the U.K. Westwood described the species in that year and he assumed that it was imported on living plants or in the packings of Orchidaceae from Mexico. Now this species has spread all over the world and attacks many plant families and genera (Russell, 1977). In 1926, a tomato grower drew the attention of the English entomologist Speyer to black pupae among the normally white scales of the greenhouse whitefly. From the black pupae, parasitoids emerged that were identified as *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) (Speyer, 1927). Within a few years a research station in England was supplying 1.5 million of these parasitoids annually to about 800 nurseries in Britain. During the 1930s *E. formosa* was shipped to some other European countries, Canada, Australia and New Zealand. After World War II, the use of *E. formosa* was discontinued because newly introduced insecticides provided control on most greenhouse crops.

The interest in the use of natural enemies revived after the resistance to pesticides in the two-spotted spider mite, *Tetranychus urticae*, reached such levels that chemical control became impossible. An imported predatory mite, *Phytoseiulus persimilis*, successfully kept the spider-mite populations below the economic injury level (Hussey & Bravenboer, 1971). This implied that broad spectrum pesticides could not be applied for control of other pests because these would negatively affect the natural enemy. Thus, attention focused on natural enemies of the other pests in the greenhouse. In the 1970's enormous whitefly outbreaks took place in Western Europe, among others because of increasing resistance to pesticides of the whiteflies, and interest in the parasitoids increased again (Wardlow et al., 1972). The knowledge already available from previous applications with *E. formosa* earlier this century enhanced the development of introduction strategies for whitefly control (Vet et al., 1980).

The availability of the efficient parasitoid *E. formosa* paved the way for the development of biological and integrated control programs in greenhouses. During the past 25 years, 25 species of natural enemies have been identified and introduced against 20 pest species in greenhouses (van Lenteren & Woets, 1988; van Lenteren et al., 1992). Presently biological control of greenhouse whitefly with *E. formosa* is applied in more than 20 of the 35 countries that have a greenhouse industry. The parasitoid is applied mainly in tomato. In Western Europe alone biological control of greenhouse whitefly is applied on about 4000 ha and growers consider it a more reliable method than chemical control. The positive spin-off is reduced environmental pollution, a healthier work environment for growers and consumer appreciation of produce with less or no chemical residues.

Problem definition and research goal

Biological control of greenhouse whitefly with *E. formosa* is very reliable in such crops as tomato, sweet pepper and gherkin, but not in egg plant and cucumber. In ornamentals, such as gerbera, results are ambiguous. The introduction scheme was found by a 'trial and error' approach: natural enemies were released at different times and in different numbers, and their level of control was examined. The knowledge of regulation mechanisms at the population level is still limited. As yet there is no satisfactory explanation as to why the parasitoid introduction scheme for tomato cannot be applied reliably on other important greenhouse crops. A variety of qualitative explanations have been given for the difference in control levels, based on laboratory studies of individual behaviour and on population studies in the greenhouse. However, the main causal factors could not be identified.

Differences in control levels may be caused by differences in (1) the greenhouse temperature, (2) the life-history parameters and thus the population development of pest and natural enemy, (3) the crop structure and leaf size, (4) the leaf surface (hairiness), and (5) the whitefly distribution in the crop. Factor (1) influences the life-history parameters and (1), (3), (4) and (5) affect the parasitoids' searching behaviour and, as a result, the parasitization efficiency. Because of the multitude of relationships between the three trophic levels (crop-pest-parasitoid), the most important factors can only be evaluated after integration of all relevant processes.

Systems analysis and simulation are powerful tools for this purpose. This approach bridges the gap between knowledge at the individual level and understanding at the population level (Rabbinge et al., 1989). The present study aims at integrating existing knowledge on the major processes known to affect the whitefly-parasitoid interaction in a crop by means of an explanatory simulation model. The goal is to obtain quantitative understanding of the tritrophic system crop- greenhouse whitefly-*E. formosa* to explain failure or success of biological control. The model is *mechanistic*, that is, it explains *how* whiteflies and parasitoids, in terms of life-history parameters, and *how* parasitoids, in terms of searching efficiency, host handling and available eggs, realize the observed level of parasitism. Mechanistic explanations are helpful in understanding and improvement of biological control in practice. The model does not explain *why* the whiteflies and parasitoids choose to behave in this way, in terms of the selection pressure acting on them. Thus, it does not provide a *functional* explanation of the observed behaviour, which can be studied using optimal foraging models.

The model simulates the population dynamics of whitefly (host) and parasitoid in a crop. It is based on developmental biology of the two species and on the parasitoids' searching and parasitization behaviour in relationship to host plant characteristics and greenhouse climate. Whiteflies show a strongly clustered distribution over plants and leaves and local host densities very much affect the parasitoids' behaviour. Therefore, local interactions are very important. The model is unique in that it is an individual-based model which simulates local searching and parasitization behaviour of a large number of individual parasitoids in a whitefly-infested crop. The model

includes stochasticity and spatial structure which is based on location coordinates of plants and leaves. Individual-based models are a necessity when local interactions and stochasticity are important (De Angelis & Gross, 1992). With the model we are able to (1) explain the ability of *E. formosa* to reduce whitefly populations in greenhouses on crops like tomato, (2) improve introduction schemes of parasitoids for crops where control is more difficult to obtain and (3) predict effects of changes in cropping practices (e.g. greenhouse climate, choice of cultivars) on the reliability of biological control.

Most of the models on population dynamics developed thus far use observed functional response curves as input. The functional response curve is the relationship between the number of hosts parasitized per parasitoid per day as a function of host density. These curves are observed on leaves and then extrapolated to the crop level by deriving parasitism rates from the average host density in the crop. This implicitly assumes that the observed relationship for leaves is also valid at higher spatial levels, which is unrealistic when hosts show a strongly clustered distribution in the crop and when functional response curves are non-linear.

Outline of the thesis

When the present research project started, many experiments had been done to obtain the life-history parameters of the two species: immature development rate, immature mortality, adult longevity, sex ratio, fecundity and oviposition frequency. Furthermore, extensive studies had been done on the whitefly's host-plant preference and suitability, on selection of feeding and oviposition sites and on spatial distribution patterns (review in van Lenteren & Noldus, 1990). The parasitoids' foraging behaviour was observed in detail when the parasitoid was confined to an experimental arena for a fixed time (review in Noldus & van Lenteren, 1990).

However, little was known about the time allocation of the parasitoid on leaves when they were able to leave. The gaps in knowledge are first identified and studied experimentally in **Chapters 2, 3 and 4**, to be able to quantify the foraging process of the parasitoid from landing on a leaf until departure. These chapters describe direct-observation experiments of foraging parasitoids on tomato leaflets until leaving. Chapter 2 summarizes residence times on leaflets. In Chapter 3 the leaving tendency of the parasitoid from the leaflet and effects of several intra-patch experiences with hosts are quantified. In Chapter 4 other basic aspects of foraging on leaves are quantified, such as the parasitoids' walking speed and walking activity and host handling behaviour.

Data of Chapters 3 and 4 are used as input in the simulation model described in **Chapters 5, 6 and 7**. In these chapters, the foraging behaviour of *E. formosa* is studied using a stochastic simulation model at three spatial scales: in a small experimental arena, on a tomato leaflet and on a tomato plant. The models are validated with experimental data. This information helps to understand quantitative effects of the parasitoid on whitefly populations at a much larger spatial and time scale: in a crop during a growing season.

In **Chapters 8 and 9**, life-history parameters of the greenhouse whitefly and *E. formosa* are reviewed. With data from literature, the relationships between life-history parameters and temperature are estimated by non-linear regression.

Chapter 10 describes the final model which simulates the population dynamics of the pest insect-parasitoid interaction in a tomato crop. This model comprises several submodels, one of which is the model of the parasitoids' foraging behaviour on tomato leaflets, described in Chapter 6. Data of Chapters 8 and 9 for tomato are used as input to describe the developmental biology of the two species. The model simulates behaviour of individuals and includes stochasticity and spatial structure which is based on location coordinates in the canopy. The model is validated with population counts from experiments with and without introduction of *E. formosa* in small greenhouse compartments and in a large commercial greenhouse. A sensitivity analysis of the model extracts the most important properties of parasitoid, whitefly and crop which favour biological control.

The study is concluded with a summarizing discussion in **Chapter 11** that demonstrates the scientific and practical implications of this study and prioritizes the future plans for further research.

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Chapter 2

Residence times of the whitefly parasitoid *Encarsia formosa* on tomato leaflets

ABSTRACT

Individual *Encarsia formosa* parasitoids were observed continuously on either clean, honeydew-contaminated and whitefly-infested tomato leaflets until the parasitoids flew away. The median residence time on clean leaflets was about 20 min at 20, 25 and 30°C, and was the same on infested leaflets when no hosts were encountered. Encounters with unparasitized and parasitized whitefly larvae, and contact with honeydew prolonged the residence time of the parasitoid on the leaflet. Even when many parasitized black whitefly pupae (unsuitable hosts) were encountered and rejected, the parasitoid still was arrested on that leaflet. *E. formosa*'s walking pattern seemed to be random, and parasitoids showed no preference for searching on the upper or lower leaf side when no hosts where encountered. There is also no preference for the edge or for the middle of a leaf. Walking and flight activity of the parasitoids was hardly observed at 15 and 18°C. Many parasitoids became inactive after periods when the barometric pressure decreased than when stable or increasing.

INTRODUCTION

The parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) has been used since the 1920s to control the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). At present biological control is commercially successful in several greenhouse vegetables (van Lenteren & Woets, 1988). The reliable application of this parasitoid was supported by an intensive research program. Part of this research consisted of direct observation of host searching, host selection, host discrimination, parasitization, and host feeding behaviour (van Lenteren et al., 1976a and b; Nell et al., 1976; van Lenteren et al., 1980). Still, little is known about the time allocation of parasitoids on leaves. In greenhouses most of the leaves are uninfested, as average whitefly densities are extremely low when biological control is successful (Eggenkamp-Rotteveel Mansveld et al., 1978). So, the parasitoids spend much time searching for hosts. They move from leaf to leaf and the time they stay on each leaf has great impact on the parasitization efficiency and, thus, on the level of biological control.

E. formosa is a synovigenic, solitary larval parasitoid of the greenhouse whitefly. In order to reproduce, the parasitoid searches for the sessile whitefly immatures by flying or hopping from leaf(let) to leaf(let), without distinguishing between infested and clean plants or leaves before landing (Noldus & van Lenteren, 1990; Sütterlin & van Lenteren, in prep.). Once on a leaf it starts walking and drumming the leaf with its antennae. Hosts are only present on the lower leaf side. Upper leaf sides may be covered by honeydew produced by hosts in higher leaf layers.

On encounter, a host can be rejected after an inspection with the antennae (antennal rejection) or can be rejected or accepted for oviposition or host feeding after insertion of the ovipositor (ovipositorial rejection, oviposition or host feeding respectively) (van Lenteren et al., 1980).

The aim of this study was to examine time allocation of *E. formosa* on leaves. This information will later be used to estimate the parasitization efficiency of the parasitoid with the help of a simulation model (Chapters 5, 6, 7 and 10). Experiments were done on: (1) clean tomato leaflets, (2) leaflets with honeydew, (3) leaflets with a low number of unparasitized hosts, and (4) leaflets which were depleted by conspecifics earlier and only bear parasitized hosts. As the temperature usually varies between 15 and 30°C in greenhouses, the effect of this temperature range was also tested.

MATERIAL AND METHODS

Plants

Tomato plants (*Lycopersicon esculentum* var. 'Moneymaker') were grown in a greenhouse compartment at 20-24°C, L16:D8 and 70% RH. Each week a fertilization treatment was carried out and in autumn, leaves were sprayed sequentially with Rubigan, Nimrod, Baycor and Daconil against powdery mildew. These fungicides are not harmful for whitefly and parasitoid immatures (Koppert Biological Systems, pers. comm.). Plants were used when 4-6 weeks old and about 60 cm in height. Leaflets on which observations were carried out were fully grown and 22.5 $cm^2 \pm 6.3SD_{n-1}$ (n=110) in size.

Greenhouse whitefly

Greenhouse whiteflies were reared on tomato var. 'Moneymaker' in a greenhouse compartment at approximately 24°C, L16:8D and 50% RH. The whitefly had been reared on this tomato cultivar for 20 years.

Low densities of 1 or 4 unparasitized larvae per leaflet were obtained by placing clip-on leaf cages (2.5 cm) bearing 1 female and 1 male adult whitefly on a clean tomato plant. For all other treatments (see below), a clean tomato plant was placed in a plant cage with a large number of whitefly adults. After 16-24 h the whiteflies were removed from the leaflets and the plant was transferred to a whitefly-free compartment. Whitefly immatures develop from the egg stage to four successive larval stages (L1-L4), a prepupal and a pupal stage (Chapter 8). The L3, L4 and prepupa are preferred by *E. formosa* for oviposition (Nell et al., 1976). After 17-21 days at 22°C and 50% RH larvae were of stage L3-L4. Fully grown leaflets with a correct number of L3/L4 larvae were chosen shortly before the start of an observation.

To produce recently-parasitized whitefly larvae, a few parasitoids were released 1-7 h before an observation on a leaflet bearing unparasitized L3/L4 larvae. Whitefly larvae were considered to be parasitized after an oviposition posture lasting longer than

120 s was observed (van Lenteren et al., 1976b). The leaflet was then used for observation. At the end of the observation the larvae were dissected to check if each oviposition posture had resulted in an egg deposited in the host.

To produce black parasitized whitefly pupae, plants with unparasitized L3 larvae were placed in cages with about 50 parasitoids for 24 h at 22°C. After 9-10 days at 22°C the parasitoid immature pupated in the host pupa, which then turned black. Fully grown leaflets with the correct number of hosts were chosen shortly before the start of an observation.

Honeydew was collected on upper sides of leaflets by placing an infested leaflet slightly above a clean leaflet in a holder for 24 h at 22°C. The infested leaflet bore 15.9 ± 5.1SD (n=30) immature whiteflies (all stages) per 0.196 cm^2. Leaflets remained attached to their plants. Leaflets with honeydew on the upper leaf side were checked for (dropped) whitefly immatures, which were then removed. A large amount of honeydew was thus collected on leaflets in the same way as in a natural situation: with natural droplet size and with small pieces of exuviae.

Parasitoids

Parasitoids were delivered as black pupae on paper cards by Koppert Biological Systems (Berkel en Rodenrijs, the Netherlands), where *E. formosa* is reared on tobacco leaves. Cards were placed in glass petri dishes (5 cm in diameter) at 20-24°C with a droplet of honey one day before each observation when the observations were done at 25 and 30°C respectively. Most parasitoids emerged in early morning hours. Lights were switched on at least 2 h before observation. When observations were done at 20°C, petri dishes were also placed at 20°C to avoid a temperature decline, which might influence the parasitoids' activity. For each observation a naive female of *E. formosa*, not older than 24 h was used.

When the observations were done at 15 or 18°C, parasitoids emerged at 25°C and were kept at that temperature during the day. During the night they were placed at 12°C. This pre-treatment was done to be sure of parasitoids with a full batch of mature eggs (high temperature exposure) and to avoid a temperature decline shortly before the observations (low temperature exposure), as in the other replicates. Therefore, these naive parasitoids were 24-48 h old. At 18°C two other pre-treatments were also done: black pupae were placed at 18°C (n=10) or at 20-24°C (n=13) for emergence, and observation was done on the day of emergence.

From at least 1 h before the start of the observation parasitoids were kept separately in a polysaccharid capsule (2.5x0.8 cm).

Experimental set-up

The observations were carried out on tomato leaflets in a climate room at a constant temperature (±1°C) and 70±5% RH. At the start of each observation a single naive *E. formosa* female was introduced on a leaflet placed in a glass vial (5.5x1.5 cm) filled with water. This vial was attached to the stem in the middle of a tomato plant. Leaflet angle was about 45°. Five plants surrounded the plant to mimic the light conditions of a crop and to provide the parasitoid with ample opportunity to hop or fly to another leaflet. Light intensity at the observed leaflet was 5775 lux. Continuous observation started directly after the introduction of the parasitoid. When the parasitoid was on the lower leaf side it was observed through a stereo microscope; when it was on the upper leaf side it was followed by eye.

The residence time, the search time and the host handling time were recorded using the computer software package 'The Observer' (Noldus, 1991). Throughout the experiment, the position of the parasitoid on the leaflet was recorded: the upper leaf side, the lower leaf side, or whether the parasitoid was on the edge or not. Edge width was taken the same as the width of the parasitoids' searching path (0.5 mm). An observation stopped when the parasitoid flew from the leaflet. When the parasitoid walked off the petiole, which was only rarely observed, or when no foraging activity occurred for more than 60 min the observation was not included in the analysis. Observations were also excluded when a parasitoid left within 180 s, because this was clearly due to disturbance of the parasitoid during introduction.

Two types of experiments were conducted. In experiment I no hosts were present. This was done to study the effect of temperature, the side of the leaflet on which the parasitoid was introduced, and the presence of honeydew. Seven combinations of these factors were tested (n is the number of successful observations): (1) 15°C, without honeydew, parasitoid introduced on upper leaf side (n=32), (2) 18°C, without honeydew, parasitoid introduced on upper leaf side (n=66), (3) 20°C, without honeydew, parasitoid introduced on upper leaf side (n=26), (4) 25°C, without honeydew, parasitoid introduced on upper leaf side (n=38), (5) 30°C, without honeydew, parasitoid introduced on upper leaf side (n=46), (6) 25°C, without honeydew, parasitoid introduced on lower leaf side (n=43) and (7) 25°C, with honeydew, parasitoid introduced on upper leaf side (n=22).

In experiment II a varying number of unparasitized or parasitized hosts were present on the lower leaf side. This was done to estimate the effect of encounters with hosts. In this experiment the ambient temperature was always 25°C, honeydew was absent and the parasitoid was introduced on the lower leaf side. Three host *types* were distinguished: unparasitized, recently-parasitized by a conspecific, and black parasitized by a conspecific. The only difference between the 6 treatments was the number of hosts and the host type: (1) 1 unparasitized L3/L4 larva (n=24), (2) 4 unparasitized L3/L4 larvae (n=25), (3) 1 recently-parasitized L3/L4 larva (n=54), (4) 4 recently-parasitized L3/L4 larvae (n=41), (5) 4 black parasitized pupae (n=32) and (6) 77 to 200 black parasitized pupae (n=20).

Table 1. Mean residence time (s) of *E. formosa* on clean tomato leaflets. SD_{n-1} and number of replicates given between brackets.

Temperature (°C)	15	18	20	25	25	30
Leaf side of introduction	upper	upper	upper	upper	lower	upper
Residence time	>>3600 (-;32)	>>3600 (-;66)	1484 a (1242;26)	1415 a (828;38)	1034 a (1053;43)	1739 a (1979;46)

Kruskal-Wallis test, P=0.243. Different letters in a row indicate significant differences. Overall mean=1450 (1417;153), median=1014.

RESULTS

Residence time

Residence times of *E. formosa* on clean leaflets are given in Table 1. At 15 and 18°C parasitoids did not fly away from the leaflets. Twelve and eight observations were continued the next morning (16-24 h later) respectively and in all cases the parasitoid was still on the leaflet, close to the place were it was observed the day before. At 18°C, observations were done in autumn 1990 and repeated in summer 1991 after different pre-treatments of the parasitoids. Only two parasitoids, which also had emerged at 18°C, flew away from the leaflet. At temperatures of 20, 25 and 30°C, residence times on clean tomato leaflets were the same. The leaf side on which the parasitoids were introduced to also did not influence residence times.

Table 2 shows the residence times on infested leaflets when no hosts were discovered by the parasitoid. Host number and type did not affect the residence times. The mean residence time on infested leaflets when no encounters occurred (1681 s) was equal to the residence time on clean leaflets (1450 s) (Mann-Whitney U test, P=0.132, n=54 and 153 respectively). In the treatments with unparasitized hosts, most parasitoids (95.9%) did discover hosts, because in these treatments the parasitoids were introduced close to a host in the middle of the leaflet.

Residence times were higher when hosts were discovered by the parasitoids and then the number and type of hosts encountered played an important role (Table 2). Mean times were longest (8660 s) when 4 unparasitized hosts were present. The residence time on uninfested leaflets with honeydew (5133 s) was significantly higher than on clean leaflets (Mann-Whitney U test, $P=4.94*10^{-6}$, n=18 and 153 respectively).

These long residence times were not caused by parasitoids spending a larger amount of time sitting still or preening. The parasitoids' searching or walking activity (the time walking while drumming on the leaf surface as a percentage of the total time on the leaf, excluding host handling time) was not influenced by temperature at 20°C or up, the leaf side of introduction, the presence of honeydew and it was never affected by host encounters or ovipositions in these experiments (Chapter 4). The overall mean was 71.7±21.2SD % (median=77.0%; n=371).

The parasitoids spent most of the time on the leaf surface without being in contact with hosts (Table 2). When 4 unparasitized or recently-parasitized hosts were

Table 2. Mean residence time (s) of *E. formosa* on infested tomato leaflets when hosts were not discovered, when hosts were discovered or when honeydew was on the leaflet, time (s) on the leaf without handling hosts and time (s) until first host encounter on infested tomato leaflets when hosts were discovered, total number of host encounters and ovipositions on (all) infested tomato leaflets, at 25°C. Host types are unparasitized (unpar.), recently-parasitized (rec.par.) and black parasitized (black). SD_{n-1} and number of replicates given between brackets.

Host number	1	4	1	4	4	77-200	0	
Host type	unpar.	unpar.	rec.par.	rec.par.	black	black	honeydew	P[1]
Residence time; hosts not discovered[2]	--- (---;0)	2411 a (906;2)	1824 a (1426;28)	1148 a (879;15)	1962 a (1505;9)	--- (---;0)	---	0.220
Residence time; hosts discovered or honeydew on leaflet	4438 a (1247;24)	8660 b (1706;23)	4389 a (2048;26)	5159 a (3182;26)	4280 a (3062;23)	6485 ab (2747;20)	5133 a (3837;18)	$7.13*10^{-7}$
Time without handling hosts	4018 a (1189;24)	6979 b (1576;23)	3820 a (1934;26)	4270 a (2957;26)	4217 a (3063;23)	6005 ab (2734;20)	---	$6.50*10^{-6}$
Time until first encounter	434 ab (388;24)	708 a (809;23)	798 a (707;26)	702 ab (939;26)	1345 a (1329;23)	164 bc (139;20)	---	$2.88*10^{-6}$
Encounters with hosts	2.5 ab (1.3;24)	7.0 ac (3.2;25)	2.1 b (2.9;54)	4.2 ab (5.1;41)	2.5 b (2.7;32)	53.0 c (32.2;20)	---	$2.22*10^{-16}$
Ovipositions in hosts	0.79[3] ab (0.41;24)	2.92[3] a (1.35;25)	0.13 c (0.34;54)	0.46 bc (0.78;41)	0.00 c (0.00;32)	0.00 c (0.00;20)	---	0.0

[1] Kruskal-Wallis test, followed by a distribution-free multiple comparison (α=0.05). Different letters in a row indicate significant differences.
[2] Overall mean=1681 (1312;54), median=1385. [3] Estimated from hosts turning black.

Table 3. Correlation between residence time and total number of encounters of *E. formosa* on tomato leaflets, based on six treatments (0, 1 and 4 hosts per leaflet at 25°C; the parasitoid introduced on the lower leaf side).

Host type at the time of introduction	Spearman's r_s	n
Unparasitized	0.896	92
Recently-parasitized	0.724	138
Black parasitized	0.780	95
All	0.789	239

Spearman rank correlation test (α=0.05).

present, the time without handling hosts was about 80% of the residence time on the leaflet. Even at a high host density of 77-200 black parasitized pupae, parasitoids were not in contact with hosts during 92% of the time. During this time parasitoids were walking while drumming for hosts, preening, or sitting still. Obviously, long residence times were not caused by host handling.

Host type and the number of hosts (1 or 4) did not influence the time until the first encounter, but (as expected) a higher number of hosts shortens this time (Table 2). At low host numbers, the time until the first encounter is about half of the residence time on clean tomato leaflets.

The average number of encounters and ovipositions in hosts on the leaflets are also given in Table 2. The residence time of the parasitoid was always significantly correlated with the total number of host encounters on the leaflet (Table 3). Linear regression yielded an average increase (slope) in residence time of 885.8 s per encounter on a leaflet with unparasitized hosts (r^2=0.808; n=92). The increase in residence time was much lower, i.e. 497.5 s, on a leaflet with parasitized hosts (r^2=0.447; n=170). Residence times were poorly correlated with the number of ovipositions in hosts, mainly because oviposition in black parasitized pupae was never observed.

Position on the leaflet

E. formosa changes from one leaf side to another while searching. On clean leaflets the average number of changes was 1.5 at 25°C. This increased to 6.7 when honeydew was present on the upper leaf side, due to the longer total residence time. Thus, both residence time and number of leaf side changes increased with a factor 4, so the duration of each stay on a leaf side remained the same. When 4 unparasitized hosts or 77-200 black parasitized hosts were present, the average number of leaf side changes were only 3.4 and 5.9 respectively, whereas the times without handling hosts were much higher than on clean leaflets. These data show that encounters with hosts, and especially ovipositions, prolong the duration of each stay on the lower side of the leaf. This is verified in more detail in Chapter 3.

E. formosa spent 64.5% of the time on the leaf side of introduction when no hosts were on the leaflet. This percentage was not affected by temperature at 20°C or

Table 4. Time spent by *E. formosa* on the leaf side of introduction as percentage of the total time, on tomato leaflets without hosts. SD_{n-1} and number of replicates given between brackets.

Temperature (°C)	15	18	20	25	25	30	25
Leaf side of introduction	upper	upper	upper	upper	lower	upper	upper
Honeydew on upper leaf	no	no	no	no	no	no	yes
Time on leaf side of introduction (%)	- (-;32)	- (-;66)	69.7 a (36.8;26)	64.2 a (30.9;38)	66.5 a (26.4;43)	56.1 a (35.9;46)	72.4 a (21.0;22)

Kruskal-Wallis test, P=0.277. Different letters in a row indicate significant differences. Overall mean=64.5 (31.1;175), median=65.9.

Table 5. Time spent by *E. formosa* on the lower leaf side as percentage of the total time on the leaflet excluding host handling time, on infested tomato leaflets when hosts were discovered, at 25°C. SD_{n-1} and number of replicates given between brackets.

Host number	1	4	1	4	4	77-200
Host type	unpar.	unpar.	rec.par.	rec.par.	black	black
Time on lower leaf side (%)	83.8 a (5.3;24)	79.1 a (8.9;23)	82.1 a (14.9;26)	83.9 a (17.9;26)	78.8 a (16.4;23)	78.5 a (14.2;20)

Kruskal-Wallis test, P=0.0907. Different letters in a row indicate significant differences. Overall mean=81.2 (13.8;142), median=83.5.

Table 6. Position on a tomato leaflet of *E. formosa* when flying away (% of all parasitoids which flew away, n=365) at 20, 25 and 30°C.

Position	upper edge	upper middle	lower edge	lower middle
Parasitoids (%)	63.9	21.9	5.2	9.0

higher, the leaf side of introduction, and the presence of honeydew on one leaf side (Table 4). Thus, there is no preference for upper or lower leaf sides when hosts are absent.

When hosts were discovered by the parasitoids, 81.2% of the time (excluding host handling time) was spent on the lower leaf side on which the parasitoids were introduced. This percentage was not affected by host number or type, nor even by the high number of hosts of 77-200 (Table 5). This percentage of time spent on the lower leaf side was significantly higher than on leaflets without hosts (64.5%) (Mann-Whitney U test, $P=7.63*10^{-4}$, n=142 and 175 respectively), again showing that encounters prolong the duration of each stay on the lower leaf side.

The percentage of the time (excluding host handling time) that the parasitoid spent on the leaf edge was 7.9 ± 8.8SD % (n=299) at 25°C. This percentage is similar to the edge area, which was 5.9 ± 0.8SD % (n=6) of the total leaflet surface. Thus, the time spent at different parts of the leaflet is proportional to the surface area of these

Table 7. Percentage of *E. formosa* parasitoids which were inactive (sitting still for more than 1 h) on clean, honeydew-contaminated or infested tomato leaflets. Total number of parasitoids given between brackets.

Temperature (°C)	15	18	20	25	25	25	25	30
Period	C	B,C	C	A	B	C	D	C
Inactive parasitoids (%)	100.0 (32)	97.0 (66)	59.4 (64)	14.7 (150)	8.1 (123)	11.5 (26)	32.7 (98)	30.3 (66)

Table 8. Barometric pressure and its change (mbar) during 12 h before the observations during spring/summer 1990 (period A) and during autumn 1991 (period D). SD_{n-1} and number of replicates given between brackets.

Period	spring/summer 1990		autumn 1991	
Barometric pressure	mean	change	mean	change
Active parasitoids	1019.6 a (8.1;128)	0.63 a (2.35;128)	1020.8 a (13.9;66)	1.08 a (3.72;66)
Inactive parasitoids	1015.1 a (5.6;22)	-0.30 b (2.59;22)	1018.6 a (11.2;32)	0.26 a (2.80;32)
P[1)]	0.0926	0.0189	0.435	0.572

[1)] Mann-Whitney U test (α=0.05). Different letters in a column indicate significant differences.

leaf parts.

The position on the leaflet from which the parasitoids flew away was not different for the treatments. Most parasitoids (85.8%) left from the upper leaf side (Table 6). Observation of the flight was difficult, because of the small size and black colour and the capricious flight pattern of *E. formosa*. The direction of the flight was usually upwards for the first few centimeters, but changed frequently afterwards.

Parasitoids' inactivity and barometric pressure

On particular days or parts of the day, almost all parasitoids were inactive and the observations were stopped after one hour. Because experiments were done in a climate room at constant temperatures and humidity, the barometric pressure was the only environmental factor that was not controlled. Observations were carried out in Wageningen, the Netherlands during four periods: during the spring and summer of 1990 (period A), during the autumn of 1990 (period B), during the spring and summer of 1991 (period C) and during the autumn of 1991 (period D). Table 7 shows the percentage of parasitoids which were inactive during the observations in these periods. Observations carried out at 25°C during period A and D were used to analyse the influence of barometric pressure on activity. During the observations in period B and C, the number of inactive parasitoids was insufficient.

Hourly data on barometric pressure were taken during each observation, as well as 6 and 12 h before each observation. The effect of the barometric pressure was only

apparent when the period of 12 h before each observation was taken into account. The spring and summer of 1990 was characterized by warm, sunny and relatively stable weather without frequent showers: the amplitude in barometric pressure was 1.74±1.72SD mbar (n=150) during the 12 h period for each parasitoid tested. Autumn 1991 was relatively unstable with many rainy days: the amplitude in barometric pressure was 2.51±2.50SD mbar (n=98). Table 8 shows that the change in barometric pressure (maximum minus minimum or vice versa) during 12 h before each observation was significantly different for active and inactive parasitoids during the spring and summer of 1990. For active parasitoids the average barometric pressure increased 0.63 mbar and for inactive parasitoids it decreased 0.30 mbar. During autumn 1991 the same trend was observed: for active parasitoids the average pressure increased 1.08 mbar and for inactive parasitoids it increased only slightly (0.26 mbar). This low average for inactive parasitoids, close to 0, means that more inactive parasitoids observed a decreasing pressure than the active parasitoids. However, the difference in change of barometric pressure between active and inactive parasitoids was not significant, which might be due to the relatively unstable character of the weather during this period.

DISCUSSION

For *E. formosa* the residence time on a clean tomato leaflet varied greatly but averaged about 20 min. At 15 and 18°C parasitoids were hardly searching and residence times were extremely long. During the present study it appeared that on a particular day or part of the day when the barometric pressure had decreased, many parasitoids became inactive. Similar effects have been reported for other insects (Lanier & Burns, 1978; Ankney, 1984; Steinberg et al., 1992). On infested leaflets when hosts were not encountered by *E. formosa*, the residence time was equal to that on clean leaflets, indicating that the parasitoid does not detect hosts from a (short) distance. *E. formosa*'s walking pattern seemed to be random, and parasitoids showed no preference for the upper or lower leaf side when no hosts were encountered. There is also no preference for the edge or for the middle of a leaf. Van Lenteren et al. (1976a) showed that different host stages are encountered in proportion to their size, and inferred random searching from this.

Contact with honeydew or encounters with unparasitized and parasitized hosts arrested the parasitoid on the leaflet. The presence of a film of honeydew with small pieces of exuviae prolonged the average residence time to 85 min. When 4 unparasitized hosts were present, the residence time was 144 min. Again, a high variation was observed. Even when parasitized black whitefly pupae were encountered and immediately rejected, the parasitoid was arrested on the leaf and up to 134 of such encounters were observed at high densities before take off. These long residence times were not caused by host handling or by a reduction in walking activity of the parasitoids. The observed residence times show that each encounter, and especially

each oviposition in unparasitized hosts, prolong the total duration on the leaf and the duration of each stay on the lower leaf side, where hosts are present. This is verified in more detail in Chapter 3.

Honeydew is apparently associated with the presence of hosts by the parasitoid. Van Vianen & van der Veire (1988) also showed an increase in time on the leaf after *E. formosa* discovered honeydew. Hågvar & Hofsvang (1991) show longer visit times when honeydew was encountered in several aphid parasitoid species.

The residence times on clean and infested tomato leaflets are very similar to that on cucumber leaves, which were almost 5 times larger: Van Eck-Borsboom (1979) measured an average residence time of 19.3 min ($\pm$16.9SD_{n-1}; n=99) on clean leaves at 25°C, 70.9 min ($\pm$79.9; n=55) on leaves with one droplet of honeydew per 10 cm^2 and 155.7 min ($\pm$102.6; n=15) on leaves when on average 3 unparasitized hosts were discovered. A correlation between residence time and leaf size (range 43-160 cm^2; n=99) was not found. However, on much larger leaves (e.g. gerbera) higher residence times were found (about 1 h on clean leaves, Sütterlin et al., 1993). A correlation between the residence time on a clean leaf and the number of parasitoids that had visited that leaf before (on the same day) was not found either, indicating that the parasitoid does not detect or react to earlier conspecifics directly, but only by encountering parasitized hosts.

A very large proportion of the parasitoids (95.9%) discovered the unparasitized hosts in a relatively short time. This is because during the treatment with *unparasitized* hosts, the parasitoids were introduced close to the hosts, which were always in the middle of the leaflet due to the use of leaf cages for whitefly oviposition. In the other treatments with 1 or 4 *parasitized* hosts, where parasitoids were not introduced near the hosts, 48-72% of the parasitoids discovered the hosts. On cucumber and gerbera leaf discs with a comparable host density, Li et al. (1987), Godthelp (1989) and Kusters (1990) found that 65% of the parasitoids discovered unparasitized hosts, which shows that detection of unparasitized hosts is not different from that of parasitized hosts.

Ledieu (1976) and Hussey et al. (1976) found *E. formosa* more often on heavily infested leaves of the crop and concluded that this was the result of detection from a distance, probably due to attraction by the honeydew that is excreted by the whiteflies. Popov & Zabudskaya (1982) observed more parasitoids in the olfactometer chamber with heavily infested leaves compared to clean leaves, but it is not clear from the paper if this was due to the parasitoids' first choise. Noldus & van Lenteren (1990), Bouwman et al. (1992) and Sütterlin & van Lenteren (in prep) re-examined this problem by direct observation of individual parasitoids in wind tunnels, olfactometers and plant cages. They concluded that the parasitoid does not distinguish between infested and uninfested plants or leaves from a distance (maximally 1.5 m) and that leaves are visited randomly. The present study showed that, once on a leaf, parasitoids are arrested after having contacted hosts or honeydew, which explains the increasing parasitoid density on infested leaves in time.

In conclusion, the present study resulted in the following essential additions to earlier work on *E. formosa*: (1) parasitoids searched at random without a preference for the upper or lower leaf side, or for the edge or middle of a leaf, (2) the residence time on clean tomato leaflets was about 20 min and equal to that on infested leaves on which no hosts are encountered, (3) parasitoids were arrested on the leaf by encounters with, and especially by ovipositions in unparasitized hosts, by encounters with parasitized (unsuitable) hosts and by contact with honeydew, (4) parasitoids were arrested on the lower leaf side by encounters with hosts, (5) many parasitoids became inactive when the barometric pressure had decreased. These new findings have important consequences for the interpretion and explanation of the overall parasitization efficiency of *E. formosa* in the field.

Time series of the present study have been used to derive the patch leaving mechanism for *E. formosa*. The parasitoids' *tendency* of leaving (probability per unit of time to leave) and its reciprocal, the giving up time, were estimated by means of the proportional hazards model (Chapter 3). The *tendency* of changing from one leaf side to the other, and the influence of different intra-patch experiences with hosts were also tested. This was done because comparison of total residence *times* is handicapped because the number, timing and sequence of encounters with hosts can never be kept equal among replicates.

The new data are used in a stochastic simulation model of the foraging behaviour of *E. formosa* (Chapters 5, 6, 7 and 10). Based on these simulations, we are able to judge in what situations *E. formosa* can be used as an efficient biological control agent.

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Chapter 3

The influence of intra-patch experiences and temperature on the time allocation of the whitefly parasitoid *Encarsia formosa*

ABSTRACT

The effect of experiences, such as contact with honeydew, rejections of hosts and ovipositions in hosts, and of temperature, on the time allocation of individual *Encarsia formosa* female parasitoids on tomato leaflets have been studied. Behavioural records were analysed by means of the proportional hazards model. Analyses were carried out at two levels: (1) the tendency of leaving and (2) the tendency of changing from one leaf side to another. The patch-leaving behaviour of *E. formosa* can be described by a stochastic threshold mechanism, which is characterized by a certain tendency (probability per time) to leave. The median time from being placed on the leaflet or, if it occurred, from the latest encounter with a host until leaving was 18.6 min. The median time for changing from one leaf side to the other was initially 11.6 min and dropped to 5.7 min after both leaf sides had been visited. The effect of temperature, ranging from 20 to 30°C, was negligible. The presence of honeydew as well as the first oviposition in an unparasitized host decreased the tendency to leave, thus increasing the giving up time (GUT) since latest encounter with a host. Encounters with parasitized hosts did not affect the GUT since latest encounter; as a result the total residence time increased. After the first oviposition in an unparasitized host the tendency of changing from the lower leaf side on which hosts were present to the upper side was decreased. The presence of honeydew did not affect the tendency of changing leaf sides.

INTRODUCTION

Foraging by a parasitoid involves a series of steps that brings it progressively closer to their hosts (Salt, 1935; Doutt, 1964; Vet & Dicke, 1992; and for an extensive review of all phases see Nordlund et al., 1981). When searching in a host poor environment, or when most hosts in a certain patch have been exploited, the motivation to leave such an area and to start searching for a more profitable patch should be initiated.

The question of when to leave a patch optimally is one of the main issues in optimal foraging theory. Several strategies have been modelled (Charnov, 1976; Iwasa et al., 1981; McNair, 1982; McNamara & Houston, 1987; Green, 1987). The best known hypotheses for patch-leaving mechanisms are: (a) a patch is left after a fixed number of hosts is parasitized, (b) the parasitoids leave the patch after a fixed period of time and (c) the parasitoids leave after the oviposition or encounter rate falls below a certain threshold (Gibb, 1962; Krebs, 1973; Murdoch & Oaten, 1975; Waage, 1979).

Waage (1979) was among the first to study effects of intra-patch experiences on leaving decisions of parasitoids empirically. He predicted that ovipositions in unparasitized hosts should increase the time spent in a patch since the latest oviposition (giving up time, GUT). Encounters with parasitized hosts, however, are suggested to

result in a decrease. Most of the optimal foraging theories are based on a priori modelling, since the relative importance of several factors in determining when a patch is left is pre-set in the models. Predictions can be compared qualitatively with empirical data. An important extension to a priori modelling is to quantify the relative effects of several factors on patch-leaving decisions from the empirical data, by using statistical models (see Haccou et al., 1991; Hemerik et al., 1993).

Much research has been done on host searching, host selection and parasitization of the whitefly parasitoid *Encarsia formosa*. Little is known about the time allocation on leaves at low host densities when the parasitoid gradually depletes a patch. Here, we study the influence of different experiences and of temperature on the time allocation of this parasitoid on a tomato leaflet, i.c. the probability per unit time of leaving the leaflet (leaving tendency) or to change from the lower to the upper leaf side or vice versa (tendency of changing leaf sides). Presence of honeydew was considered a factor because parasitoids can be expected to react to this host associated cue, which is also used as a food source. Ovipositions are incorporated as another factor, because they can give information about the quality of the patch. Rejections of hosts are included as relevant since encounters with parasitized hosts can give information about patch depletion.

E. formosa Gahan (Hymenoptera: Aphelinidae) is a synovigenic, solitary larval parasitoid of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). Once on the leaf the wasp starts walking and drumming the leaf surface with its antennae. Hosts are only present on the lower leaf side. Upper leaf sides may be covered by honeydew produced by hosts in higher leaf layers. On encounter, a host can be rejected after an inspection with the antennae (antennal rejection) or can be rejected or accepted for oviposition or host feeding after an insertion of the ovipositor (ovipositorial rejection, oviposition or host feeding) (van Lenteren et al., 1980).

Experiments were carried out in which individual parasitoids were observed continuously either on clean leaflets, on leaflets with honeydew, or on leaflets with unparasitized and parasitized hosts. Analysis of total residence times should be discouraged because number, timing and sequence of encounters and the resulting handling behaviours can never be kept equal among replicates. The statistical models that we applied to analyse the experimental data are special applications of the proportional hazards model (Cox, 1972; Kalbfleisch & Prentice, 1980). This model was chosen because it is a stochastic model, it makes no assumptions about how probabilities change with time, it is easily adapted to different situations and censored data, which inevitably occur in behavioural research (see Bressers et al., 1991), are handled accurately. When one studies the giving up time (GUT) since the latest encounter of a parasitoid, the encounter with a host causes a censored observation of the searching time, because it is not known when the parasitoid would have left if the host had not been encountered. The GUT will be underestimated when these censored observations are neglected. Another advantage of this approach is that the outcome can

directly be incorporated as input in stochastic simulation models of insect behaviour (Chapters 5, 6, 7, and 10).

MATERIAL AND METHODS

Details on the growing of tomato plants, the rearing and pre-treatment of whiteflies and parasitoids and on the production of tomato leaflets covered with a film of honeydew, or leaflets with a certain number of unparasitized or recently parasitized L3/L4 larvae or black parasitized pupae can be found in Chapter 2. Recently parasitized whitefly larvae were parasitized by conspecifics 1-7 h before the observation and black parasitized pupae 9-10 days (at 22°C) before the observation.

Experimental set-up

The observations were carried out on tomato leaflets in a climate room at a constant temperature (±1°C) and 70±5% RH. At the start of each observation a single *E. formosa* female was introduced on a leaflet placed in a glass vial (5.5x1.5 cm) filled with water. This vial was attached to the stem in the middle of a tomato plant. Leaflet angle was about 45°. Five plants surrounded the plant to mimic the light conditions of a crop and to provide the parasitoid with ample opportunity to hop or fly to another leaflet. Light intensity at the observed leaflet was 5775 lux. Continuous observation started directly after the introduction of the parasitoid. When the parasitoid was on the lower leaf side it was observed through a stereo microscope; when it was on the upper leaf side it was followed by eye.

The following behavioural components were recorded using the computer software package 'The Observer' (Noldus, 1991): a) searching, b) standing still/ eating honeydew/ preening, c) drumming the host with antennae, d) oviposition posture, and e) host feeding. Throughout the experiment, the position of the parasitoid on the leaflet was recorded: the upper leaf side, the lower leaf side, or whether the parasitoid was on the edge or not. Edge width was taken the same as the width of the parasitoids' searching path (0.5 mm). An observation stopped when the parasitoid flew from the leaflet or when it walked off the petiole, which was rarely observed. When no foraging activity occurred for more than 60 min, the observation was stopped and not included in the analysis. Observations were also excluded when a parasitoid left within 180 s, because this was clearly due to disturbance of the parasitoid during introduction.

Two types of experiments were conducted. In experiment I no hosts were present and in experiment II a varying number of unparasitized or parasitized hosts were present on the lower leaf side. Experiment I was done to study the effect of temperature, the side of the leaflet on which the parasitoid was introduced to and the presence of honeydew, on the leaving tendency and the tendency of changing leaf sides. Five combinations of these factors were tested: (1) 25°C, without honeydew, parasitoid introduced on upper leaf side (n=39), (2) 25°C, without honeydew, parasitoid introduced on lower leaf side (n=45), (3) 25°C, with honeydew, parasitoid introduced

on upper leaf side (n=24), (4) 20°C, without honeydew, parasitoid introduced on upper leaf side (n=29) and (5) 30°C, without honeydew, parasitoid introduced on upper leaf side (n=50).

Experiment II was conducted to estimate the effect of encounters with hosts on the leaving tendency and the tendency of changing leaf sides. Therefore, whitefly immatures were present on the lower leaf side. In this experiment the ambient temperature was always 25°C, honeydew was absent and the parasitoid was introduced on the lower leaf side. As a control, the group of 45 replicates from experiment I was taken. The only difference between the 6 treatments with hosts was the number of hosts and whether or not they were parasitized by a conspecific: (1) 1 unparasitized L3/L4 larva (n=24), (2) 4 unparasitized L3/L4 larvae (n=27), (3) 1 recently-parasitized L3/L4 larva (n=43), (4) 4 recently-parasitized L3/L4 larvae (n=43), (5) 4 parasitized black pupae (n=41) and (6) 77 to 200 parasitized black pupae (n=23).

It is not necessary to aim at equal number of replicates, because time periods between subsequent encounters were analysed (see description of the model) and each replicate differs in number of such time periods.

THE REGRESSION MODEL

The proportional hazards model is formulated in terms of the hazard rate, which is the probability per unit time that a certain event (a so-called failure) occurs. The hazard rate can be considered here as the tendency of a parasitoid to leave a leaflet or to change to the other side of the leaflet. It is assumed that parasitoids have a basic tendency to perform a certain behaviour (base line hazard), which is reset after certain renewal points. Renewal points occur here at times of encounters with hosts. These clearly interrupt searching of *E. formosa* due to the relative long handling times. The observed hazard rate is assumed to be the product of the base line hazard and a factor that gives the joint effect of a set of p covariates $z_1,....,z_p$. The covariates are, for instance, the intra-patch experiences, such as the occurrence of ovipositions (with values 0,1,2, ...) or the absence or presence of honeydew (with value 0 or 1 respectively). They are called fixed since they do not change between two successive encounters. The general form of the model with fixed covariates is:

$$(1) \qquad h(t;z) = h_0(t)\ \exp\{\sum_{i=1}^{p} \beta_i\ z_i\}$$

where $h(t;z)$ denotes the observed hazard rate, $h_0(t)$ the base line hazard, t the time since the latest renewal point and $\beta_1,....,\beta_p$ the relative contributions of the fixed covariates $z_1,....,z_p$. The form of the base line hazard in time is left unspecified; $h_0(t)$ as well as $\beta_1,....,\beta_p$ are estimated from the data by means of likelihood maximization (for further details, see Haccou & Hemerik, 1985; Kalbfleisch & Prentice, 1980). The test statistic is distributed as a χ^2 with p degrees of freedom. The test procedure is explained in Hemerik et al. (1993). The name 'proportional hazards model' stems from

the assumption that for different values of z_i the hazard rates $h(t;z)$ are proportional. This multiplicative effect can be tested (see Haccou & Hemerik, 1985).

Leaving tendency

The data used in the regression model were the observed time periods of each parasitoid from being placed on the leaflet until the first encounter with a host, between successive encounters, and from the last encounter until leaving the leaflet. During such periods, the parasitoid can either search for hosts, stand still, preen or eat honeydew. When no encounters occurred, only one time period was observed: the total residence time on the leaflet. An encounter with a host caused a censored observation of the time until leaving. Sometimes censored observations were caused by parasitoids walking off the leaflet on the petiole, or by the experimenter. The renewal points for the leaving tendency were the moments of being placed on the leaflet and the moments of resuming search after encounters with hosts.

The tendency of leaving the leaflet in experiment I is given by equation (1) with 4 fixed covariates, namely (a) the presence or absence of honeydew on the upper leaf side, (b) the effect of a temperature of 20°C in comparison to the higher regimes (25 or 30°C), (c) the effect of a temperature of 30°C in comparison to the lower regimes (20 or 25°C) and (d) the side of the leaflet on which the parasitoid was introduced.

In experiment II the effect of the following fixed covariates on the leaving tendency were estimated: (a) the time since being placed on the leaflet, (b) the number of antennal rejections of a recently-parasitized host, (c) the number of antennal rejections of a parasitized black host, (d) the number of ovipositorial rejections of a recently-parasitized host, (e) the number of ovipositions in a recently-parasitized host (superparasitism) and (f) the number of ovipositions in an unparasitized host. The effects of host feedings or rejections of unparasitized hosts could not be analysed because these behaviours were rarely observed in the experiments.

Tendency of changing leaf sides

The data used in the regression model were the observed time periods on a particular leaf side from the beginning on that leaf side until the first encounter, between successive encounters on that leaf side and from the last encounter until changing to the other leaf side. When no encounters occurred on a particular leaf side, the observed time period equalled the total time from the beginning on that leaf side until changing leaf sides again. When analysing time periods on upper or lower leaf sides, censors were caused by encounters with hosts, by parasitoids flying away from the leaflet, or sometimes by parasitoids walking off the leaflet or by the experimenter. Renewal points were the moments of changing to the leaf side under consideration and the moments of resuming search after encounters with hosts.

In experiment I the tendency of changing leaf sides is given by equation (1) with 5 fixed covariates: the first three covariates of the leaving tendency (a,b and c), plus (d) the time since being placed on the leaflet, and (e) whether or not both leaf sides have been visited.

The tendency of changing leaf sides in experiment II is given by equation (1) with 7 fixed covariates, namely the first six covariates of the leaving tendency (a,b,c,d,e and f), plus (g) whether or not both leaf sides have been visited.

RESULTS

Leaving tendency

The estimated leaving tendency and the effects of several covariates are given in Table 1. The basic leaving tendencies (base line hazards; probability of leaving per unit of time) in Experiment I and II were approximately constant over time and almost equal (Table 1A). The combined effect of all covariates is significant in both experiments (Table 1B).

A film of honeydew with small pieces of exuviae on the upper leaf side strongly reduced the leaving tendency of the parasitoid. The multiplication factor $\exp(\beta)$ is below 1, which results in a lower hazard rate $h(t,z)$ according to equation (1): time periods on leaflets with honeydew were much higher than on clean leaflets. The leaf side on which the parasitoid started and the temperature did not influence the leaving tendency significantly on clean leaflets (Table 1C).

The effect of honeydew is shown graphically after stratification of the data (Figure 1). The cumulative base line hazards over time were approximately straight lines, so the probability of leaving remained nearly constant over time and can be estimated by the slope. In this case the maximum likelihood estimator is given by the total number of failures divided by the total failure plus censor times of all replicates of a treatment. However, the failure-to-censor ratio must be high. This was not the case in Experiment II: encounters with hosts resulted in many censored observations, thus making this estimate of the base line hazard less reliable.

Graphical goodness of fit tests can be performed by making plots of the 'residuals'. If a variable has a multiplicative effect, these plots are straight lines through the origin with a slope of 45 degrees (Kalbfleisch & Prentice, 1980; Haccou & Hemerik, 1985). Figure 2 shows the 'residuals' of Experiment I and II.

Because leaving tendency remained constant over time, the fraction of parasitoids that remain on a leaflet over time (the survival function) follows an exponential distribution. Thus the median time period on a leaflet can be estimated by ln(2) divided by the leaving tendency. This results in a median residence time of 1116 s (18.6 min) on clean tomato leaflets and 5978 s (99.6 min) on uninfested tomato leaflets containing a film of honeydew with small pieces of exuviae on the upper leaf side.

In experiment II the first oviposition in an unparasitized host strongly reduced the leaving tendency (Table 1C), resulting in an increase in the time period since the latest encounter until leaving (GUT since latest encounter). This is graphically shown after stratification in Figure 3. In a preliminary study the effect was tested for all realized ovipositions ranging from 0 to 4, but no clear difference was found for the

Table 1A. Estimated leaving tendency (base line hazard in s^{-1}) in experiment I and II.

Experiment I	0.000621
Experiment II	0.000732 [1)]

[1)] Estimated without censors due to encounters.

Table 1B. The value of the test statistic T (df) for the combined effect of all covariates on the leaving tendency in experiment I and II.

Experiment I	39.28 (4) *
Experiment II	22.90 (6) *

*: $P < 0.05$

Table 1C. Estimated effects (multiplication factor exp β) of covariates on the leaving tendency in experiment I and II and the value of the test statistic T.

	Effect	T (df)
Experiment I		
Introduction on upper leaf side	0.7788	1.23 (4)
Honeydew on upper leaf side	0.1867	27.05 (4) *
Temperature 20°C	0.9343	0.07 (4)
Temperature 30°C	0.7027	2.37 (4)
Experiment II		
Time since being placed on leaflet[1)]	1.0000	1.89 (6)
Antennal rejection of recently-parasitized hosts	1.1351	3.73 (6)
Antennal rejection of parasitized black hosts	0.9948	0.03 (6)
Ovipositorial rejection of recently-parasitized hosts	0.7255	3.63 (6)
Oviposition in recently-parasitized hosts	0.8422	1.01 (6)
Oviposition in unparasitized hosts[2)]	0.4648	16.02 (6) *

*: $P < 0.05$. [1)] Effect given per second. [2)] Effect given when covariate is 0/1 for no/one or more events.

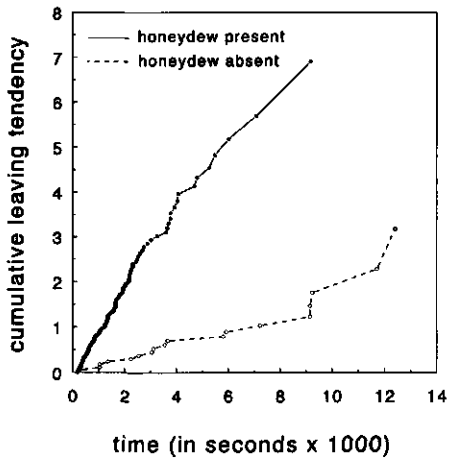

Figure 1. Cumulative leaving tendency (cumulative hazard rate) in experiment I, when a film of honeydew with small pieces of exuviae is absent or present on the upper leaf side.

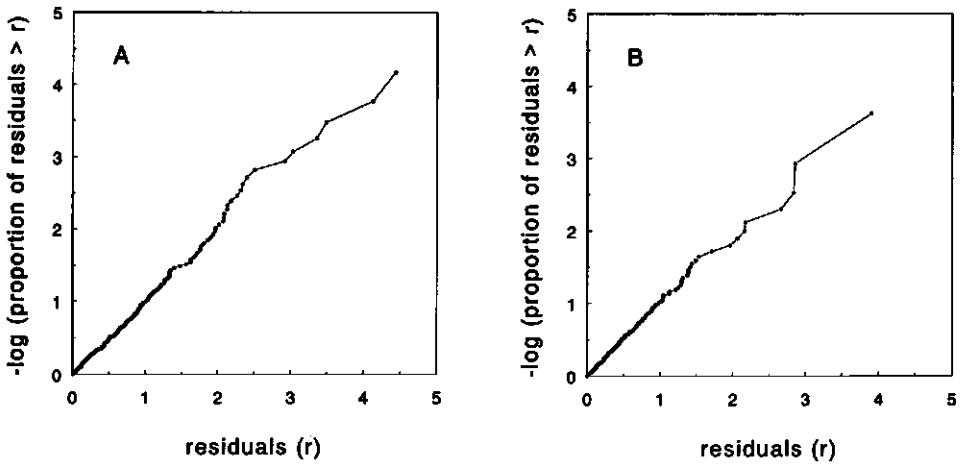

Figure 2. Graphical test for goodness of fit (-log survivor of the residuals) of the model for the leaving tendency of experiment I (A) and II (B).

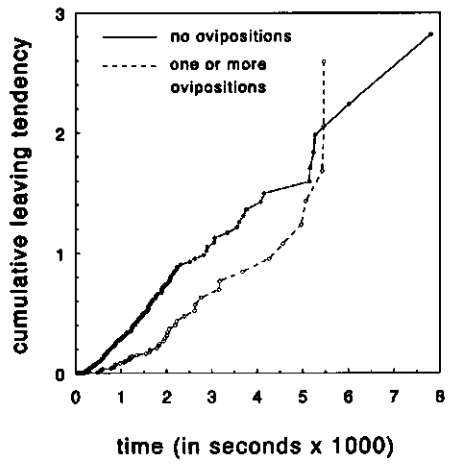

Figure 3. Cumulative leaving tendency (cumulative hazard rate) in experiment II for no or one or more ovipositions in unparasitized hosts.

effect after one or more ovipositions.

Time since being placed on the leaflet and encounters with parasitized hosts did not affect the leaving tendency significantly (Table 1C), so the GUT since latest encounter was not affected. Even encounters with black parasitized hosts did not affect the leaving tendency, although leaflets with 77 to 200 black hosts were used in the experiments. On these leaflets, the number of encounters was on average 53 (range 12-134).

As a consequence, each encounter with hosts, whether or not parasitized, increased the residence time on a leaflet, even when the GUT since latest encounter is not changed. The median GUT since latest encounter with parasitized or unparasitized hosts was 1116 s (18.6 min) if no oviposition had occurred. This time period increased to 2401 s (40 min) after the first oviposition in an unparasitized host.

Tendency of changing leaf sides

In a preliminary analysis the effect of all covariates was tested for many realized values. If the effect did not differ when a covariate was 1 or higher, the final analysis was done with the covariate being 0 or 1 for zero or more than zero events respectively.

The estimated tendency of changing from one leaf side to the other and the effects of the covariates are given in Table 2. The basic tendencies (base line hazards) in Experiment I and II were about the same. Again cumulative base line hazards over time were approximately straight lines. Encounters with hosts on the lower leaf side in experiment II resulted in a low failure-to-censor ratio, thus making the estimate of the base line hazard from lower to upper leaf side less reliable (Table 2A).

The basic tendency of changing leaf sides was almost equal for lower and upper leaf side (Table 2A). The median time period on the lower leaf side since the beginning on that leaf side or, if it occurred, since the latest encounter on that leaf side, was in Experiment I initially 724 s (12.1 min). On the upper leaf side in Experiment I and II median times were respectively 636 (10.6 min) and 745 s (12.4 min).

The combined effect of all covariates were significant in both experiments (Table 2B). After the first oviposition in an unparasitized host the tendency of changing from lower to upper leaf side was strongly decreased (Figure 4), thus increasing the time since the latest encounter on the lower leaf side (where hosts were present) to 1288 s (21.4 min).

After both leaf sides had been visited by the parasitoid, the tendency of changing leaf sides increased strongly on both leaf sides in experiment I. As a result, the median times were shorter: 400 s (6.7 min) and 286 s (4.8 min) on the lower and upper leaf side respectively. Also in experiment II the tendency of changing from lower to upper leaf side increased after both leaf sides had been visited. A similar, but not significant effect was found for the tendency of changing from upper to lower leaf side.

The presence of a film of honeydew with small pieces of exuviae on the upper leaf side did not influence the tendency of changing from upper to lower leaf side. In general, the tendency of changing leaf sides was not affected by the time since being placed on the leaflet, the temperature and encounters with parasitized hosts.

Table 2A. Estimated tendency of changing leaf sides (base line hazard in s^{-1}) in experiment I and II.

	From lower to upper side	From upper to lower side
Experiment I	0.000958	0.00109
Experiment II	0.00129 [1)]	0.000931

[1)] Estimated without censors due to encounters.

Table 2B. The value of the test statistic T (df) for the combined effect of all covariates on the tendency of changing leaf sides in experiment I and II.

	From lower to upper side	From upper to lower side
Experiment I	33.60 (4)	60.15 (5) *
Experiment II	212.33 (7) *	67.25 (7) *

*: $P < 0.05$

Table 2C. Estimated effects (multiplication factor exp β) of covariates on the tendency of changing leaf sides in experiment I and II and the value of the test statistic T.

	From lower to upper side		From upper to lower side	
	Effect	T (df)	Effect	T (df)
Experiment I				
Time since being placed on leaflet[1)]	1.0000	0.14 (4)	1.0000	0.01 (5)
Both leaf sides visited	1.8072	10.84 (4) *	2.2258	19.35 (5) *
Honeydew on the leaf side	-	-	0.9034	0.25 (5)
Temperature 20°C	0.6210	2.23 (4)	0.7989	0.61 (5)
Temperature 30°C	0.6316	9.23 (4)	1.9440	12.33 (5) *
Experiment II				
Time since being placed on leaflet[1)]	1.0000	0.57 (7)	0.9999	7.47 (7)
Antennal rejection of recently-parasitized hosts[2)]	1.3716	4.42 (7)	1.7151	4.81 (7)
Antennal rejection of parasitized black hosts[2)]	1.1134	0.55 (7)	2.7547	29.70 (7) *
Ovipositorial rejection of recently-parasitized hosts[2)]	0.8542	0.81 (7)	2.3901	15.15 (7) *
Oviposition in recently-parasitized hosts[2)]	0.9268	0.16 (7)	1.0046	0.00 (7)
Oviposition in unparasitized hosts[2)]	0.5616	15.11 (7) *	0.7999	0.94 (7)
Both leaf sides visited	3.3797	93.82 (7) *	1.5196	8.00 (7)

*: $P < 0.05$. [1)] Effect given per second. [2)] Effect given when covariate is 0/1 for no/one or more events.

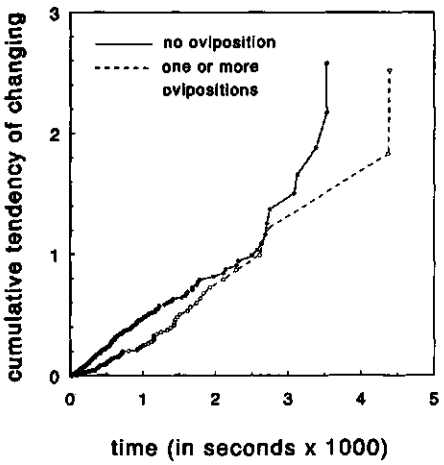

Figure 4. Cumulative tendency of changing from lower to upper leaf side (cumulative hazard rate) in experiment II for no or one or more ovipositions in unparasitized hosts.

DISCUSSION

Leaving a leaf side or a leaflet can be described by a certain probability per unit of time, resulting in a great variation in GUT since latest encounter. For *E. formosa* on tomato leaflets this probability is approximately constant over time and the median time period that the parasitoids remain on a leaflet is 18.6 min after landing or after their latest encounter with a host. This time is equal on clean and on infested leaves when no hosts were encountered, so once on the leaf the parasitoid is not arrested by the presence of hosts at a short distance on the same leaf. This time is also not influenced by temperature ranging from 20 to 30°C. Such daily temperature fluctuations are common in the field and as they do not influence the distribution of the sessile hosts, there is no need for the parasitoid to change its leaving tendency.

The presence of a film of honeydew with small pieces of exuviae and the first oviposition in an unparasitized host decrease the leaving tendency of *E. formosa* on tomato leaflets. This increases the GUT since landing or since the latest encounter to a median of about 100 and 40 min respectively, without affecting the walking pattern, speed or activity (van Lenteren et al., 1976; Chapter 4). These observed responses increase the likelihood of encountering hosts in a natural, clumped host distribution. Honeydew is apparently associated with the presence of hosts. The majority of honeydew is produced by the preferred L3, L4 and prepupal whitefly stages (Lei Hong & Xu Rumei, 1993; Madueke, 1979). Van Vianen & van der Veire (1988) observed an increase in time on the leaf after *E. formosa* discovered honeydew. Hågvar & Hofsvang (1991) review longer visit times when honeydew was present for several aphid parasitoids.

Haccou et al. (1991) and Hemerik et al. (1993) found a multiplication factor for GUT (since latest oviposition) of 1/0.87 and 1/0.80 per oviposition after ovipositions in unparasitized hosts for *Leptopilina heterotoma* and *L. clavipes* respectively. These parasitoids are mainly time-limited (Driessen & Hemerik, 1992). The effect on GUT (since latest encounter) for *E. formosa* is initially stronger, namely a multiplication factor of 1/0.46 for the first oviposition. The second, third and fourth oviposition give no additional effect. *E. formosa* can be egg-limited or time-limited, depending on the situation. Once on a patch with hosts all 8-10 eggs can be laid within one hour, whereas maturation of new eggs takes more time (van Vianen & van Lenteren, 1986). Also Sugimoto & Tsujimoto (1988) found that the parasitoid *Chrysocharis pentheus* stayed longer on a patch after the first encounter with a host.

Encounters with parasitized hosts do not affect the leaving tendency and the resulting GUT since latest encounter of *E. formosa*, even though experiments were conducted in which more than 100 of such encounters were realized. Although the leaving tendency does not increase after such encounters, parasitoids are arrested and the residence time on a leaflet does increase. When encounters with parasitized hosts are a good indicator of the presence of unparasitized hosts, there is no need for the parasitoids to increase the leaving tendency after rejections when they are not time-limited. In greenhouses this is usually the case, because not all unparasitized hosts on a leaflet are parasitized by one *E. formosa*. This is caused by the parasitoids' random walking pattern and short residence time at low host densities and by egg-limitation at higher densities.

Haccou et al. (1991) found no effect of encounters with parasitized hosts on the GUT since latest oviposition of *Leptopilina heterotoma*. This parasitoid is not arrested by such encounters. For *L. clavipes*, the effect was dependent on whether previous ovipositions had occurred (Hemerik et al., 1993). Van Lenteren (1991) discussed the fact that early encounters of *L. heterotoma* with parasitized hosts might increase the tendency of staying on the patch, but later, when the ratio of unparasitized to parasitized hosts is low, encounters might result in the opposite. However, in an analysis in which the data of *E. formosa* were stratified according to the number of encounters with parasitized hosts, even a high number of encounters of 10 to 134 had no effect on the leaving tendency. In another analysis of the data hosts were distinguished between hosts parasitized by the same female or by a conspecific. In the first set-up the ratio of unparasitized to parasitized hosts decreased during observation from 1 to 0 in many cases and in the latter it remained always 0. In both cases, encounters with parasitized hosts did not have any effect on the leaving tendency of *E. formosa*.

Summarizing, the present paper showes the following additions and differences to earlier work: (1) *E. formosa* is arrested on the leaf by contact with honeydew and by encounters with, and especially by ovipositions in unparasitized hosts; (2) the parasitoid is even arrested by encounters with parasitized (unsuitable) hosts; (3) the parasitoid is not arrested by the presence of hosts which are not encountered; (4) parasitoids usually leave from the upper leaf side, because on this leaf side no

encounters with hosts occur; (5) the parasitoid does not make a distinction between the upper and lower leaf side when searching for hosts, whereas whitefly immatures are only present on the lower leaf side; (6) the parasitoid is arrested on the lower leaf side by encounters with, and especially by ovipositions in unparasitized hosts; (7) the parasitoid is also arrested on the lower leaf side by encounters with parasitized hosts; and (8) the parasitoid is not arrested on the honeydew-contaminated leaf side. Ledieu (1976) and Hussey et al. (1976) found *E. formosa* more often on heavily infested leaves of a crop and concluded that this was the result of host detection from a distance. Noldus & van Lenteren (1990) showed by direct observation of individual parasitoids that they do not distinguish between infested and clean plants or leaves before landing. The present study showes that the increasing number of parasitoids on infested leaves can be explained by the arrestment effect after landing.

The patch-leaving behaviour of *E. formosa* can be described by a stochastic threshold mechanism: the parasitoid leaves after the host *encounter* rate falls below a certain threshold (encounters per time, which is the reciprocal of GUT). This threshold is not fixed however, but shows a great variation, and can be described by a probability. Three differences with the model of Waage (1979) are that (1) in our statistical model the relative importance of different factors is based on the data; (2) *Venturia canescens* leaves a patch when the *oviposition* rate falls below a certain threshold and encounters with parasitized hosts do not influence patch times; and (3) the threshold (and thus the GUT) in the model of Waage (1979) is assumed to be deterministic and never varies at a constant host density and timing of ovipositions. As Waage (1979) noticed, the observed GUT (since last oviposition) was often shorter than some previous interval between ovipositions on the patch, which could not be explained by the model. For *E. formosa* stochasticity plays an important role, as observed standard deviations were large and equalled the mean GUT values.

The proportional hazards model is appropriate to analyse data on time allocation because it is a stochastic model. Another advantage of this approach is that the results are quantitative and can be incorporated directly into simulation models. The estimated leaving tendency and the tendency of changing leaf sides together with the significant effects of certain types of encounters with hosts and honeydew will be used as input in a stochastic simulation model of the foraging behaviour of *E. formosa* on a leaf (Chapter 6). With this model, the functional response can be simulated on a leaf in a natural situation, where the parasitoid can fly to other leaves. Based on these simulations, we are able to judge in what situation *E. formosa* can be used as an efficient biological control agent.

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Chapter 4

Foraging behaviour of the whitefly parasitoid *Encarsia formosa* on tomato leaflets

ABSTRACT

Individual *Encarsia formosa* parasitoids were observed continuously until the parasitoids flew away, either on clean tomato leaflets, on leaflets with honeydew, or on leaflets with unparasitized and parasitized whitefly larvae. Encounters with unparasitized and parasitized whitefly larvae, and contact with honeydew arrested the parasitoids on the leaflet. The walking speed increased linearly from 0.179 to 0.529 mm/s between 15 and 25-30°C. The walking activity showed another relationship with temperature: it was below 10% at 15 and 18°C, and increased to about 75% at 20, 25 and 30°C. It was not affected by host encounters or by 1 to 4 ovipositions. The total handling time of hosts was between 1.8-21.8% of the total time on the leaflet. Self-superparasitism was not observed. Conspecific-superparasitism did occur in 14% of the encounters with hosts containing a parasitoid egg, but was not observed anymore when the parasitoid egg had hatched. Experienced parasitoids superparasitized as often as naive females. The foraging behaviour of *E. formosa* from landing on a leaf until departure has now been quantified and is discussed.

INTRODUCTION

Biological control of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae), with the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) has been applied since the 1920s and is at present commercially used with success in several greenhouse vegetables (van Lenteren & Woets, 1988). An intensive research program backed the reliable application of this parasitoid. Part of this research consisted of direct observation of host searching, host selection, host discrimination, parasitization, and host feeding behaviour (van Lenteren et al., 1976a and b; Nell et al., 1976; van Lenteren et al., 1980). Most of these experiments were, however, conducted during a fixed time period at high densities of unparasitized hosts on leaves removed from the plant. Little is known about these processes at low host densities when the parasitoid gradually depletes a patch and leaves, or when the parasitoid visits an already depleted patch, more typical of conditions under which whitefly is controlled by *E. formosa*.

E. formosa is a synovigenic, solitary larval parasitoid of the greenhouse whitefly. In order to reproduce, *E. formosa* has to search for the sessile whitefly immatures. The parasitoid moves from leaf(let) to leaf(let) by flying or hopping, without distinguishing between infested and clean plants or leaves before landing (Noldus & van Lenteren, 1990; Sütterlin & van Lenteren, in prep.). Once on a leaf it starts walking and drumming the leaf with its antennae. Hosts are only present on the lower leaf side. Upper leaf sides may be covered by honeydew produced by hosts in higher leaf layers. On encounter, a host can be rejected after an inspection with the

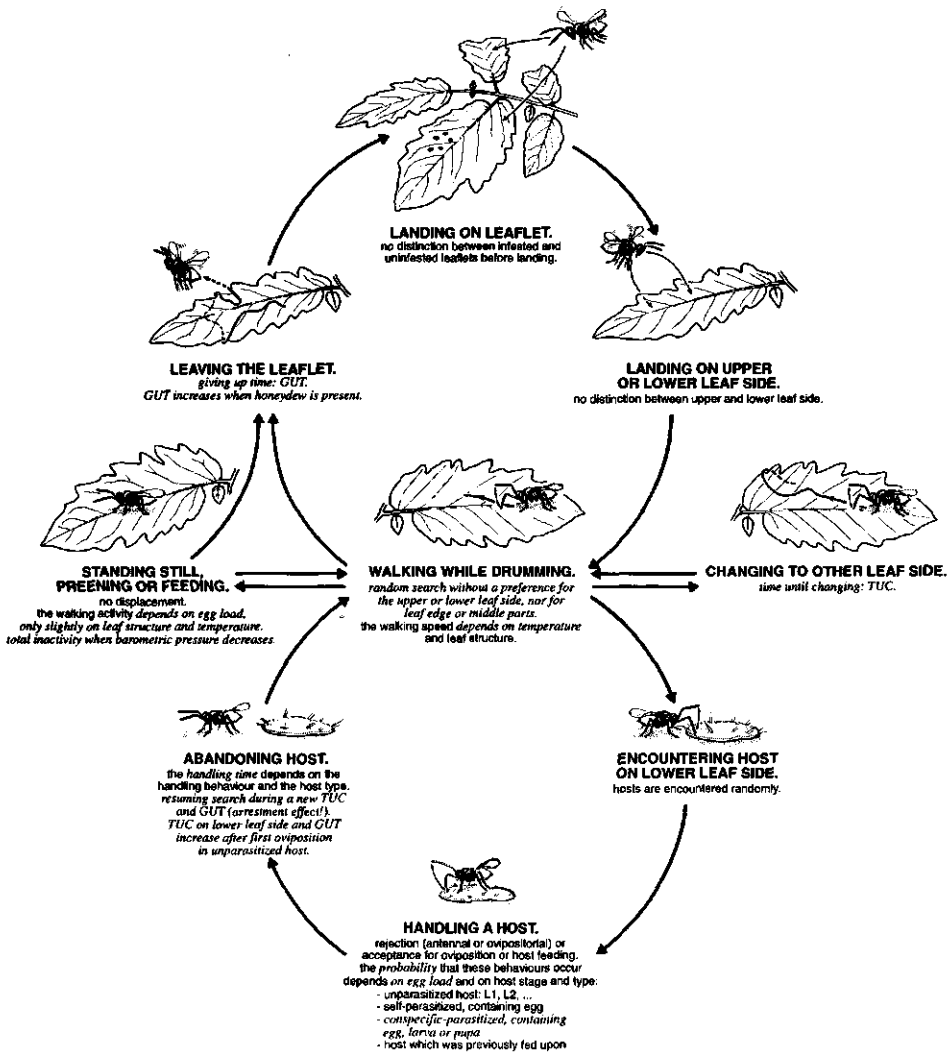

Figure 1. Overview of the foraging behaviour of *Encarsia formosa* on a tomato leaflet. Gaps in knowledge which were quantified by the present experiments are given in italics. Data on time allocation of the parasitoid (TUC: the time until changing leaf sides; GUT: the giving up time) can be found in Chapter 3. The body length of the wasp is 0.6 mm.

antennae (antennal rejection) or can be rejected or accepted for oviposition or host feeding after insertion of the ovipositor (ovipositorial rejection, oviposition or host feeding, respectively) (van Lenteren et al., 1980).

In greenhouses where biological control is successful, average whitefly densities are usually extremely low, and vary between 0 and 0.2 whitefly pupae per plant during a growing season (Eggenkamp-Rotteveel Mansveld et al., 1978). Most of the leaves are not infested and the parasitoids spend much time searching for hosts. The rate at which they hop or fly from leaf to leaf depends on the host situation and thus on the time which they stay on a particular leaf. The aim of this study was to quantify the whole foraging process from landing on a leaf until departure (see Figure 1). Later, this information will be used to estimate the parasitization efficiency of the parasitoid with the help of a simulation model (Chapters 5, 6, 7, and 10). Experiments were done on (1) clean tomato leaflets, (2) leaflets with honeydew, (3) leaflets with a *low* number of *unparasitized* hosts, and (4) leaflets which were depleted by conspecifics earlier and only bear *parasitized* hosts. As the temperature usually varies between 15 and 30°C in greenhouses, the effect of these temperatures on the foraging behaviour was also tested. Individual parasitoids were observed continuously on both leaf sides until they flew away, a procedure which has not been followed until now.

MATERIAL AND METHODS

Details on the growing of tomato plants, the rearing of whiteflies and parasitoids and on the production of tomato leaflets covered with a film of honeydew, or leaflets with a certain number of unparasitized or recently parasitized L3/L4 larvae or black parasitized pupae can be found in Chapter 2. Recently parasitized whitefly larvae were parasitized by conspecifics 1-7 h before the observation and black parasitized pupae 9-10 days (at 22°C) before the observation. To produce parasitized whitefly larvae (L4) containing a parasitoid larva, a few parasitoids were released on a leaflet bearing unparasitized L3/L4 larvae. These leaflets remained attached to the plants and were kept in cages at 25°C for 6 d. This was 2 days before pupation of the parasitoid immature and blackening of the host. Whitefly larvae were considered to be parasitized after an oviposition posture lasting longer than 120 s was observed (van Lenteren et al., 1976b). At the end of the observation the larvae were dissected to check if each oviposition posture was successful.

Details on the age and pre-treatments of the parasitoids can be found in Chapter 2. In one case, which will be specified later, experienced parasitoids were tested, which had one oviposition in an unparasitized L3 larva the day before the observation. They were kept in glass petri dishes (5 cm in diameter) with a droplet of honey at 25°C and aged 24-48 h at the time of observation.

Experimental set-up: direct observations

The observations were carried out on tomato leaflets in a climate room at a constant temperature (±1°C) and 70±5% RH. At the start of each observation a single naive *E. formosa* female was introduced on a leaflet placed in a glass vial (5.5x1.5 cm) filled with water. This vial was attached to the stem in the middle of a tomato plant. Leaflet angle was about 45°. Five plants surrounded the plant to mimic the light conditions of a crop and to provide the parasitoid with ample opportunity to hop or fly to another leaflet. Light intensity at the observed leaflet was 5775 lux. Continuous observation started directly after the introduction of the parasitoid. When the parasitoid was on the lower leaf side it was observed through a stereo microscope; when it was on the upper leaf side it was followed by eye.

The following behavioural components were recorded using the computer software package 'The Observer' (Noldus, 1991): a) searching, b) standing still/ eating honeydew/ preening, c) drumming the host with antennae, d) oviposition posture, and e) host feeding. Throughout the experiment, the position of the parasitoid on the leaflet was recorded: the upper leaf side, the lower leaf side, or whether the parasitoid was on the edge or not. Edge width was taken the same as the width of the parasitoids' searching path (0.5 mm). An observation stopped when the parasitoid flew from the leaflet. When the parasitoid walked off the petiole, which was only rarely observed, or when no foraging activity occurred for more than 60 min the observation was not included in the analysis. Observations were also excluded when a parasitoid left within 180 s, because this was clearly due to disturbance of the parasitoid during introduction.

Two types of experiments were conducted. In experiment I no hosts were present. This was done to study the effect of temperature, the side of the leaflet on which the parasitoid was introduced, and the presence of honeydew. Seven combinations of these factors were tested (n is the number of successful observations): (1) 15°C, without honeydew, parasitoid introduced on upper leaf side (n=32), (2) 18°C, without honeydew, parasitoid introduced on upper leaf side (n=66), (3) 20°C, without honeydew, parasitoid introduced on upper leaf side (n=26), (4) 25°C, without honeydew, parasitoid introduced on upper leaf side (n=38), (5) 30°C, without honeydew, parasitoid introduced on upper leaf side (n=46), (6) 25°C, without honeydew, parasitoid introduced on lower leaf side (n=43) and (7) 25°C, with honeydew, parasitoid introduced on upper leaf side (n=22).

In experiment II a varying number of unparasitized or parasitized hosts were present on the lower leaf side. This was done to estimate the effect of encounters with hosts. In this experiment the ambient temperature was always 25°C, honeydew was absent and the parasitoid was introduced on the lower leaf side. Three host *types* were distinguished: unparasitized, recently-parasitized by a conspecific, and black parasitized by a conspecific. The only difference between the 6 treatments was the number of hosts and the host type: (1) 1 unparasitized L3/L4 larva (n=24), (2) 4 unparasitized L3/L4 larvae (n=25), (3) 1 recently-parasitized L3/L4 larva (n=54), (4) 4 recently-parasitized L3/L4 larvae (n=41), (5) 4 black parasitized pupae (n=32) and (6) 77 to 200 black parasitized pupae (n=20).

Two complementary treatments were carried out to test the effect of previous experience with hosts and the presence of a parasitoid larva in the host. As in experiment II, the ambient temperature was 25°C, honeydew was absent and the parasitoid was introduced on the lower leaf side. The behaviour of the parasitoid was followed until handling of the first encountered host ended: (1) 1 recently-parasitized L3/L4 larva, experienced parasitoid (n=29) and (2) 1 parasitized L4 larva containing a parasitoid larva, naive parasitoid (n=20).

Experimental set-up: walking speed

The experiment was carried out by observation of an individual parasitoid on the lower leaf side of a clean tomato leaflet. Leaflets were fully grown and about two weeks old (from the fifth leaf out of 10, counted from the top of the plant). Observations were carried out in a climate room at a constant temperature of 15, 20, 25, and 30°C (±1°C) and 70±5% RH for 21, 21, 20 and 20 replicates respectively. A leaflet was placed upside down into a petri dish (5.1 cm in diameter). On the leaflet a perspex ring (inside diameter 2.4 cm) was placed to create a fixed and restricted searching arena. At the start of each replicate a single, naive *E. formosa* female was introduced into this arena, after which the petri dish was closed and mounted on a burette holder. Openings in the lid prevented a high humidity. The petri dish was placed upside down with an upward tilt of approximately 45° to mimic the natural position of leaves. The searching behaviour was then recorded on video for about 5 min. Later, the recordings were projected on a monitor screen (magnification 13x) and by following the parasitoid with a marker the walking patterns of the parasitoids were drawn on a transparent sheet fixed to the screen. The position of the parasitoid was marked every 10 s. All periods that the parasitoid was not walking were omitted. Walking tracks were then read into the computer with a x-y digitizer. The (magnified) tracks were subdivided into 2 mm parts, which is 0.5x the (magnified) step length of the parasitoid. A computer analysis of the tracks resulted into the average distance covered while walking per unit time: walking speed.

RESULTS

Searching for hosts

Residence times of *E. formosa* on clean and honeydew-contaminated leaflets are given in Table 1. At 15 and 18°C parasitoids did not fly away from the leaflets. At temperatures of 20°C or up, residence times on clean leaflets were not affected by temperature or the leaf side on which the parasitoids were introduced to. Contact with honeydew arrested the parasitoid on the leaflet.

During this time parasitoids were walking while drumming for hosts, preening, or sitting still. The searching or walking activity of *E. formosa* can be expressed as the time walking while drumming on the leaf surface as a percentage of the total time on the leaf, excluding host handling time. Table 1 shows that walking activity was low

Table 1. Mean residence time (s) and walking activity (time walking while drumming on the leaf surface as a percentage of the total time on the leaflet) of *E. formosa* on tomato leaflets without hosts. SD_{n-1} and number of replicates given between brackets.

Temperature (°C)	15	18	20	25	25	30	25	
Leaf side of introduction	upper	upper	upper	upper	lower	upper	upper	
Honeydew on upper leaf side	no	no	no	no	no	no	yes	P[1]
Residence time	>>3600 (-;32)	>>3600 (-;66)	1484 a (1242;26)	1415 a (828;38)	1034 a (1053;43)	1739 a (1979;46)	5133 b (3837;18)	$6.27*10^{-5}$
Walking activity (%)	10.1[2] (6.5;32)	8.4[2] (8.4;64)	70.1 a (26.4;26)	63.1 a (25.4;38)	69.2 a (22.0;43)	68.8 a (27.5;46)	75.7 a (23.4;22)	0.239

[1] Kruskal-Wallis test (α=0.05). Different letters in a row indicate significant differences. [2] Calculated during first hour.

Table 2. Mean residence time (s) and total host handling time (as a percentage of the total residence time) of *E. formosa* on infested tomato leaflets when hosts were discovered, walking activity (time walking while drumming on the leaf surface as a percentage of the total time on the leaflet, excluding host handling time) and number of host encounters and ovipositions on (all) infested tomato leaflets, at 25°C. Host types are unparasitized (unpar.), recently-parasitized (rec.par.) and black parasitized (black). SD_{n-1} and number of replicates given between brackets.

Host number	1	4	1	4	4	77-200	
Host type	unpar.	unpar.	rec.par.	rec.par.	black	black	P[1]
Residence time; hosts discovered	4438 a (1247;24)	8660 b (1706;23)	4389 a (2048;26)	5159 a (3182;26)	4280 a (3062;23)	6485 ab (2747;20)	$8.09*10^{-8}$
Handling time (%)	9.6 ab (4.9;24)	19.3 b (11.1;23)	13.2 ab (9.6;26)	21.8 ab (20.0;26)	1.8 c (3.7;23)	8.0 a (7.6;20)	$2.48*10^{-11}$
Walking activity (%)	86.2 a (9.1;24)	76.5 ab (14.9;25)	72.6 b (15.1;54)	65.2 b (20.9;41)	78.1 ab (13.2;32)	79.7 ab (10.3;20)	$1.72*10^{-5}$
Encounters	2.5 ab (1.3;24)	7.0 ac (3.2;25)	2.1 b (2.9;54)	4.2 ab (5.1;41)	2.5 b (2.7;32)	53.0 c (32.2;20)	$2.22*10^{-16}$
Ovipositions	0.79[2] ab (0.41;24)	2.92[2] a (1.35;25)	0.13 c (0.34;54)	0.46 bc (0.78;41)	0.00 c (0.00;32)	0.00 c (0.00;20)	0.0

[1] Kruskal-Wallis test, followed by a distribution-free multiple comparison (α=0.05). Different letters in a row indicate significant differences. [2] Estimated from hosts turning black.

Table 3. Mean walking activity (time walking while drumming on the leaf surface as a percentage of the total time on the leaflet, excluding host handling time) of *E. formosa* before the first or after the last oviposition or encounter. SD_{n-1} and number of replicates given between brackets.

Host-	Oviposition in unparasitized hosts				Oviposition in recently-parasitized hosts				Encounter with black pupae			
number	1		4		1		4		1		77-200	
Period	before	after	before	after	before	after	before	after	before	after	before	after
Walking-activity	81.1 a (22.7;24)	88.1 a (8.9;24)	66.8 a (35.1;23)	80.0 a (12.5;23)	75.1 a (16.4;6)	77.5 a (9.7;6)	72.0 a (22.6;13)	71.7 a (15.8;13)	75.6 a (20.1;23)	82.1 a (14.3;23)	78.8 a (19.9;20)	65.1 a (23.4;20)
P[1)]	0.415		0.0974		0.575		0.675		0.207		0.0762	

[1)] Wilcoxon signed rank test for pairwise comparison (α=0.05). Different letters in a row indicate significant differences.

Table 4. Mean walking speed (mm/s) of *E. formosa* on clean tomato leaflets. SD_{n-1} between replicates, number of replicates (parasitoids) and total number of 10" tracks given between brackets

Temperature (°C)	15	20	25	30
Walking speed	0.179 a (0.0696;21;412)	0.307 b (0.156;21;550)	0.618[1)] c (0.264;20;385)	0.441[1)] c (0.118;20;408)

Kruskal-Wallis test, $P=4.65*10^{-10}$, followed by a distribution-free multiple comparison (α=0.05). Different letters in a row indicate significant differences.
[1)] When combined: 0.529 (0.221;40;793).

at 15 and 18°C, but was not influenced by temperature at 20°C or up. It was also not influenced by the leaf side of introduction and the presence of honeydew at 25°C.

Residence times on infested leaflets when no hosts were discovered by the parasitoids (1681±1312SD s; median: 1385 s) were equal to that on clean leaflets (1450±1417SD s; median: 1014 s) (Mann-Whitney U test, P=0.132, *n*=54 and 153 respectively). Residence times were much higher when hosts were discovered by the parasitoids and then the number and type of hosts encountered played an important role (Table 2).

These long residence times were not caused by parasitoids spending a larger amount of time sitting still or preening. Table 2 shows the walking activity on infested leaflets. Some differences in walking activity between treatments were observed. However, these differences were not caused by the type of hosts encountered: Table 3 shows that the walking activity was never affected by encounters with hosts or by ovipositions in these experiments, where the number of ovipositions varied from 0 to 4. The walking activity on infested leaflets was equal to that on clean leaflets at 20, 25 and 30°C (Mann-Whitney U test, P=0.152, *n*=175 and 196). The overall mean was 71.7±21.2SD % (*n*=371, median=77.0%).

Walking speed measurements are given in Table 4. Walking speed increased rapidly with temperature from 15 until 25°C. A difference between 25 and 30°C was not found.

Host handling

Every parasitoid-host contact was followed by drumming the host with the antennae. The average number of encounters and ovipositions in hosts on the infested leaflets are given in Table 2. Oviposition did occur in recently-parasitized hosts (superparasitism), but was never observed in black parasitized whitefly pupae.

The total time spent handling the hosts was low compared to the total residence time (Table 2). When 4 unparasitized or recently-parasitized L3/L4 larvae were available, about 20% of the residence time was spent on handling hosts. Even at a high host density of 77-200 black parasitized pupae, handling hosts took only 8.0% of the residence time (Table 2). Most of the time the parasitoid was walking, preening or sitting still on the leaf surface. Obviously, long residence times were not caused by host handling.

The handling time following an encounter with a host of stage L3/L4 depended on whether the host was rejected or accepted for oviposition or host feeding (Table 5). The time needed to reject a host after contact with the antennae was rather short (5-35 s, depending on the host type) compared to the other handling behaviours. The handling time for oviposition and for ovipositorial rejection of a host was always equal (Mann-Whitney U tests), and was 298-654 s depending on the host type. The total time for host feeding was quite long (1063-1626 s).

The time for an oviposition and the time for an antennal rejection seems to depend on the host type. Time of oviposition in unparasitized hosts was shorter than that in parasitized or superparasitized hosts (Mann-Whitney U tests). Antennal rejection

Table 5. Mean handling time (total time including drumming etc., in s) per handling behaviour of an L3/L4 larva by *E. formosa*, at 25°C. SD_{n-1} between replicates and number of replicates (parasitoids) given between brackets.

Host type	Unparasitized	Recently parasitized			Parasitized 6 days before	Black pupae	Superparasitized
		Self	Conspecific		Conspecific	Conspecific	Self
			Naive	Experienced			
Antennal rejection	35.0 (-;1)	5.0 (2.9;40)	15.6 (8.8;30)	26.2 (11.0;15)	19.2 (12.0;14)	8.0 (3.9;42)	9.1 (7.0;16)
Ovipositorial rejection	349.4[1] (53.4;5)	298.3[2] (43.9;4)	480.2 (360.8;11)	452.3 (253.1;5)	387.8 (292.3;6)	415.8 (313.1;8)	394.0 (66.2;2)
Oviposition	362.0[1] (100.6;31)	-[2]	654.9 (310.0;19)	472.5 (251.4;8)	-	-	646.6 (-;1)
Host feeding	1626 (1025;2)	1425 (-;1)	1063.5 (1201.4;4)	-	-	-	-

[1] Estimated from hosts turning black; when combined (with 11 other data): 349.5 (88.7;47). [2] Oviposition posture observed, hosts not dissected.

Table 6. Handling behaviours on L3/L4 larvae by *E. formosa* at 25°C (% of total number of encounters).

Host type	Unparasitized	Recently parasitized			Parasitized 6 days before	Black pupae	Superparasitized
		Self	Conspecific		Conspecific	Conspecific	Self
			Naive	Experienced			
% antennal rejection	0.9	95.0	72.7	55.2	70.0	98.9	95.5
% ovipositorial rejection	22.5[1]	4.2[2]	8.5	17.2	30.0	1.1	3.0
% oviposition	74.8[1]	0.0[2]	14.2	27.6	0.0	0.0	1.5
% host feeding	1.8	0.8	4.6	0.0	0.0	0.0	0.0
Total encounters	111	119	176	29	20	1138	67

[1] Estimated from hosts turning black. [2] Oviposition posture observed, hosts not dissected.

of self-parasitized and self-superparasitized hosts and of black parasitized pupae was shorter than for other host types. The handling time for oviposition and for ovipositorial rejection varied less when hosts were unparasitized compared to parasitized hosts. The handling times by naive and experienced females were equal.

The probability of a host rejection, an oviposition or a host feeding after encountering a host can be estimated by the percentage of the total number of encounters spent on each handling behaviour. For host stage L3/L4 they depended on the host type encountered (Table 6). The percentage ovipositions (success ratio) was highest in unparasitized hosts (74.8%) and did not change during these experiments, when the number of ovipositions increased from 0 to 4. An oviposition posture was rarely observed in hosts recently parasitized by the same female. However, oviposition does occur when hosts were recently parasitized by a conspecific: 14.2% of such encounters resulted in a superparasitization. This did not change significantly for experienced females, at least the success ratio did not decrease. Host handling behaviour of experienced wasps did not differ from that of naive wasps. When the host was parasitized 6 days before and contained a parasitoid larva, oviposition was not observed anymore. When the hosts were black parasitized pupae or superparasitized by the same female, they were almost always rejected after antennal contact.

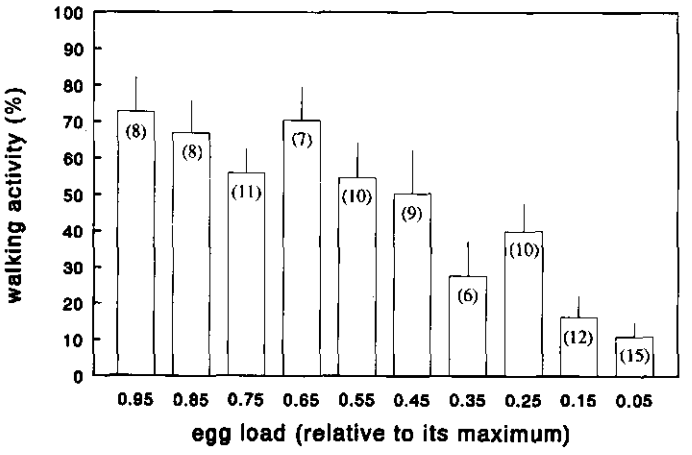

Figure 2. Walking activity (time walking while drumming on the leaf surface as a percentage of the total time on the leaf, excluding host handling time) of *Encarsia formosa* on cucumber during an oviposition sequence, derived from 11 observations by Hulspas-Jordaan (1978). Bars represent standard errors; the number of replicates (periods between successive encounters >25 s) is given between brackets.

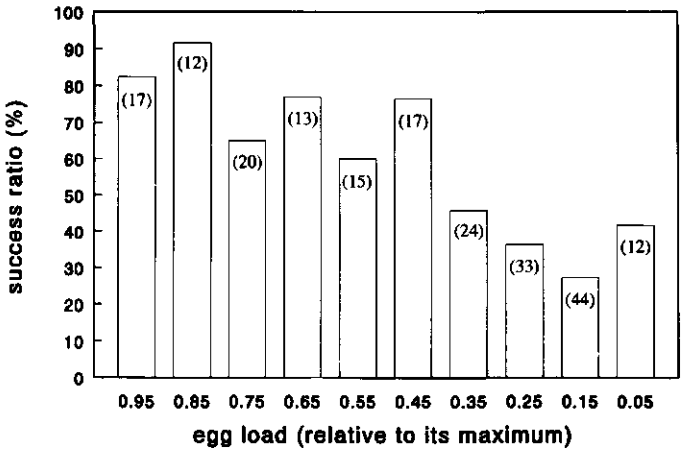

Figure 3. Success ratio (% of the total number of encounters with L3 or L4 larvae resulting in an oviposition) of *Encarsia formosa* on cucumber during an oviposition sequence, derived from 11 observations by Hulspas-Jordaan (1978). The number of encounters is given between brackets.

DISCUSSION

The median residence time of *E. formosa* on clean tomato leaflets was about 20 min. Contact with honeydew or encounters with unparasitized and parasitized hosts arrested the parasitoid on the leaflet. The parasitoids spent maximally 20% of the residence time on host handling. About 75% of the remaining time was spent on walking while drumming for hosts at temperatures above 20°C. The average walking activity was quite constant: it did not change with temperature above 20°C, it was the same on leaflets with honeydew, and it was not influenced by encounters with or ovipositions in hosts in these experiments on the premise that the total number of ovipositions remained low. The egg storage capacity of *E. formosa* is generally 8-10 mature eggs per female (van Vianen & van Lenteren, 1986; Kajita & van Lenteren, 1982). If more than 4 eggs are laid, walking activity decreases. This became particularly clear after re-analysis of Hulspas-Jordaan's (1978) data on *E. formosa* foraging for hosts on cucumber. These results show that when more than 4 eggs have been laid, walking activity decreases with decreasing egg load (Figure 2). This result is supported by recent observations of Sütterlin & van Lenteren (1993) on gerbera, who also found a decreasing walking activity after more than 4 ovipositions until the egg load was depleted. Further, they showed that the walking activity increased again after new eggs had matured.

The walking activity on tomato seems to be slightly higher than on gerbera and cucumber leaves, where an activity of about 60% was observed (see Appendix I). Differences in walking speed between host plants are much more obvious (Hulspas-Jordaan & van Lenteren, 1978). The walking speed is also more sensitive to

temperature: it increased rapidly from 0.179 to 0.529 mm/s between 15 and 25-30°C on tomato. The same trend was found for gerbera leaves (Sütterlin & van Lenteren, in prep.). Hulspas-Jordaan & van Lenteren (1978) found a walking speed on tomato of 0.3 mm/s (n=12) at 24°C, which is low compared to the present study. However, their number of replicates was low, the walking arena was smaller and the curvimeter they used to determine walking speed was much less precise than the digitizer used in our experiments (see also Li et al., 1987). Even for gerbera leaves, which are hairier than tomato, Sütterlin & van Lenteren (in prep.) measured a higher walking speed of 0.39 mm/s (n=60) at 25°C, when using the same method as we did.

Host handling does not seem to be influenced by the host plant. No differences were found in handling times and success ratios on unrelated host plants like tomato, cucumber, gerbera and poinsettia (see below). Handling seems to depend entirely on the stage of the greenhouse whitefly immature which is encountered by the parasitoid (Nell et al, 1976) and whether or not hosts are parasitized, superparasitized or host-fed.

The total handling time (including drumming etc.) for oviposition and for ovipositorial rejection of an unparasitized host is about 6 min on tomato, which is similar to recent findings on poinsettia, gerbera and cucumber (see Appendix I). As in the present study, no significant differences were found in earlier data between the total handling time for oviposition and for ovipositorial rejection. Differences in the time for an oviposition posture for oviposition and for ovipositorial rejection were not found either (see Appendix I). Thus, the 100-second criterium of van Lenteren et al. (1976b) for oviposition posture resulting in an egg deposition is not very accurate. Hosts have to be dissected to be sure of an egg deposition.

The only difference between the time for oviposition and for ovipositorial rejection was their variation, which was lower in case of an oviposition: the average coefficient of variation (SD_{n-1}/mean) was 25 and 63% respectively when hosts were unparasitized, and was caused by variation in the duration of the oviposition posture (see Appendix I).

In the present study the success ratio in unparasitized hosts (74.8%) might seem quite high when compared to other data (see Appendix I). Nell et al. (1976) found on average 42.6% ovipositions in unparasitized L4 larvae on cucumber and tomato, when parasitoids could lay all their eggs. Unfortunately, the relationship with egg load was not studied. Hulspas-Jordaan (1978) found on average 49.0% ovipositions in L3 or L4 larvae on cucumber, when parasitoids could lay all their eggs. Re-analysis of these data showed that the success ratio depended on egg load. It was about 80% when the parasitoids had a full egg load, but decreased significantly when more eggs were laid (Figure 3). The same was recently found on gerbera (Sütterlin & van Lenteren, in prep.). In our experiment the parasitoids never laid more than 4 eggs and were thus not depleted, which explains the high success ratio.

Self-superparasitism was not found for *E. formosa* (see also Appendix I). Conspecific-superparasitism did occur in 14% of the contacted hosts containing a parasitoid egg, but was not observed anymore when the parasitoid egg had hatched. Experienced wasps did not reject more parasitized hosts than naive females.

At 15 and 18°C, the parasitoids were standing still for most of the time and did not fly. Usually they walked only for the first few minutes. This is contrary to van Lenteren & van der Schaal (1981), who found a lower temperature threshold for searching and oviposition of 12°C. However, it does agree with Enkegaard (1992) who found a strong reduction in the functional response curve on leaves for *E. formosa* at 16°C compared to 22°C, when parasitoids were reared at 22°C. A possible explanation might be that the temperature at which the parasitoids were reared has been increased during the last decade, causing a considerable shift in the lower temperature threshold of *E. formosa* for searching and oviposition.

In conclusion, the present study showed the following essential additions to earlier work on *E. formosa*: (1) parasitoids were arrested on the leaf by encounters with and ovipositions in unparasitized hosts, by encounters with parasitized (unsuitable) hosts and by contact with honeydew, (2) walking activity decreased with decreasing egg load, (3) walking speed increased with increasing temperature, (4) the percentage of encounters resulting in an oviposition (success ratio) decreased with decreasing egg load, (5) host handling did not depend on the host plant, (6) handling time for oviposition did not differ from that of ovipositorial rejection, (7) self superparasitism was not observed, (8) conspecific superparasitism was only observed when parasitized hosts contained a parasitoid egg, and not anymore when parasitized hosts contained a parasitoid larva or pupa, (9) host handling behaviour of experienced wasps did not differ from that of naive wasps, and (10) parasitoids became active only at temperatures above 18°C. Particularly findings (1), (2), (3), (4) and (10) have important consequences for the overall parasitization efficiency of *E. formosa*.

More detailed information on time allocation of the parasitoids on leaves can be found in Chapters 2 and 3. In these studies, residence time, time on upper and lower leaf side, time until changing to the other leaf side, and the giving up time were analyzed. The influence of different intra-patch experiences with hosts were also tested and the patch leaving mechanism of *E. formosa* is discussed. With these new findings the complete foraging process from landing on a leaf until departure has now been described and quantified (Figure 1). Next, this information will be used in a stochastic simulation model of the foraging behaviour of *E. formosa* (Chapters 5, 6 and 7). Based on these simulations, we are able to judge in what situations *E. formosa* can be used as an efficient biological control agent.

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APPENDIX I. ESSENTIAL DATA.

Almost all data listed below originate from unpublished M.Sc. theses. They are used for comparison with the present results and in simulation models of the foraging behaviour.

Walking activity:
Clean cucumber leaf: 57.8%, n=99 (van Eck-Borsboom, 1979).
Infested cucumber leaf: 63.7%, n=59 (Li et al., 1987).
Cucumber leaf before the first oviposition: 72.7±27.2SD %, n=8 (Hulspas-Jordaan, 1978).
Clean gerbera leaf (var.'Parade'): 58.8±24.2SD %, n=21 (Sütterlin et al., 1993).
Gerbera leaf before the first oviposition: 59.5±27.5SD %, n=10 (Sütterlin et al., 1993).
Gerbera leaf before the first encounter with a host: 60.1%, n=55 (Godthelp, 1989).
Gerbera leaf before the first encounter with a host: 44.6%, n=30 (Kusters, 1990).

Handling time:
Oviposition in unparasitized hosts:
Poinsettia: 333.0±85.3SD s, n_h=74 handlings (Boisclair, 1990).
Gerbera (var.'Parade'): 333.7±78.9SD s, n=10 parasitoids (Sütterlin & van Lenteren, in prep.).
Tomato and cucumber: 249.7±76.8SD s, n_h=76 (Sevenster-van der Lelie, 1974).
Tomato: 248.8±40.6SD s, n=10 (van Lenteren & van der Schaal, 1981, at 25°C).

Ovipositorial rejection of unparasitized hosts:
Poinsettia: 251.4±157.3SD s, n_h=24 (Boisclair, 1990).
Gerbera (var.'Parade'): 372.1±233.3SD s, n=14 (Sütterlin & van Lenteren, in prep.).

Oviposition posture in unparasitized hosts, resulting in oviposition:
Cucumber: 216.2±63.5SD s, n_h=129 (Hulspas-Jordaan, 1978).
Tomato and cucumber: 209.5±46.0SD s, n_h=179 (Sevenster-van der Lelie, 1974).

Oviposition posture in unparasitized hosts, resulting in ovipositorial rejection:
Cucumber: 218.6±140.5SD s, n_h=19 (Hulspas-Jordaan, 1978).
Tomato and cucumber: 194.0±144.1SD s, n_h=173 (Sevenster-van der Lelie, 1974).

Antennal rejection of unparasitized hosts:
Tomato and cucumber, all host stages: 10.9 s, n_h=1178 (van Lenteren et al., 1980).
Poinsettia, L3/L4 stage: 21.6±17.2SD s, n_h=64 (Boisclair, 1990).

Host feeding of unparasitized hosts:
Tomato and cucumber: 917.3±411.2SD s, n_h=19 (Sevenster-van der Lelie, 1974).

Antennal rejection of parasitized hosts:
Tomato and cucumber, all host stages: 9.7 s, n_h=244 (van Lenteren et al., 1980).

The percentage of the total number of encounters spent on each handling behaviour:
Poinsettia; the first encounter with unparasitized L3/L4 larvae: 33% antennal rejection, 18% ovipositorial rejection, 49% oviposition, and 0% host feeding; n=139 encounters (Boisclair, 1990).
Cucumber and tomato; unparasitized L4 larvae; parasitoids laid all their eggs: 28.0% antennal rejection, 23.9% ovipositorial rejection, 42.6% oviposition, and 5.5% host feeding; n=254 (Nell et al., 1976).

Cucumber; unparasitized L3/L4 larvae; parasitoids laid all their eggs: 38.0% antennal rejection, 9.2% ovipositorial rejection, 49.0% oviposition, and 3.7% host feeding; n=271 (Hulspas-Jordaan, 1978). Tomato and cucumber; self-parasitized L4 larvae: 97.5% antennal rejection and 2.5% ovipositorial rejection; n=158 (van Lenteren et al., 1976b).

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Chapter 5

Analysis of foraging behaviour of the whitefly parasitoid *Encarsia formosa* in an experimental arena: a simulation study

ABSTRACT

Foraging behaviour of *Encarsia formosa* was analysed with a stochastic simulation model of the searching parasitoid during a fixed time in an experimental arena with immatures of the greenhouse whitefly, *Trialeurodes vaporariorum*. The model is based on searching, host selection and handling behaviour, and on the physiology of the parasitoid. Outputs of the model were the number of hosts encountered, parasitized or killed by host feeding. The simulation results agreed well with observations on leaves of several crops. Mean number of encounters, ovipositions and host feedings increased with host density to a maximum of 25 encounters, 6.5 ovipositions and 1.5 host feedings during 2 h at 25°C. The number of ovipositions on the leaf at low host densities was strongly affected by the parasitoids' walking speed and walking activity, the probability of oviposition after encountering a host and the initial egg load. At high densities, the initial and maximum egg load were most important. A Type II functional response curve was found, which may be the result of the 'experimental' procedure where a parasitoid was confined to a patch during a fixed time.

INTRODUCTION

Biological control of the greenhouse whitefly, *Trialeurodes vaporariorum*, with the parasitoid *Encarsia formosa* is commercially applied with success in several greenhouse vegetables, such as tomato (van Lenteren & Woets, 1988). Much basic research backed the reliable application of the parasitoid in the field, such as studies on host searching, host selection, host discrimination and host handling behaviour of the parasitoid (van Lenteren et al., 1976a,b; Nell et al., 1976; van Lenteren et al., 1980) and on foraging behaviour and time allocation on leaves (Chapters 2, 3 and 4). *E. formosa* is a synovigenic and solitary parasitoid. In order to reproduce, *E. formosa* has to search for the sessile whitefly hosts. The parasitoid forages on a leaf by walking and drumming and hosts are encountered randomly (van Lenteren et al., 1976a; Chapter 2). After an encounter, four behaviours on that host can be distinguished: the parasitoid may reject the host after contact with the antenna (antennal rejection) or after contact with the ovipositor (ovipositorial rejection), she may parasitize (oviposition) or she may use the host as a food source (host feeding) (van Lenteren et al., 1980). About ten days after oviposition the immature parasitoid pupates in the host pupa, which then turns black.

As yet there is no satisfactory explanation as to why the parasitoid introduction scheme for tomato cannot be applied reliably on some other important greenhouse crops, such as cucumber and gerbera. To better understand the tritrophic system host

plant- greenhouse whitefly- *E. formosa* which can help to explain failure or success of biological control, a simulation model of the population dynamics of the pest insect-parasitoid interaction was developed. The model is based on developmental biology of the two species and on the parasitoid's searching and parasitization behaviour in relationship to host plant characteristics and greenhouse climate. Demographic input data can be found in Chapters 8 and 9. The model consists of several submodels, one of which is presented here.

The submodel presented here simulates the foraging behaviour of the parasitoid. In order to understand quantitative effects of the parasitoid's foraging behaviour on whitefly populations in a crop, this behaviour is first studied at a much smaller spatial scale. Input parameters for an *E. formosa* female searching for hosts during a fixed time in an experimental arena were used in the present simulations. The simulated number of hosts encountered, parasitized and killed by host feeding were validated with experimental data. A sensitivity analysis showed the most important behavioural or physiological parameters, which affect the number of hosts encountered and parasitized.

From the simulation results at different host densities, the parasitoids' functional response can be determined. The functional response is the relationship between the number of parasitizations of an individual parasitoid per unit of time as a function of host density. Holling (1965) distinguished three types of functional responses: (I) a linear increase of number of parasitizations with host density until a maximum level is reached, (II) a rise in parasitization which decelerates as host density increases until a maximum level is reached and (III) a sigmoid increase with host density. The shape of the curve helps to understand the dynamics of the host-parasitoid interaction at the population level.

In case of a Type II response, percentage parasitism declines with increasing host density (inversely density-dependent). According to theory, this will tend to have a destabilizing effect on the dynamics of host and parasitoid. A high host density on the leaf thus 'dilutes' the per capita parasitization pressure caused by one parasitoid. In case of a Type III (S shaped) response, density-dependence occurs and populations tend to be stabilized (see e.g. Murdoch & Oaten, 1975; Oaten & Murdoch, 1975). However, functional responses are only one factor in determining the dynamics at the population level. The effect on the population level depends on the balance between the 'dilution' effect and, for instance, aggregation of parasitoids on leaves (see e.g. Hassell & May, 1974; Chesson & Murdoch, 1986; Reeve et al., 1989; Pacala et al., 1990). From the simulation results at different host densities, the number of encounters, ovipositions (parasitizations) and host feedings in relationship to density can be generated for *E. formosa* searching during a fixed time in an experimental arena. The model will later be extended and used at larger spatial scales, such as (whole) leaves, plants and canopies (Chapters 6, 7 and 10).

THE SIMULATION MODEL

A stochastic Monte Carlo simulation model was developed for the foraging behaviour of the parasitoid. In the simulations presented in this chapter the parasitoid is searching on the infested side of a leaf(let) during a fixed time and cannot reach the other leaf side or leave. In Chapter 6 the model is extended and used to simulate the searching parasitoid during a single visit to a tomato leaflet, where the parasitoid is able to move from one leaf side to the other and can fly away. In Chapter 7 the model is extended and simulations are done for the parasitoid on a tomato plant where the parasitoid is able to fly from leaflet to leaflet and can move from one leaf side to the other. The description of the three models is given here.

Stochasticity means that processes occur with a certain probability, for instance in the model presented here, an encounter with a certain host stage or the resulting handling behaviour on that host. Some input parameters are not fixed but drawn from a continuous distribution function to mimic its observed variation, such as the handling time, the walking activity, and when the parasitoid is searching on a leaf or plant, the time period that the parasitoid searches on the leaf until leaving and the time period on a particular leaf side until changing to the other leaf side. Each computer run simulates one foraging parasitoid. The searching and parasitization results for each parasitoid are unique due to the stochastic processes and therefore the simulation must be repeated for many parasitoids. As a result, Monte Carlo simulations yield information about the mean and variation of a population of parasitoids. The same approach was used by Sabelis (1981) and van Batenburg et al. (1983) to simulate prey-predator and host-parasitoid interactions at the individual level.

Input parameters were obtained from several experiments (see below). For the model of the foraging behaviour in an experimental arena they are:

- number of all immature hosts per leaf(let)
- size (mean diameter) of all immature host stages
- width of the parasitoids' searching path
- walking speed of the parasitoid
- walking activity of the parasitoid
- variation in walking activity
- the probability of a certain handling behaviour to occur after encountering a host
- handling time for each handling behaviour
- variation in handling time for each handling behaviour
- initial egg load of the parasitoid (number of mature eggs per female at the beginning of the experiment)
- maximum egg load of the parasitoid (egg storage capacity)
- relative egg maturation rate of the parasitoid
- maximum number of host feedings per parasitoid per day
- leaf(let) size
- temperature
- time step of simulation

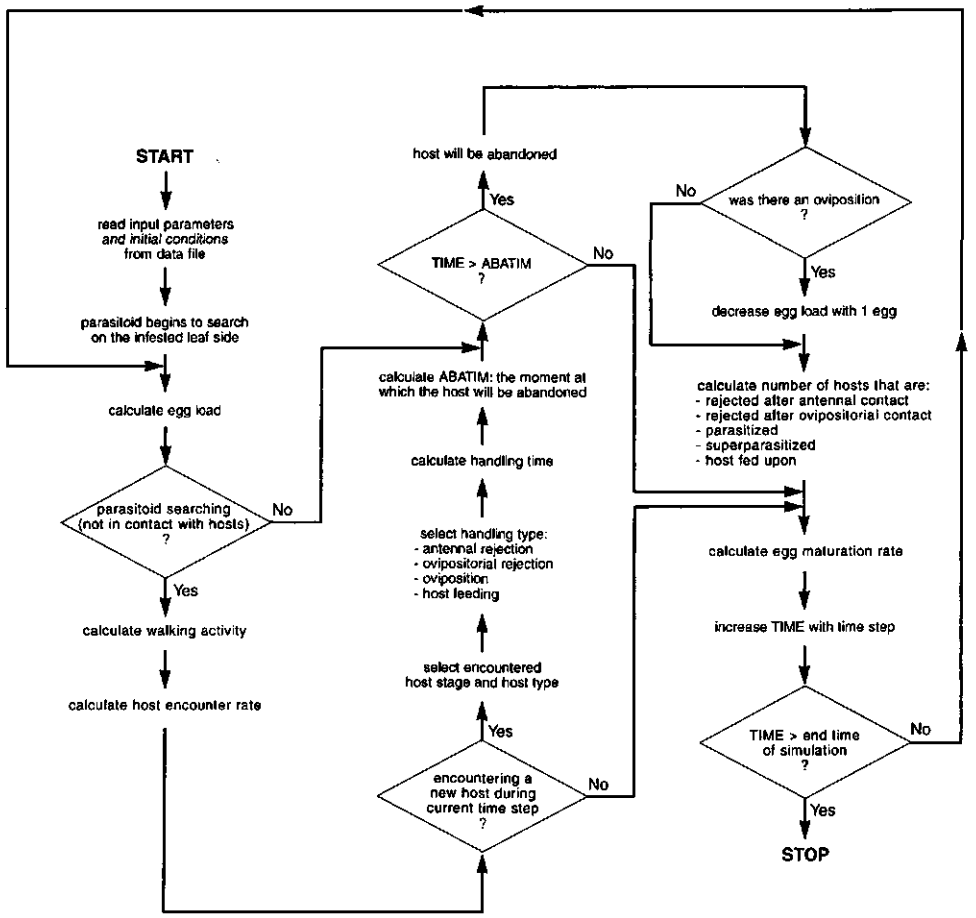

Figure 1. Flow diagram of the foraging behaviour of one *E. formosa* female in an experimental arena.

- end time of simulation

Extra input parameters for the models of foraging behaviour on a tomato leaflet and on a plant (Chapters 6 and 7) are:

- parasitoids' tendency of changing from the lower to the upper leaf side
- parasitoids' tendency of changing from the upper to the lower leaf side
- the effects of intra-patch experiences on the tendencies of changing leaf sides
- parasitoids' tendency to leave the leaflet
- the effects of intra-patch experiences on the leaving tendency
- probability of landing on the lower leaf side of the leaflet, compared to the upper side

For simulation of the searching parasitoid on a tomato plant (Chapter 7) a few more parameters are needed as input:

- number of leaflets on the plant
- number of infested leaflets
- number of each immature host stage on each infested leaflet
- probability of landing on a particular leaflet

The model for one parasitoid searching in an experimental arena during a fixed time is presented in the flow diagram of Figure 1. The model is initialized with the number of hosts per leaf for each stage. The time step of simulation was taken 1.2 s, much smaller than the smallest time coefficient in the model (handling time for antennal rejection of a parasitized host), which is needed for accurate numerical integration. Accuracy was tested by comparing the simulation results with those obtained at a time step double or half in size. Number of replicates (parasitoids) was always 100, which was sufficient for a low standard error of the mean (SE<5%). During the simulation, the initial condition of each replicate was taken the same. Therefore, variation in body size between parasitoids or in number of ovarioles per female was not taken into account.

Walking speed and activity

The parasitoid walks with a certain speed. Walking speed does not account for periods that the parasitoid is standing still. It depends on leaf structure (Hulspas-Jordaan & van Lenteren, 1978; Li et al., 1987) and on temperature (Chapter 4). Walking speed data for tomato were taken from Chapter 4.

Walking activity is defined here as the percentage of time walking while drumming on the leaf surface compared to the total time on the leaf without handling hosts. In the model, a value for walking activity is drawn from a normal distribution (after arcsin transformation) to mimic the large variation for one parasitoid as was observed during experiments. Mean and coefficient of variation (SD_{n-1}/mean) on tomato were 75% and 0.30 respectively (Chapter 4). The walking activity was a little lower on cucumber and gerbera and it decreased with decreasing egg load, after about 4 eggs were laid (Chapter 4). In the model, the mean walking activity was kept at its maximum value until the egg load was depleted for 50%, and then decreased linearly

to zero with egg load. The walking activity was low at temperatures below 18°C (Chapter 4) and was set to 5%.

Encounter probability

In the model six host *stages* are distinghuished which can be parasitized or host-fed upon: the larval stages L1, L2, L3, L4, and the prepupa (PP) and pupa (PU) (Nell et al., 1976). After parasitization or host feeding, six host *types* are distinguished: (1) unparasitized hosts, (2) parasitized hosts containing an egg laid by the same female, (3) parasitized hosts containing an egg laid by a conspecific, (4) parasitized hosts containing a parasitoid larva from a conspecific, (5) parasitized hosts containing a parasitoid pupa (black pupae) and (6) hosts which are fed upon. To summarize: hosts are divided into 36 host *classes* which can only be present on the lower leaf(let) side.

E. formosa is searching randomly on a leaf(let) without preference for a particular leaf side or part (van Lenteren et al., 1976a; Chapter 2). The observed walking pattern is not influenced by veins and never becomes tortuous (van Lenteren et al., 1976a) and is independent of the number of leaf hairs on cucumber (Li et al., 1987). Therefore the walking pattern does not have to be described for the simulations, but the calculation of the encounter rate suffices. Skellam (1958) derived an equation for the encounter rate RE (encounters per time):

$$(1) \qquad RE = (WI_p + DM_h) * WS * ACT * DENS$$

in which WI_p is the width of the parasitoids' searching path (in mm), DM_h is the mean diameter of the host (in mm), WS is the walking speed of the parasitoid (in mm/sec), ACT is the walking activity of the parasitoid (expressed as fraction of time) and DENS is the host density (in number/mm^2). The mean diameter of the host stages was calculated as the average of length and width, which are given by van Lenteren et al. (1976a). *E. formosa* searches by drumming the leaf surface with the antennae, meanwhile turning slightly to the left and right. From video analyses the width of the searching path was estimated as twice the head width (head width given by van Vianen & van Lenteren, 1986a). The sum of WI_p and DM_h represents the width of the encounter path and the product of WS and ACT the net rate of movement of the parasitoid.

The probability PE of an encounter during a time step dt, can be derived from the Poisson distribution, which is commonly used to describe random processes:

$$(2) \qquad PE = 1 - \exp(-RE*dt)$$

By drawing a number between 0 and 1 with a random generator, an encounter is simulated when this number is below PE. In this way, encounters with all possible host classes can be simulated.

Handling of hosts

Each encounter will be followed by one of the four handling behaviours, which occur at a certain probability, depending on host stage and host type. The host plant does not have an effect (Chapter 4). These probabilities were estimated by the percentage of encounters resulting in antennal rejection, ovipositorial rejection, oviposition and host feeding. For unparasitized hosts, they were taken from Nell et al. (1976), for parasitized hosts by the same female from van Lenteren et al. (1976b) and for parasitized hosts by a conspecific female from Chapter 4. In the first two studies the parasit oids depleted their eggs. Unfortunetaly, the relationship between the probability of each handling behaviour and egg load was not examined. In Chapter 4 it was found that the probability of oviposition (success ratio) in unparasitized hosts decreased linearly during the observations when the relative egg load decreased from 1 (full batch of mature eggs) to 0 (no eggs). Table 1 shows the results of linear regression, as derived from the observational protocols of Hulspas-Jordaan (1978). Although the number of parasitoids was low (11), only the relationship for the probability of host feeding was not clear. These results were confirmed by recent experiments of Sütterlin & van Lenteren (in prep.) on gerbera. For the model, probabilities depending on egg load were derived. They were based on the mean values of Nell et al. (1976), because these were obtained for all whitefly stages and were based on many replicates, and on the slope of Table 1.

E. formosa is a solitary parasitoid. During an oviposition, one egg will be laid. Superparasitism by a conspecific may occur, depending on the parasitoid stage in the host (Chapter 4). Self superparasitism was not observed and is neglected in the model. An observed maximum number of 3 host feedings per parasitoid per day is used (Fransen & van Montfort, 1987; Arakawa, 1982).

Host handling takes a certain amount of time. For *E. formosa*, handling times were low compared to the total time on the leaf (Chapter 4). In the model, handling time is drawn from a normal distribution, of which mean and variation depends on type of behaviour and host type. The host plant does not have an effect (Chapter 4). For unparasitized hosts handling times were derived from Boisclair (1990), Sütterlin & van Lenteren (in prep.) and Chapter 4 and for parasitized hosts from Chapter 4. The time for host feeding and its variation were taken from Sevenster-van der Lelie (1974), because the number of replicates was higher than in other studies. When handling of an encountered host stops and the host is abandoned, host numbers of each host class change due to oviposition or host feeding. Therefore, densities for each host stage and type are recalculated in the model. When an encountered host is abandoned, the parasitoid resumes searching on the leaf.

Egg maturation

In the model, the parasitoid starts with a full batch of mature eggs of 8.9. This maximum egg load is based on data of van Vianen & van Lenteren (1986a) who observed on average 8.9 ovarioles per parasitoid (n=1452). About 1 mature egg per ovariole was observed at 0.5 day after emergence (Kajita & van Lenteren, 1982; van

Table 1. Linear regression between the probability of each handling behaviour to occur after encountering a host and egg load (relative to its maximum), as derived from Hulspas-Jordaan (1978) (n=10 egg load classes).

Probability of:		r^2
antennal rejection =	0.502 - 0.429 * egg load	0.495
ovipositorial rejection =	0.153 - 0.160 * egg load	0.601
oviposition =	0.290 + 0.628 * egg load	0.766
host feeding =	0.0559 - 0.0391 * egg load	0.151

Vianen & van Lenteren, 1986b). *E. formosa* is a synovigenic parasitoid. When the egg load of the parasitoid drops below its maximum value due to oviposition, egg maturation starts. The egg maturation rate at a certain time ($dEGG_t/dt$, in number of mature eggs per female per hour) depends on the egg load at that time (EGG_t), as was shown by van Vianen & van Lenteren (1986b): it is at its maximum when the egg load is zero and decreases linearly with increasing egg load, until the maximum egg load (EGG_{max}) is reached. It is simulated as a deterministic process:

$$(3) \qquad dEGG_t/dt = C * (EGG_{max} - EGG_t)$$

in which the constant C is the relative egg maturation rate (in 1/h) and can be solved analytically from equation (3). The value C was derived at a constant temperature from data of Kajita & van Lenteren (1982), who counted the number of mature eggs at 0 and 16 h after emergence of 5 parasitoids at 5, 10, 15, 20 and 25°C. The maximum egg load in their experiments was 7.7. A linear relationship with temperature (TEMP) was then found:

$$(4) \qquad C = -0.0205+0.004032 * TEMP;\ r^2=0.828\ (n=5)$$

According to equation (3) and (4), the maximum egg maturation rate is 0.7 eggs/h when the parasitoid depleted her eggs at 25°C. Many parasitoids need to host feed to obtain nitrogenous compounds, which are necessary to produce eggs (Jervis & Kidd, 1986). However, Gast & Kortenhoff (1983) and van Lenteren et al. (1987) found that *E. formosa* females which were refrained from host feeding laid the same number of eggs than females which were able to host feed. They suggested that parasitoids that do not feed on hosts obtain the nitrogenous compounds from the honeydew of the whiteflies. Therefore, in the model we assume that egg maturation is not affected by host feeding.

Time allocation

Data on time allocation are only used as input in the models for searching parasitoids on a tomato leaflet and on a plant (Chapters 6 and 7). The median giving up time (GUT) of *E. formosa* after landing on a tomato leaflet or, if it occurred, from the latest encounter with a host until leaving was 18.6 min. The median time for changing from one leaf side to the other (TUC) was initially 11.6 min, and dropped to 5.7 min after both leaf sides had been visited (Chapter 3). GUT and TUC showed a great variation. In Chapter 3 two characteristics were quantified to describe the time allocation of *E. formosa* on a tomato leaflet: the parasitoids' leaving tendency, i.e. the probability per unit of time to leave the leaflet and the parasitoids' tendency of changing leaf sides, i.e. the probability per unit of time to change from one leaf side to the other.

The leaving tendency and the tendency of changing leaf sides sometimes changed after the parasitoid had an experience with a host. Intra-patch experiences with the host are e.g. contact with honeydew, antennal or ovipositorial rejections of hosts and ovipositions. The effect on the leaving tendency and the tendency of changing leaf sides were quantified as multiplication factors (Chapter 3). The first oviposition in an unparasitized host as well as the presence of a film of honeydew decreased the leaving tendency strongly, thus increasing the GUT since latest encounter. Encounters with parasitized hosts did not affect the leaving tendency and the resulting GUT since latest encounter. As a consequence, each encounter with hosts, whether or not parasitized, lead to longer residence times on the leaf.

The first oviposition in an unparasitized host also decreased the tendency of changing from the lower leaf side, where hosts are present, to the upper side, leading to longer visit times at the lower leaf side. Presence of honeydew did not affect the tendency of changing leaf sides. Both the leaving tendency and the tendency of changing leaf sides were not affected by the leaf side on which the parasitoid began to search, the time since the beginning of searching on the leaf and the temperature above 18°C.

Each time after landing on the leaflet and when a host is abandoned, a value for GUT is derived in the model from an exponential distribution, as was observed in Chapter 3:

(5) $GUT = -\ln(X)/T$

in which T is the leaving tendency (in $time^{-1}$), and X is a random number between 0 and 1. The parasitoid leaves when this time is reached without a next host encounter. The leaving tendency of the parasitoid is calculated from the basic tendency and, in case an experience with a host has occurred earlier which influences this tendency, its multiplication factor. For instance on a clean leaflet or after each host encounter, the leaving tendency is equal to the basic tendency of 0.000621 s^{-1}. When the first oviposition in an unparasitized host has occurred, the basic tendency will be multiplied by 0.46. GUT is then -ln(X)/0.000621 s on clean leaflets or after each host encounter and increases to -ln(X)/0.000286 s after the first oviposition on the leaflet. For median

times, X is set to 0.5 which yields 18.6 and 40.4 min respectively. In the model, minimum GUT was set to 100 s, because observed times since the last encounter until leaving were never smaller than this value.

During GUT, the parasitoid either walks while searching or does not walk at all (stands still, preens or eats honeydew). The average walking activity in the experiments on tomato, which were used to estimate the leaving tendency and the resulting GUT, was 75% (Chapter 4). In the model, the GUT of equation (5) was prolonged when the mean walking activity dropped below 75% due to a decreasing egg load, to include the long resting periods of the parasitoid. In this way, the GUT that the parasitoid really *walks* was always equal.

At the beginning of searching on a particular leaf side or each time when a host is abandoned on that leaf side, the time that the parasitoid stays on that leaf side (TUC) is calculated in the same way. TUC was also exponentially distributed. A value for TUC is derived according to equation (5), in which T is now the tendency to change from one leaf side to the other. Both tendencies of changing from the lower leaf side to the other and vice versa are calculated from each basic tendency and, in case an experience with a host has occurred earlier which influences this tendency, its multiplication factor (Chapter 3).

In summary, important processes in the model characterizing the tritrophic relationship between host plant, host insect and the parasitoid as influenced by temperature are:

- the walking speed which depends on host plant (leaf structure) and temperature
- the walking activity which depends on egg load and leaf structure and which is low at temperatures below 18°C
- the probability of each handling behaviour after encountering a host which depend on host stage, host type and on egg load
- handling time and its variation which depend on handling behaviour and host type
- the relative egg maturation rate which depends on temperature

For searching parasitoids on a tomato leaflet and on a plant (Chapters 6 and 7), two other important processes are:

- the basic tendency to change from one leaf side to the other which depends on host plant (leaf size), the first oviposition in an unparasitized host on that leaf side and on whether both leaf sides have been visited.
- The basic tendency to leave which depends on host plant (leaf size), honeydew on the leaf and on the first oviposition in an unparasitized host.

RESULTS

Validation

Direct observations of searching parasitoids on a cucumber, poinsettia and bean leaf infested with immatures of the greenhouse whitefly by Hulspas-Jordaan (1978), Boisclair (1990) and Gast & Kortenhoff (1983) were used to validate the model. Experiments were done with parasitoids on leaves in petri dishes during a fixed time, where they could not leave or reach the other leaf side. The leaves were infested with a high number of unparasitized hosts and exposure times were one, two or three hours. Experiments during an exposure time much longer than the residence time on leaves in the field, such as those of Fransen & van Montfort (1987) during 24 h, were not taken to validate the model, because the behaviour may change when parasitoids cannot leave a patch for a long time.

Almost all input parameters for the model were derived independently from the validation experiments (see description of the model). Only the observations of Hulspas-Jordaan (1978) were used to estimate the (relative) increase or decrease of the probability of each handling behaviour on unparasitized hosts (see Table 1). These results, however, were confirmed by recent experiments of Sütterlin & van Lenteren (in prep.) on gerbera.

Results of the validations are given in Figures 2-4. Simulated confidence intervals were very small, due to the high number of replicates. As data on walking speed of the parasitoid on bean leaves were not available, data for sweet pepper leaves were used. Bean and sweet pepper leaves are both smooth without leaf hairs and walking speeds are assumed to be similar. Input data on walking speed for cucumber and sweet pepper were taken from Hulspas-Jordaan & van Lenteren (1978) and for poinsettia from separate experiments of Boisclair (1990). The mean walking activity on the three host plants when the parasitoids had a full batch of mature eggs was taken 70%.

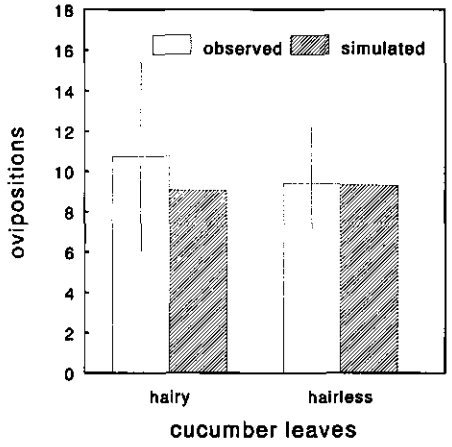

Figure 2. Observed and simulated number of ovipositions of *E. formosa* on hairy and hairless cucumber leaves. Bars represent the 95% confidence interval. Experimental set-up (n=8 and 5 respectively): 25 L3 and 25 L4 (unparasitized) greenhouse whitefly larvae on 3.5 cm^2 exposed to 1 parasitoid for 180 min at 24°C (Hulspas-Jordaan, 1978). Simulations were done for 100 replicates.

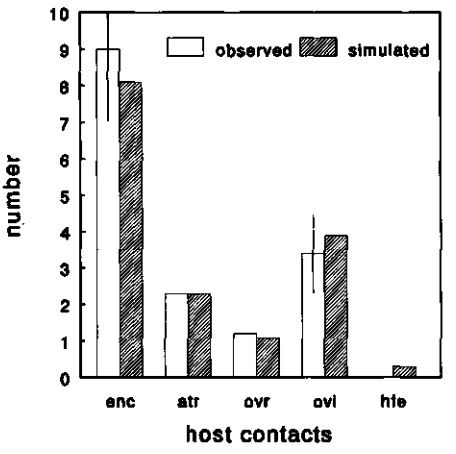

Figure 3. Observed and simulated number of encounters (enc), antennal rejections (atr), ovipositorial rejections (ovr), ovipositions (ovi) and host feedings (hfe) of *E. formosa* on a poinsettia leaf. Bars represent the 95% confidence interval. Experimental set-up (n=22): 11 L3 and 11 L4 (unparasitized) greenhouse whitefly larvae on 7.07 cm^2 exposed to 1 parasitoid for 60 min at 20°C (Boisclair, 1990). Simulations were done for 100 replicates.

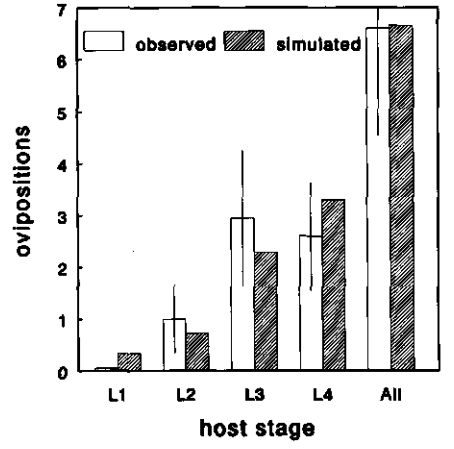

Figure 4. Observed and simulated number of ovipositions of *E. formosa* in L1, L2, L3, L4 and in all larvae on a bean leaf. Bars represent the 95% confidence interval. Experimental set-up (n=20): 20 L1, 20 L2, 20 L3 and 20 L4 (unparasitized) greenhouse whitefly larvae on 19.6 cm^2 exposed to 1 parasitoid for 120 min at 25°C (Gast & Kortenhoff, 1983). Simulations were done for 100 replicates.

Functional response

A parasitoid searching on the infested side of a tomato leaflet was simulated for 2 h. Host numbers were 6, 12, 24,..., 480 and the host stages L1, L2, L3, L4, prepupa (PP) and pupa (PU) were equally available. Temperature was always 25°C and tomato leaflet size was 22 cm^2 (one-side).

Under these conditions, mean number of encounters, number of ovipositions and host feedings increased with host density to a maximum level of 25 encounters, 6.5 ovipositions and 1.5 host feedings after 2 h (Figure 5). Variation resulted from the random encounter of hosts, the variable walking activity of each parasitoid, the variable handling behaviour of an encountered host and from the variable handling times. The functional response resembles a Type II curve. At host densities of 0, 1, 2,..., 6 L3

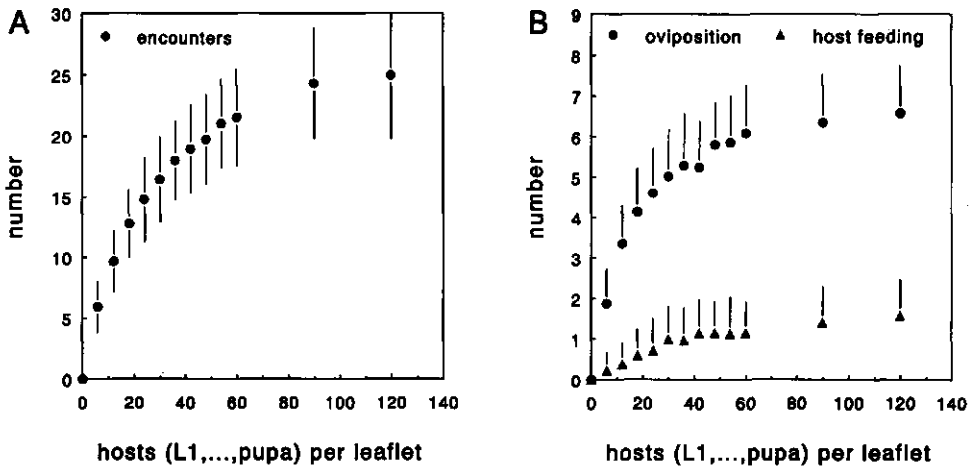

Figure 5. Simulated number of (A) encounters and (B) ovipositions and host feedings of *E. formosa* after 2 h on the infested leaf side of a tomato leaflet (22 cm^2). Bars represent the standard deviations (n=100).

larvae per leaflet, a linear increase in number of encounters and ovipositions was simulated. At a density of only 1 L3 larva per leaflet, 60% of the parasitoids discovered the larva within the exposure time of 2 h. Per parasitoid, an overall mean of 0.92 encounters, 0.46 ovipositions and 0.01 host feedings were simulated after 2 h.

The simulated distribution of encounters over different host stages is given in Figure 6A for 24 and 480 hosts per leaflet. They are expressed as percentages of the total number of encounters for all stages together. The same is done for ovipositions and host feedings (Figures 6B-C). Host density did not affect the distribution of encounters. Even the smallest stage (L1) was encountered quite often, compared to the larger stages. As the initial number of each host stage on the leaflet was equal, the distribution of encounters is only determined by their mean diameter (see equation (1)).

The distribution of ovipositions over different host stages is determined by a combination of being encountered (size) and the probability of oviposition after encountering a host (success ratio), of which the latter played the most important role. The simulated distribution of ovipositions over different host stages shifted towards the most preferred host stage at a lower egg load. This can be clearly seen at a high host density (Figure 6B), and is the result of a decreasing success ratio when egg load decreases (see Table 1). In the model, this decrease was taken linear with equal slope for all stages, so the success ratios of the most preferred stages become relatively higher at a lower egg load.

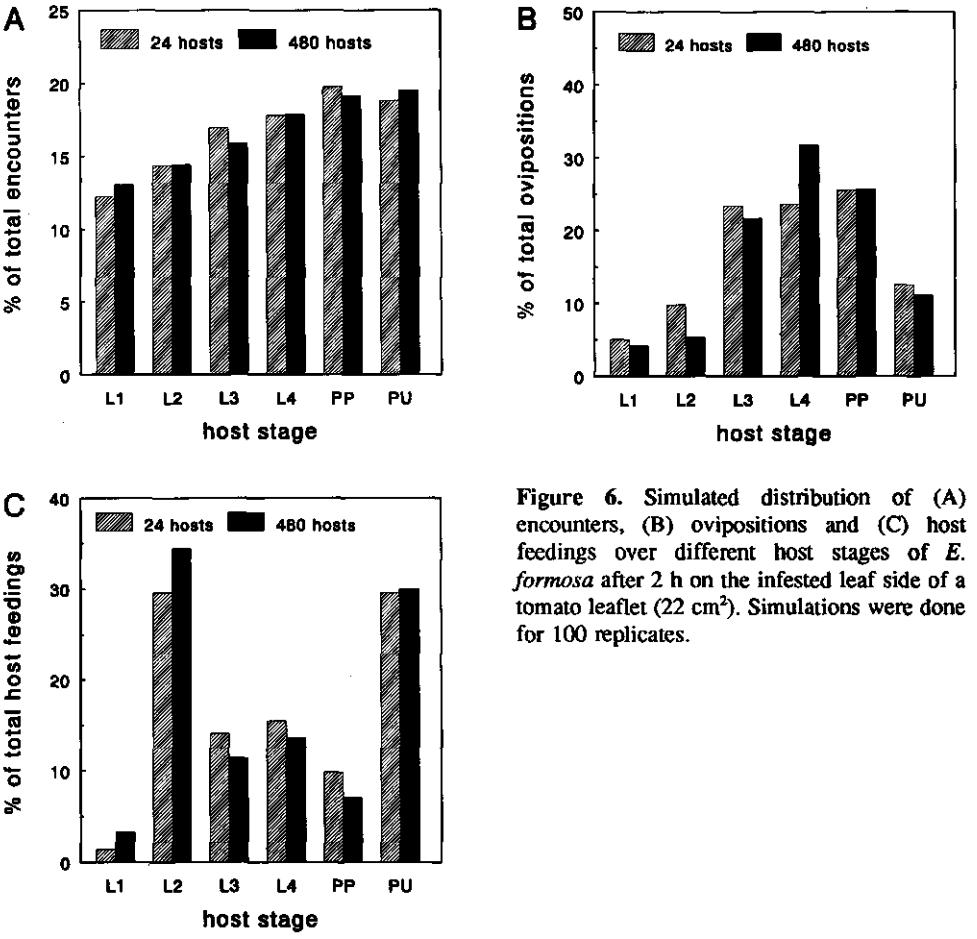

Figure 6. Simulated distribution of (A) encounters, (B) ovipositions and (C) host feedings over different host stages of *E. formosa* after 2 h on the infested leaf side of a tomato leaflet (22 cm^2). Simulations were done for 100 replicates.

Sensitivity analysis

Parasitoids foraging under the same conditions as simulated for the functional response were simulated again (see above). Now, the *change* in mean number of encounters and ovipositions was simulated after the value of one particular input parameter was decreased with 25% compared to the 'standard run'. This was done for 13 input parameters at a host density of 6, 24 and 480 hosts per leaflet. These densities corresponded with a low, medium and high number of ovipositions respectively (2.06, 4.71 and 7.50), compared to the maximum egg load of 8.9. SE/mean for the 100 replicates of the standard run was 3.75, 1.96 and 2.17% for the number of encounters and 4.64, 2.63 and 1.61% for the number of ovipositions for the three host densities respectively. Results are shown in Figure 7, in which input parameters resulting in long

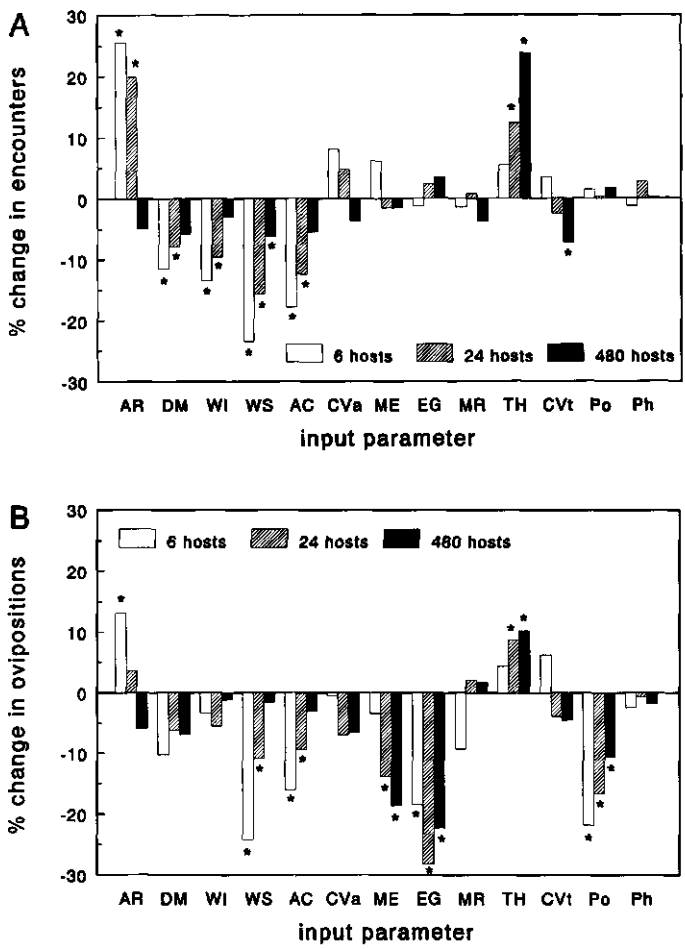

Figure 7. Change (%) in number of (A) encounters and (B) ovipositions of *E. formosa* after 2 h on the infested leaf side of a tomato leaflet (22 cm^2), when the value of one particular input parameter was decreased with 25%. Simulations were done for 100 replicates. Input parameters are leaf area (AR), diameter of host stages (DM), width of the parasitoids' searching path (WI), walking speed (WS), walking activity (AC), coefficient of variation of walking activity (CVa), maximum egg load (ME), initial egg load (EG), egg maturation rate (MR), handling time (TH), coefficient of variation of handling time (CVt), probability of oviposition after encountering a host (success ratio, Po) and probability of host feeding after encountering a host (Ph). Bars marked by * are significantly different from 0 (Student t-test on population mean; α=0.05).

bars are the most important in determining the number of encounters or ovipositions. Increasing instead of decreasing each input parameter yielded about the same absolute change in the output under study.

At a high host density, the number of encounters after 2 h was strongly influenced by and most sensitive to the handling time (TH, Figure 7A). Other parameters were less important. At a low host density, more parameters were important, especially the walking speed (WS), the walking activity (AC) and the leaf area (AR).

The number of ovipositions at a high host density was most sensitive to the initial and maximum egg load (EG and ME, Figure 7B), which is caused by egg limitation of the parasitoid. Again, more parameters were important at a low host density: the walking speed (WS) and walking activity (AC), the probability of oviposition (Po) and the initial egg load (EG). The latter still played an important role at a low host density, whereas the number of encounters was not affected (Figure 7A).

The influence of the temperature was simulated and is shown in Figure 8. At 18°C the number of encounters and ovipositions were strongly reduced, because the walking activity as observed in experiments was very low at that temperature (Chapter 4). At 20°C the mean number of encounters and ovipositions was always significantly lower than at 25 or 30°C. A reduction of 41.7 and 33.5% respectively was simulated compared to 25°C at a host density of 6 per leaflet. At higher host densities, the reduction in the number of encounters and ovipositions was smaller: 29.5 and 17.8% at 24 hosts per leaflet and only 8.9 and 5.2% at 480 hosts per leaflet respectively. This reduction is caused by a reduction in walking speed of 39.2% at 20°C compared to 25-

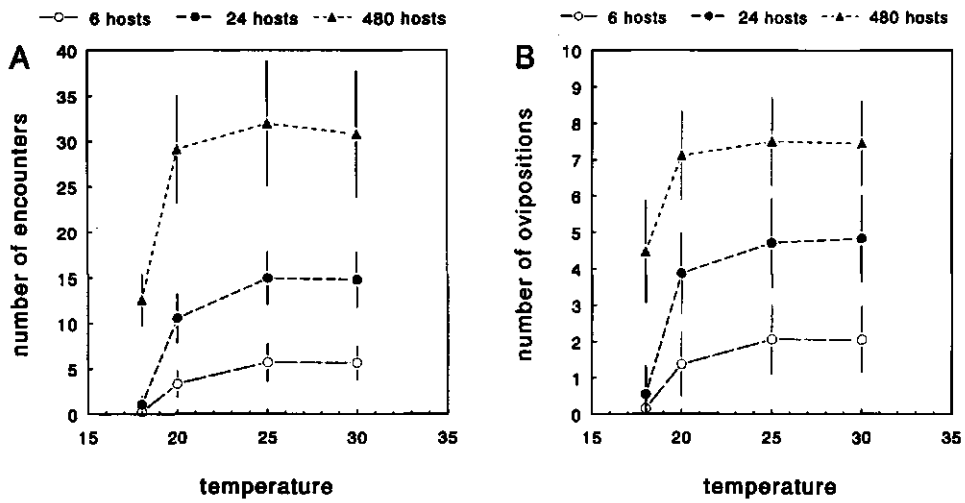

Figure 8. Simulated number of (A) encounters and (B) ovipositions of *E. formosa* after 2 h on the infested leaf side of a tomato leaflet (22 cm^2) at different temperatures. Bars represent the standard deviations (n=100).

30°C (Chapter 4). A change in the egg maturation rate with temperature did not play a role, because that parameter was unimportant in a time period of 2 h, according to Figure 7.

DISCUSSION

The simulation results agreed well with observations on cucumber, poinsettia and bean leaves. The probability of a host rejection, an oviposition or a host feeding after encountering a certain host stage were obtained from host populations of mixed stage distribution (Nell et al., 1976). The excellent validation results make it likely that they do not change when only the most preferred stages (L3 and L4) are offered, as was done in the validation experiments.

As simulated number of encounters are similar to the observed number, the hypothesis of random host encounter seems to be correct. The walking pattern of the parasitoid was not simulated by generating angular deviations from observed frequency distributions. Instead, the equation of Skellam (1958) for random encounter was used. Van Lenteren et al. (1976a) observed that the walking pattern of *E. formosa* was not influenced by veins and never became tortuous; hosts stages were encountered according to their size and number. Noldus & van Lenteren (1990) show that *E. formosa* does not use chemical cues to locate hosts or infested leaves. As two experiments used to validate the model were done at a very small spatial scale, influence of edges on walking pattern seems to be absent. In Chapter 2 it was observed that walking along edges did hardly occur and that a preference for a particular leaf part was absent.

A strong reduction in the simulated number of encounters and ovipositions at 18°C was caused by a very low walking activity. During recent experiments a very low walking activity was found at 15 and 18°C after different pre-treatments of the parasitoids (Chapters 2 and 4). This does not agree at all with earlier findings of van Lenteren & van der Schaal (1981), who found a temperature threshold of 11.4-12°C for searching and oviposition. However, it does agree with Enkegaard (1992) who found a much lower the functional response curve for *E. formosa* on hosts of *Bemisia tabaci* at 16°C compared to 22°C. Parasitoids were reared at a constant temperature of 22°C. A possible explanation may be that during the last decade, the temperature at which the parasitoids were reared has been increased and/or temperature fluctuations have been decreased, causing a shift in the lower temperature threshold for searching and oviposition.

At high host densities and temperatures above 18°C, the number of ovipositions of *E. formosa* after 2 h was close to the initial egg load, which was the most important parameter in such a short period. Even at a low host density, initial egg load played an important role for the number of ovipositions, whereas the number of encounters was not affected. This was caused by the effect of egg load on success ratio (see Table

1), which is an important parameter at low host densities. Also important at low densities were the parasitoids' walking speed and walking activity.

The shape of the simulated functional response resembled a Type II curve. This agrees with empirical data of *E. formosa* obtained in petri dish experiments of Arakawa (1981), Fransen & van Montfort (1987) and Lopez Avila (1988). At low densities of 1 to 6 hosts per 22 cm^2, a linear increase in number of encounters and ovipositions was simulated. Burnett (1958a,b) also found a linear increase in number of hosts parasitized at comparable host densities, although the experimental set-up was different. He released 20 parasitoids at the same time, resulting in a high parasitoid-host ratio. In fixed-time laboratory experiments, the Type II functional response is frequently observed for predators and parasitoids of insects or mites (reviews in Lessels, 1985; Stiling, 1987; Walde & Murdoch, 1988). The deceleration of the curves with increasing host density has generally been attributed to an increase in non-searching activities or to egg limitation, as observed by deBach & Smith (1941) and Collins et al. (1981) respectively. For *E. formosa*, both play a role and a decrease in walking activity and success ratio is responsable for the effect.

Sabelis (1981) simulated a Type II response for predatory mites foraging for spider mites using different simulation approaches, of which Monte Carlo simulation and stochastic queueing technique (finite state Markov model) yielded similar results close to the observations. In the present study a Monte Carlo model was chosen to simulate the foraging behaviour of *E. formosa* on a small spatial scale (single leaves) when host numbers are low. Under these conditions, the natural enemy gradually depletes the patch and host densities will change rapidly. Steady states cannot be assumed as will be done when using the Markov model (Sabelis, 1985, 1986).

Type II functional responses can be described by the time budget or disc equation (Holling, 1959). An important assumption for that equation is that host density remains constant. When the natural enemy gradually depletes the patch, the equation of Rogers (1972) is more suitable. The shape of the curve is described by the 'handling time' (T_h) and the attack rate (a'). The maximum level of the functional response is determined by the maximum number of handling times that can be fitted into the total time available. For *E. formosa*, the simulated maximum level of 7 ovipositions would result in a T_h of 17 min, which is much higher than the observed total handling time of 5.5 min for oviposition (Chapter 4). Fernando & Hassell (1980) showed that real handling times are much lower than estimated T_h values for several predator-prey interactions. Obviously, the estimated T_h also includes the times taken for standing still, preening, rejection, host feeding and egg maturation.

Estimated T_h values for *E. formosa* vary from 12-17 to 48 min (Arakawa, 1981; Fransen & van Montfort, 1987) and with *Bemisia tabaci* as host, from 78 to 120 min (Lopez Avila, 1988; Enkegaard, 1992). The rate of approach to the plateau at a low host density is the searching efficiency or the attack rate, a' (Holling, 1959). The attack rate based on the present simulations was 1.0 cm^2/h. Estimated a' values were 1.5 cm^2/h (Fransen & van Montfort, 1987) and with *B. tabaci* as host, 1.5-2.6 cm^2/h (Lopez Avila, 1988; Enkegaard, 1992). T_h and a' are just parameters to *describe* the

functional response curve. They depend on temperature, exposure time and, when host densities are not equal, on the experimental arena or spatial scale of the experiments, as was observed for *E. formosa* by Enkegaard (1992). Thus, comparison of T_h and a' of different experiments is often not possible. A description of observed functional responses is not sufficient and explanatory simulation studies, based on the basic processes, are necessary to increase insight in quantitative effects.

Type III (S-shaped) functional responses have been found for parasitoids confined to a patch for a fixed time (see examples of Hassell et al., 1977; Pandey et al., 1982,1984; Shirota et al., 1983; Carton et al., 1987; Kumar et al., 1994). For *Venturia (Nemeritis) canescens* this shape resulted from an increase in the searching intensity or activity (Hassell et al., 1977). Such an accelerating response can also be caused by a decreasing time spent handling the hosts, as found for the parasitoid *Aphelinus thomsoni* (Collins et al., 1981). For *E. formosa* Type III responses may in principle be the result of an increase in the parasitoid's walking speed, the walking activity or the success ratio or by a decrease in the handling time after encounters or ovipositions. Such changes were never found for *E. formosa* during direct observations (van Lenteren et al., 1976a; Sütterlin & van Lenteren, in prep.; Chapter 4).

A potentially important component of parasitoid behaviour is omitted in fixed-time experiments. A parasitoid confined to a patch for a fixed length of time is forced to remain there, whereas in the field it may emigrate to search for better patches. The Type II response of *E. formosa*, as derived from the simulations, may be caused by the 'experimental' procedure that was followed. Van Lenteren & Bakker (1978) mention two possibilities for obscuring a Type III response, when parasitoids are confined to a patch: (1) the small experimental arena, which causes even the lowest host densities to be too high to detect the increasing attack rate and (2) the parasitoid cannot leave the arena, which increases the probability to detect hosts at a low density. The functional response curve on a leaf may change in more natural situations where the parasitoid can leave. Type III responses may result when an accelerating increase in residence time with host density occurs. The next step in our analysis of the foraging behaviour of *E. formosa* will be a study where parasitoids can fly away from the leaf (Chapter 6).

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Chapter 6

Analysis of foraging behaviour of the whitefly parasitoid *Encarsia formosa* on a leaf: a simulation study

ABSTRACT

Foraging behaviour of *Encarsia formosa* was analysed with a stochastic simulation model of the searching parasitoid during a single visit to a tomato leaflet infested with immatures of the greenhouse whitefly, *Trialeurodes vaporariorum*, from which the parasitoid can fly away. The model is based on host searching, host selection, host handling and patch leaving behaviour, and on the physiology of the parasitoid. Outputs of the model were the residence time of the parasitoid on the leaflet and the number of hosts encountered, parasitized or killed by host feeding. The mean residence time and the mean number of encounters, ovipositions and host feedings on the leaflet increased with host density to a maximum of 14.0 h, 209.3 encounters, 15.6 ovipositions and 2.9 host feedings. The shape of the curves resembles a Type II functional response. The relationship between ovipositions per unit of residence time and host density showed a dome-shaped curve. The most important parameters affecting the number of ovipositions at low host densities were the parasitoids' initial egg load, the walking speed, the walking activity and the leaf area. At high densities, the maximum and initial egg load and the egg maturation rate were most essential.

INTRODUCTION

Biological control of the greenhouse whitefly, *Trialeurodes vaporariorum*, with the parasitoid *Encarsia formosa* is commercially applied with success in several greenhouse vegetables, such as tomato (van Lenteren & Woets, 1988). However, there is no satisfactory explanation why the parasitoid introduction scheme for tomato cannot be applied reliably on some other important greenhouse crops, such as cucumber and gerbera. This chapter is a continuation of the work described in Chapter 5, where the foraging behaviour of *E. formosa* during a fixed exposure time in an experimental arena was simulated. Under these conditions, the shape of the functional response resembles a Type II curve (Holling, 1965). However, a potentially important component of parasitoid behaviour is omitted in fixed-time experiments. A parasitoid confined to a patch is forced to remain there, whereas in the field it might emigrate to search for other patches. Van Lenteren & Bakker (1978) and Collins et al. (1981) found a shift from Type II curves in fixed-time experiments to Type III in variable-time experiments. Simulations of Luck et al. (1979) showed that an increase in giving up time after the first encounter with a host can produce a sigmoid response. The shape of the curve may change when an accelerating increase in residence time with host density occurs.

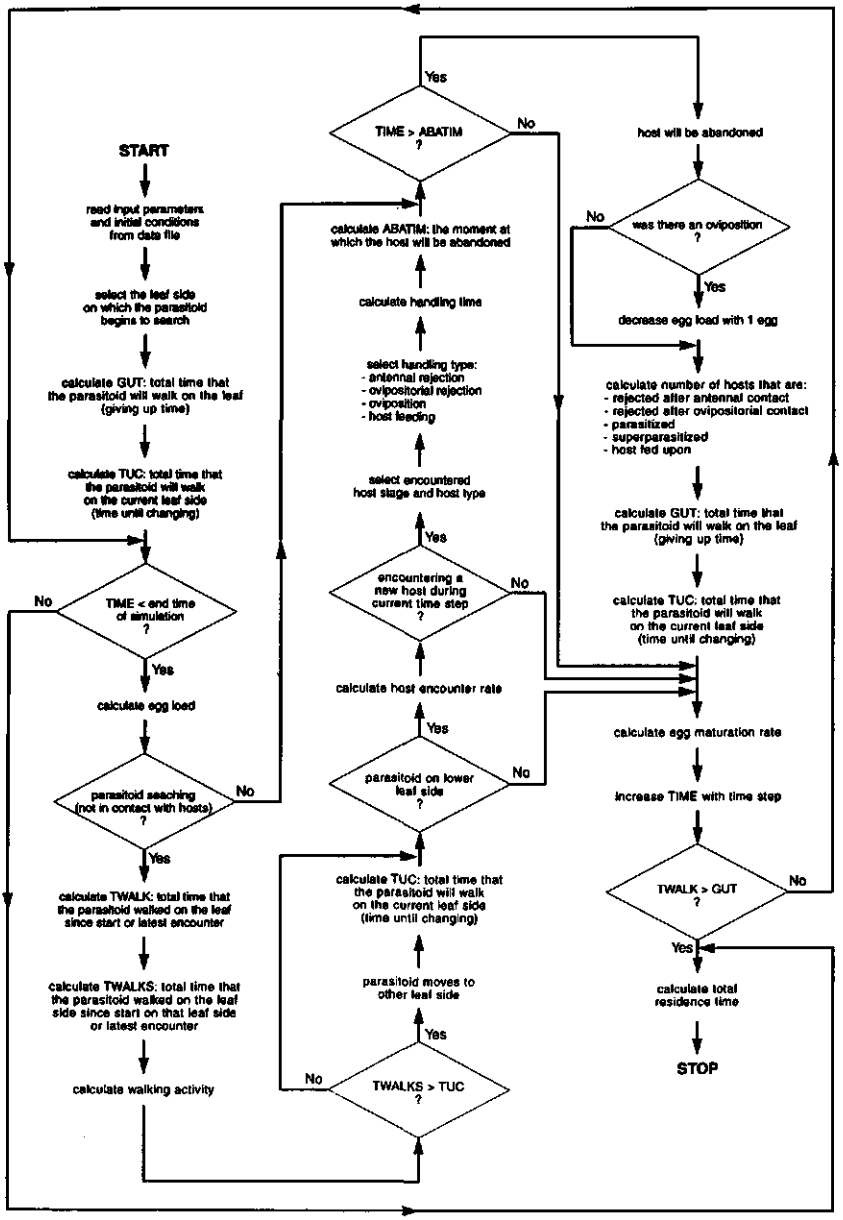


Figure 1. Flow diagram of the foraging behaviour of one *E. formosa* female on a leaf.

The model presented here simulates the foraging behaviour of the parasitoid during a single visit to a tomato leaflet. To understand quantitative effects of the parasitoids' foraging behaviour on whitefly populations in a crop, foraging behaviour is first studied at a much smaller spatial scale. The parasitoid can move from one leaf side to the other and can fly away. From the simulation results at different host densities, the parasitoids' residence time on the leaflet and the number of encounters, ovipositions and host feedings in relationship to host density were generated. The shape of the curves helps to understand the host-parasitoid interaction at the population level (see introduction of Chapter 5). A sensitivity analysis extracted the most important behavioural or physiological parameters for residence time and number of hosts encountered and parasitized. The model will later be extended and used at larger spatial scales, such as plants and canopies (Chapters 7 and 10).

THE SIMULATION MODEL

A stochastic Monte Carlo simulation model was developed for the foraging behaviour of the parasitoid during a single visit to a tomato leaflet infested with hosts. The parasitoid is able to move from one leaf side to the other and can fly away.

The model for one parasitoid is presented in the flow diagram of Figure 1. A detailed description of the processes as simulated by the model and the input parameters can be found in Chapter 5. In the model, the parasitoid starts searching on the lower side of a leaflet, where hosts can be found. The model is initialized with the number of hosts per leaflet for each stage. The time step of simulation was taken 1.2 s, about one tenth of the smallest time coefficient in the model (handling time for rejection of a parasitized host), which is needed for accurate numerical integration. Accuracy was tested by comparing the simulation results with those obtained at a time step double or half in size. As *E. formosa* does not forage in the dark (Hoogcarspel & Jobsen, 1984), the maximum time of simulation was set to a daylength of 16 h. Temperature was always 25°C. Number of replicates was 1000, except in the case of the sensitivity analysis at host density 480 where 100 replicates were sufficient for a low standard error of the mean (SE<5%). Honeydew on the leaf was assumed to be absent. During the simulation, the initial condition of each replicate was taken the same. Therefore, morphological or physiological differences between parasitoids (i.e. in body size, number of ovarioles or relative egg maturation rate) were not taken into account.

RESULTS

Validation

Validation of the simulation results was very good for parasitoids foraging during a fixed time in an experimental arena (Chapter 5). The extra input parameters for the present model, the tendency to leave and the tendencies of changing leaf sides, were derived from direct observations (Chapter 3). Therefore these experiments were only used for verification and not for independent validation. The simulated residence times and number of encounters were similar to these observations for parasitoids foraging on clean leaflets and on leaflets with 77-200 black pupae.

The experiments with one to four hosts per leaflet could not be used, because parasitoids were always released close to the hosts, whereas the model assumes random landing. Thus, experiments to validate random host encounter at low host densities were not available. At one L3 larva per leaflet, only 15.7% of the parasitoids are expected to encounter the larva according to the model, if the position of the host and the place where the parasitoid begins to search on the lower leaf side is random.

Simulation results

In the model, the parasitoid started to search on the lower side of a tomato leaflet on which the host stages L1, L2, L3, L4, prepupa (PP) and pupa (PU) were equally available. Simulation continued until the parasitoid left. Temperature was always 25°C and tomato leaflet size was 22 cm^2 (one side).

Under these conditions, the mean residence time and the mean number of encounters, ovipositions and host feedings increased with host density to a maximum of 14.0 h, 209.3 encounters, 15.6 ovipositions and 2.9 host feedings (Figures 2A-C). Variation between parasitoids resulted from the random encounter of hosts, the variable walking activity, the variable handling behaviour of an encountered host, the variable handling time and from variation in the giving up time (GUT) and the time that the parasitoid searches on a particular leaf side (TUC). Deviations from the mean were highest at 80-240 hosts per leaflet, but when expressed relative to their mean, they were highest at low host densities.

When parasitoids land on the upper leaf side, they first have to reach the lower leaf side to encounter hosts. As GUT did not depend on the leaf side on which the parasitoid began to search (Chapter 3), a larger part of the parasitoids will leave the leaflet before the first host encounter. The reduction of the mean residence time and the number of encounters and ovipositions varied between 19 and 34%, according to the model at 24 and 480 hosts per leaflet.

The shape of the curves of Figures 2A-C resembles a Type II response. The functional response is the relationship between the number of parasitizations of an individual parasitoid per unit time as a function of host density. According to the conventional definition, the number of parasitizations during an *equal* time interval have to be obtained at different host densities. A functional response curve can be generated when the number of ovipositions is expressed per unit of residence time

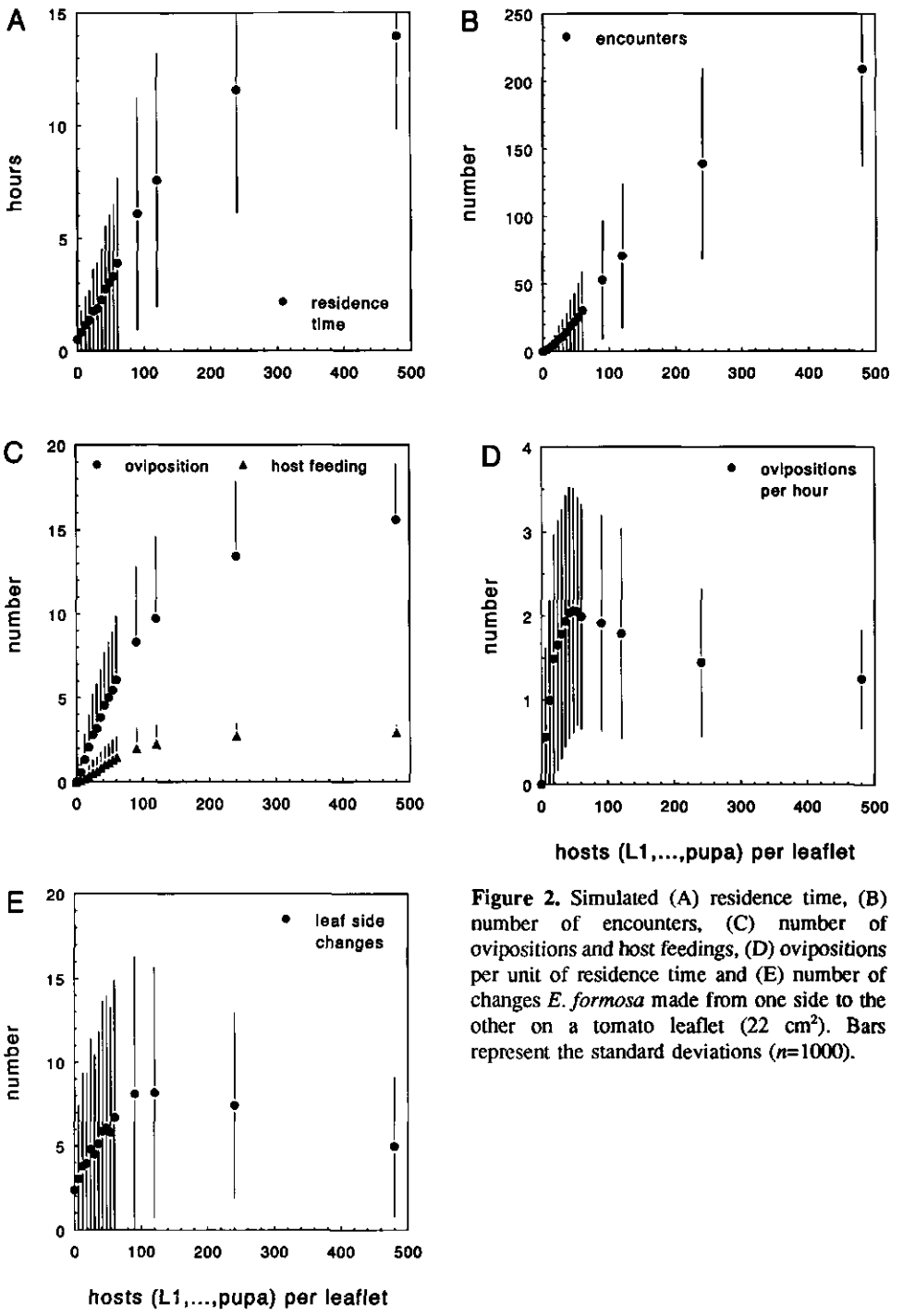


Figure 2. Simulated (A) residence time, (B) number of encounters, (C) number of ovipositions and host feedings, (D) ovipositions per unit of residence time and (E) number of changes *E. formosa* made from one side to the other on a tomato leaflet (22 cm^2). Bars represent the standard deviations (n=1000).

(Figure 2D). The resulting mean number of ovipositions per hour is an average over the total residence time. The curve increased rapidly with host density to an optimum of 2.06 ovipositions/h at 48 hosts per leaflet, after which it decreased to 1.25 at higher densities.

At low densities of 0, 1, 2,..., 6 L3 larvae per leaflet, a linear increase was simulated (Figures 2A-D). At a density of 1 L3 larva per leaflet, 15.7% of the parasitoids discovered the larva, 9.7% had a successful parasitization and 1.1% used the larva for host feeding. Thus, the probability for the larva of being killed by *E. formosa* was 10.8% during a single visit of the parasitoid to the leaflet. When the host stages are equally available, they were 3.5% for L1, 9.6% for L2, 14.8% for L3, 19.5% for L4, 16.7% for the prepupa and 12.8% for the pupa. Thus, for 100% host kill, leaflets have to be visited at least five times. The probabilities hardly changed with increasing host density until 90 hosts per leaflet, due to the initial linear increase of the number of ovipositions and host feedings with host density. The oviposition-host feeding ratio was initially 10:1 and dropped to 4.2:1 at higher densities.

Figure 2E shows the simulated number of changes the parasitoids made from one leaf side to the other. From 2.4 changes on average on clean leaflets, it increased to 8.2 at 120 hosts per leaflet, after which it decreased at higher host densities. It is clear that on tomato leaflets both leaf sides were visited quite often, whereas only on the lower leaf side hosts can be found.

The percentage of parasitoids with no encounter before leaving the leaflet (non-finders) and the percentage of parasitoids which stayed on the leaflet until the end of the day (stayers) are given in Figure 3. Especially the percentage non-finders rapidly declined with host density. At a high densities of 480 hosts per leaflet, 73.3% of the parasitoids stayed on the leaflet for the whole day and continued foraging the next morning. As honeydew prolongs the time on a leaflet (Chapter 3), the percentage non-

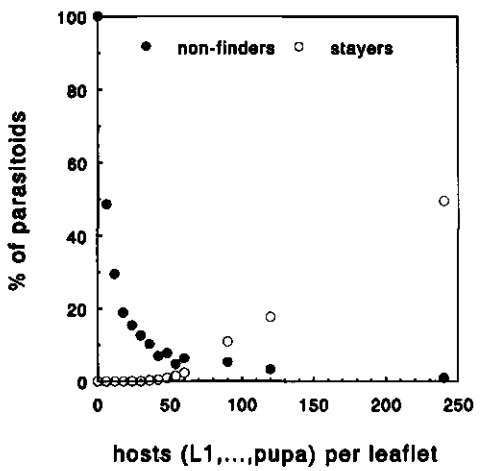


Figure 3. Simulated percentage of *E. formosa* leaving a tomato leaflet (22 cm^2) before an encounter (non-finders) and staying on the leaflet during the whole day of 16 h (stayers).

finders will decrease and the percentage stayers will increase when presence of honeydew would be included in the simulations.

The distribution of encounters over different host stages is given in Figure 4A for 24 and 480 hosts per leaflet. They were calculated as percentages of the total number of encounters for all stages together. The same was done for the number of ovipositions and host feedings (Figures 4B-C). Host density did not affect the distribution of encounters. As the initial number of each host stage was equal, the distribution of encounters was only determined by host size (see equation of Skellam, 1958). Even the smallest L1 stage was encountered quite often, because the width of the parasitoids' searching path is rather large compared to the size of L1.

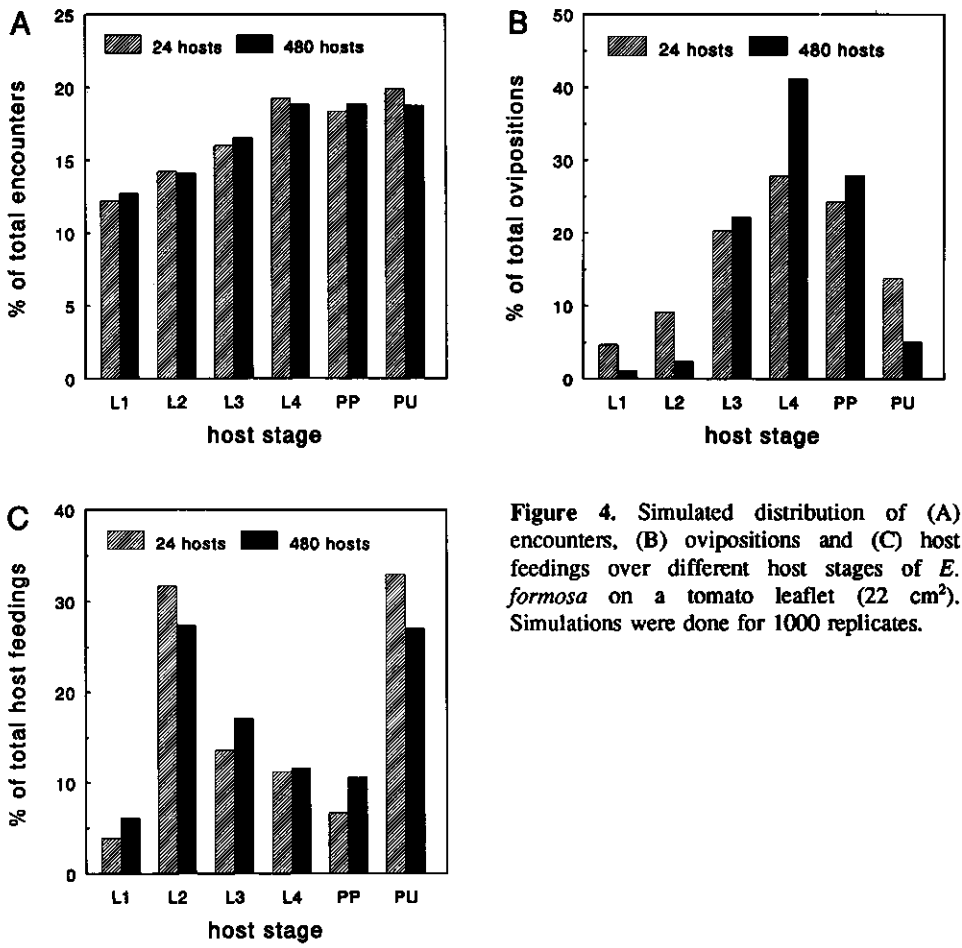
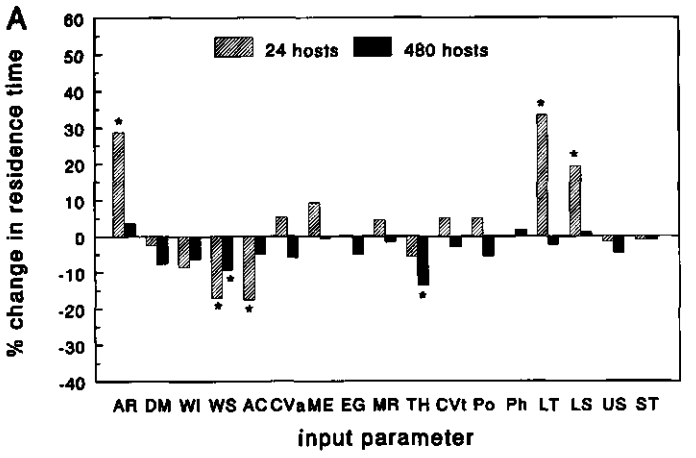


Figure 4. Simulated distribution of (A) encounters, (B) ovipositions and (C) host feedings over different host stages of *E. formosa* on a tomato leaflet (22 cm^2). Simulations were done for 1000 replicates.

The distribution of ovipositions and host feedings over different host stages was determined by a combination of hosts being encountered (size) and the probability of an oviposition (success ratio) or a host feeding after encountering a host, of which the latter played the most important role. At high host densities the distribution of ovipositions shifted to the most preferred stages L3, L4 and prepupa (Figure 4B). This is the result of a decreasing success ratio when egg load decreases (Chapter 5). In the model, this decrease was taken linear with equal slope for all stages, so the success ratio of the most preferred stages become relatively higher at a lower egg load. The distribution of host feedings over different host stages gave the opposite picture, which was caused by the slight increase in the probability for host feeding when egg load decreases.



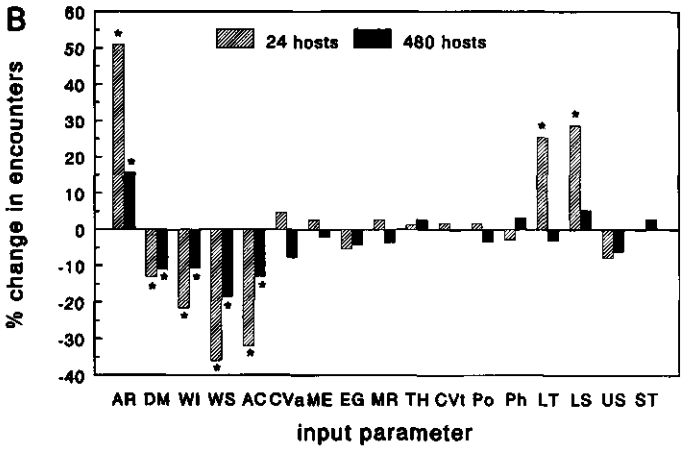
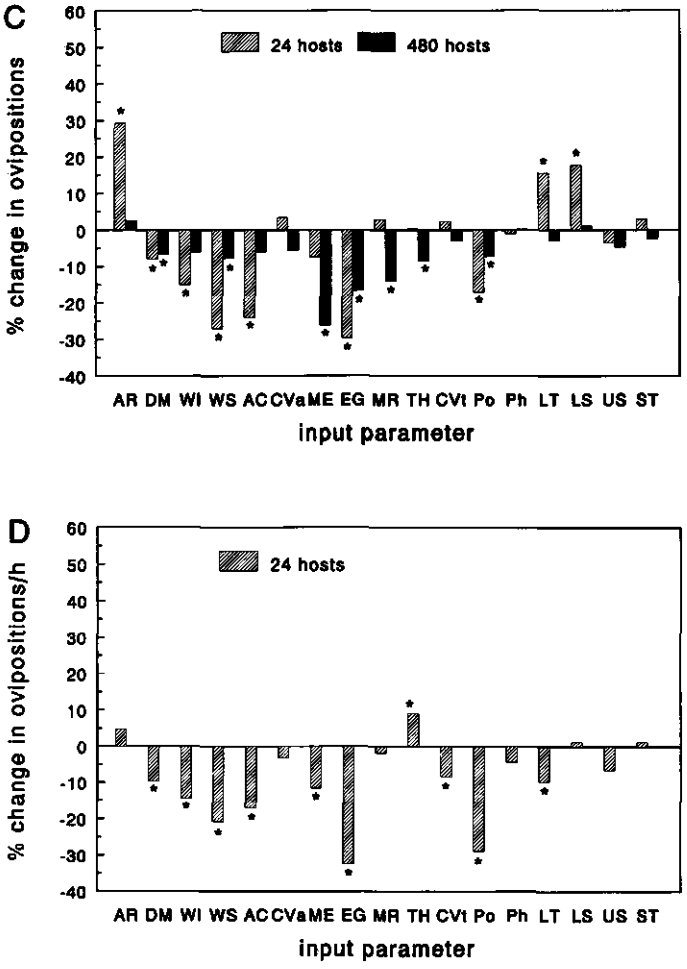


Figure 5. Change (%) in (A) residence time, (B) number of encounters, (C) number of ovipositions and (D) ovipositions per unit of residence time of *E. formosa* on a tomato leaflet (22 cm^2), when the value of one particular input parameter was decreased with 25%. Number of simulation replicates were 1000 at 24 hosts and 100 at 480 hosts. Input parameters are leaf area (AR), diameter of host stages (DM), width of the parasitoids' searching path (WI), walking speed (WS), walking activity (AC), coefficient of variation of walking activity (CVa), maximum egg load (ME), initial egg load (EG), egg maturation rate (MR), host handling time (TH), coefficient of variation of handling time (CVt), probability of oviposition after encountering a host (success ratio, Po), probability of host feeding after encountering a host (Po), leaving tendency (LT), tendency of changing from the lower leaf side to the upper (LS), tendency of changing from the upper leaf side to the lower (US), and both tendencies of changing from one leaf side to the other (ST). Bars marked with * are significantly different from 0 (Student t-test on population mean; α=0.05).



Sensitivity analysis

The *change* in residence time, number of encounters, number of ovipositions and ovipositions per unit of residence time were simulated, based on a decrease of 25% in the value for one particular parameter, compared to a 'standard run'. This was done for 17 parameters at 24 and 480 hosts per leaflet, corresponding to a low and high number of ovipositions respectively (2.8 and 15.6 per female). SE/mean for the replicates of the standard run varied between 1.96 and 3.74%. Results are shown in Figure 5, in which parameters resulting in long bars are the most essential in determining the output under study.

At a high host density, the residence time was most sensitive to the handling time (TH, Figure 5A). At a low density, more parameters were important, such as the leaving tendency (LT) and the tendency of changing from lower to upper leaf side (LS), the leaf area (AR), the walking speed (WS) and the walking activity (AC). Only the first two parameters had a direct effect on residence time. The others changed the residence time indirectly through the number of encounters with hosts.

Both residence time and number of encounters were influenced by the same parameters, especially at low densities. The number of encounters was most sensitive to the parameters used in the equation of Skellam (1958) (Figure 5B): the walking speed (WS), the walking activity (AC), the leaf area (AR), the width of the parasitoids' searching path (WI) and the size of the hosts (DM). The leaving tendency (LT) and the tendency of changing from lower to upper leaf side (LS) affected the number of encounters indirectly through the residence time.

The number of ovipositions at a high host density was strongly affected by the maximum and initial egg load (ME, EG) and the egg maturation rate (MR, Figure 5C). At a low density, egg maturation was not important anymore and essential were the initial egg load (EG), the success ratio (Po), plus the same parameters as for the number of encounters. Only the first two changed the number of ovipositions without affecting the number of encounters and the residence time (Figures 5A-B). The effect of egg load is caused by its effect on success ratio (see Chapter 5).

The number of ovipositions per unit of residence time is a measure of the parasitoids' efficiency on the leaflet. For simplicity, only results of the sensitivity analysis at a low host density are given (Figure 5D). Two of the most essential parameters were the initial egg load (EG) and the success ratio (Po). They had a direct effect on the number of ovipositions without changing the number of encounters and the residence time (Figures 5C and 5A). Also important were the parameters used in the equation of Skellam (1958), especially the walking speed (WS) and the walking activity (AC). They affected the number of ovipositions but also, to a lesser extent, the residence time indirectly through the number of encounters (Figures 5C and 5A). Compared to the number of ovipositions on the leaflet, oviposition per unit of residence time was hardly sensitive to the leaf area (AR) and the tendency of changing from the lower leaf side to the upper (LS, Figures 5C-D), because these parameters changed the number of ovipositions and the residence time in the same way (Figures 5C and 5A).

The influence of temperature is shown in Figure 6. At 18°C parasitoids were assumed not to fly away from the leaflet and the walking activity was very low, as was observed in experiments (Chapter 4). At 20°C compared to 25°C a significant reduction of 22.1% in residence time, 47.5% in number of encounters, 36.2% in number of ovipositions and 30.5% in ovipositions per unit of residence time were simulated at 24 hosts per leaflet. At 480 hosts per leaflet, differences were also significant, except for the ovipositions per unit of residence time. They were caused by a reduction of 39.2% in walking speed and of 25.1% in relative egg maturation rate at 20°C compared to

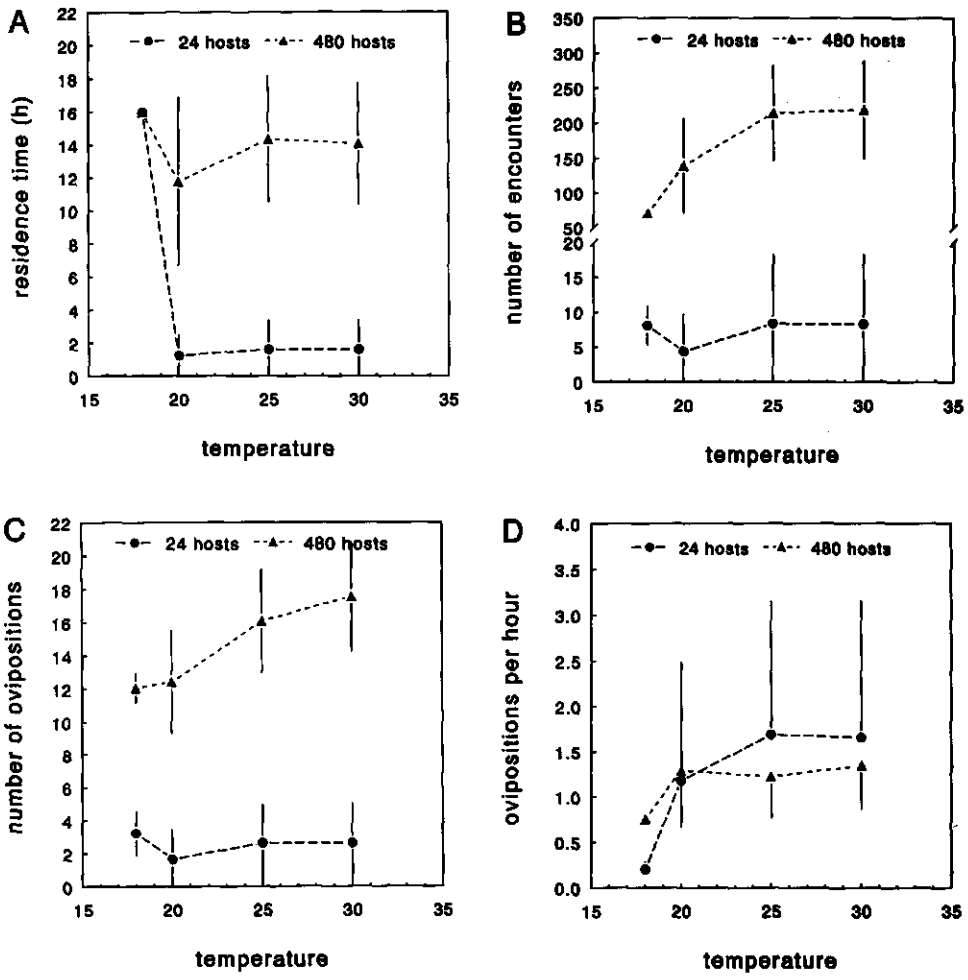


Figure 6. Simulated (A) residence time, (B) number of encounters, (C) number of ovipositions and (D) ovipositions per unit of residence time of *E. formosa* on a tomato leaflet (22 cm^2) at different temperatures. Bars represent the standard deviations (n=1000).

25°C (Chapters 4 and 5), of which the walking speed played the most crucial role according to Figure 5. At 30°C compared to 25°C a significant increase of 9.2% in number of ovipositions and of 10.1% in ovipositions per unit of residence time were simulated at 480 hosts per leaflet. This was due to an increase in the relative egg maturation rate of 25.1%.

DISCUSSION

Validation of the simulation results was very good for parasitoids foraging during a fixed time in an experimental arena (Chapter 5). The simulated residence times and number of encounters were similar to observations for parasitoids foraging on clean tomato leaflets and on leaflets with 77-200 black pupae. Independent experiments at a low host density were not available.

According to the model, *E. formosa* can parasitize 16 greenhouse whitefly immatures per day on average at 25°C, if they start searching with a full batch of mature eggs and if host density is not limiting. This means that about 7 new eggs mature during 16 h at this temperature. Fransen & van Montfort (1987) did petri dish experiments at the same conditions and found maximum oviposition of 14-19. Their experiments were done at lower host densities than simulated here, but the parasitoids could not leave. Arakawa (1981,1982) obtained maximum numbers of 14 and 20 ovipositions per day respectively.

When *Bemisia tabaci* was offered as host, Lopez Avila (1988) found a maximum of 12.8 per day and Enkegaard (1992) found 10.4 ovipositions when the parasitoids could leave the patch. Other studies show lower number of ovipositions per day (for a review see Chapter 9). This can sometimes be explained by a limiting number of hosts, the presence of large amounts of honeydew and we also expect that damaging of the parasitoids may have played a role. It is difficult to handle the minute, delicate *E. formosa* females and only with the utmost care do females survive daily transfer from one patch to another over a long period.

From the second day onwards, *E. formosa* can parasitize 11 hosts per day instead of 16, according to the model, due to egg limitation. If the parasitoid laid all eggs the preceding day, the egg maturation rate is initially 0.69 eggs/h and only 4 eggs mature during a night of 8 h at 25°C (see Chapter 5). Thus, the next morning parasitoids do not have a full batch of mature eggs.

Many parasitoids spend more time in patches of high host density (reviews in Hassell & May, 1974; Murdoch & Oaten, 1975; Godfray, 1994). For *E. formosa*, the increase in residence time with host density resembles a type II response, according to the model. This was also found for the time until first escape attempt of the parasitoids *Aphidius matricariae* and *Diaeretiella rapae* ('t Hart et al., 1978; Pandey et al., 1984). Variation in patch times was considerable, because *E. formosa* responds to its perception of host density (host encounters) rather than to actual host density. The same was found for the parasitoid *Trichogramma pretiosum* (Morrison, 1986). The

simulated number of ovipositions of *E. formosa* on leaves during a single visit increased with host density according to a Type II response. This response agrees with that found by Enkegaard (1992) when *E. formosa* could leave the patch. Collins et al. (1981) observed a Type III response for *Aphelinus thomsoni* in variable-time experiments. Van Lenteren & Bakker (1978) and van Alphen & Galis (1983) found that an increasing giving up time (GUT) after a host encounter resulted in a Type III response. Apparently, the observed increase in GUT of *E. formosa* after the first oviposition on the leaf is too weak to produce a sigmoid response, and the decreasing walking activity and success ratio is predominant in causing a decelerating increase.

The curve describing the number of ovipositions on leaves during a visit of variable duration does not meet the conventional definition of a functional response. The functional response can be derived from the number of ovipositions per unit of residence time (Hertlein & Thorarinsson, 1987). Such a curve showed a dome-shape for *E. formosa* on tomato leaflets and was neither of Type I, II or III according to the simulations. At low host densities, the increase was initially linear. Hertlein & Thorarinsson (1987) found a Type II curve for the ovipositions per unit of residence time for the parasitoid *Leptopilina boulardi*. For *E. formosa*, a decrease was simulated at higher densities, because the parasitoid shows a very low walking activity and success ratio when the egg load is low (Chapter 4). Long residence times are the result, during which oviposition hardly occurs anymore.

The number of ovipositions of *E. formosa* on tomato leaflets was sensitive to the initial egg load and the success ratio, without changing the number of encounters. Other important parameters, such as the leaf area and the parasitoids' walking speed and walking activity had an indirect effect through the number of encounters. These parameters were also the most important for the number of ovipositions of the parasitoid in an experimental arena during 2 h (Chapter 5). On tomato leaflets the parasitoids' leaving tendency and the tendency of changing from the lower leaf side to the upper also played an important role.

Two parameters had a different effect on the number of encounters or ovipositions on a tomato leaflet compared to a closed experimental arena at high host densities. Handling time did not affect the number of encounters on tomato leaflets whereas it played the most crucial role in an experimental arena during 2 h. The egg maturation rate showed the opposite for the number of ovipositions: it was only important on tomato leaflets at long exposure times. The effect of temperature above 18°C on the number of encounters and ovipositions was larger on a tomato leaflet than in an experimental arena during 2 h, due to the more important role of egg maturation. According to the model, the number of new eggs matured within 16 h by *E. formosa* on tomato leaflets with high host density was 3.5, 7.2 and 8.6 at 20, 25 and 30°C respectively.

The above are *mechanistic* explanations for the parasitoids' host encounters and ovipositions on the leaf. That is, they explain *how*, in terms of searching efficiency, the allocation of searching time, host handling and available eggs, the observed level of parasitism is realized. Mechanistic explanations can help to understand failure or

success of biological control in practice. However, they do not explain *why* the parasitoids choose to behave in this way, in terms of the selection pressure acting on them. They thus do not provide a *functional* explanation of the observed behaviour. Whether selection on parasitoid searching behaviour leads to direct, inverse, or no density dependence in parasitism across patches was studied by Lessels (1985) for a population of parasitoids.

The Type II curve for ovipositions of *E. formosa* on tomato leaflets during a single visit was also found for the parasitoid searching in an experimental arena during a fixed time (Chapter 5). However, the observed shape for an arena or leaf may be caused by the 'experimental' procedure and an S-shaped response may be obscured. Van Lenteren & Bakker (1978) mention two possibilities: (1) if the parasitoid cannot leave the arena, this increases the probability to detect hosts at a low density and (2) if the arena or leaf is small, this causes even the lowest host densities to be too high to detect an increasing attack rate. The present study shows that the first possibility can be excluded for *E. formosa*, because an S-shaped curve was not found on tomato leaflets when parasitoids were able to leave. However, the second possibility might still be relevant: a density of 1 host per tomato leaflet is still high compared to densities in the field. This must be studied at a larger spatial scale.

In a next study, the simulation model of the foraging behaviour will be extended and tested at the plant level (Chapter 7). The shape of the functional response and the mechanistic explanations may differ in a more natural situation where the parasitoid is able to fly from one leaflet to another and where host densities are much lower. The influence of host density and host distribution over leaflets will be evaluated as well.

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Chapter 7

Analysis of foraging behaviour of the whitefly parasitoid *Encarsia formosa* on a plant: a simulation study

ABSTRACT

Foraging behaviour of *Encarsia formosa* was analysed with a stochastic simulation model of the searching parasitoid during a day on a tomato plant infested with immatures of the greenhouse whitefly, *Trialeurodes vaporariorum*, on which the parasitoid is able to fly from leaflet to leaflet. The model is based on searching, host selection, host handling and patch leaving behaviour, and on the physiology of the parasitoid. Outputs of the model are the number of visited leaflets and the number of hosts encountered, parasitized or killed by host feeding. The simulation results agreed well with observations of parasitoids foraging on tomato plants. The number of encounters and ovipositions on the plant increased with host density according to a Type II functional response. At a clustered host distribution over leaflets and low host densities, the most important parameters affecting the number of ovipositions were the leaf area, the parasitoids' walking speed and walking activity, the probability of oviposition after encountering a host, the initial egg load and the ratio of search times on both leaf sides. At high densities, the maximum egg load and the giving up time on a leaflet since latest host encounter were most essential.

INTRODUCTION

Biological control of the greenhouse whitefly, *Trialeurodes vaporariorum*, with the parasitoid *Encarsia formosa* is commercially applied with success in several greenhouse vegetables, such as tomato (van Lenteren & Woets, 1988). However, there is no satisfactory explanation why the parasitoid introduction scheme for tomato cannot be applied reliably on other important greenhouse crops, such as cucumber and gerbera. This work is a continuation of the work described in Chapters 5 and 6, where the foraging behaviour of *E. formosa* was simulated in an experimental arena during a fixed time and on a tomato leaflet when the parasitoid was able to leave. Under both conditions, the number of encounters, ovipositions and host feedings increased with host density according to a Type II response (Holling, 1965). However, the leaf might be too small, which causes even the lowest host density to be too high to detect an increasing attack rate (Lenteren & Bakker, 1978). Even a density of one host per leaflet is very high compared to the situation in the field, where biologically controlled whitefly densities are usually below 0.3 pupae per plant (Eggenkamp-Rotteveel Mansveld et al., 1982a,b). Moreover, in the field the parasitoid not only can leave a patch but can proceed to another or return to the same patch again. Experiments in which parasitoids are presented with a number of discrete patches test effects of patch selection. The shape of the functional response may change in a more natural situation

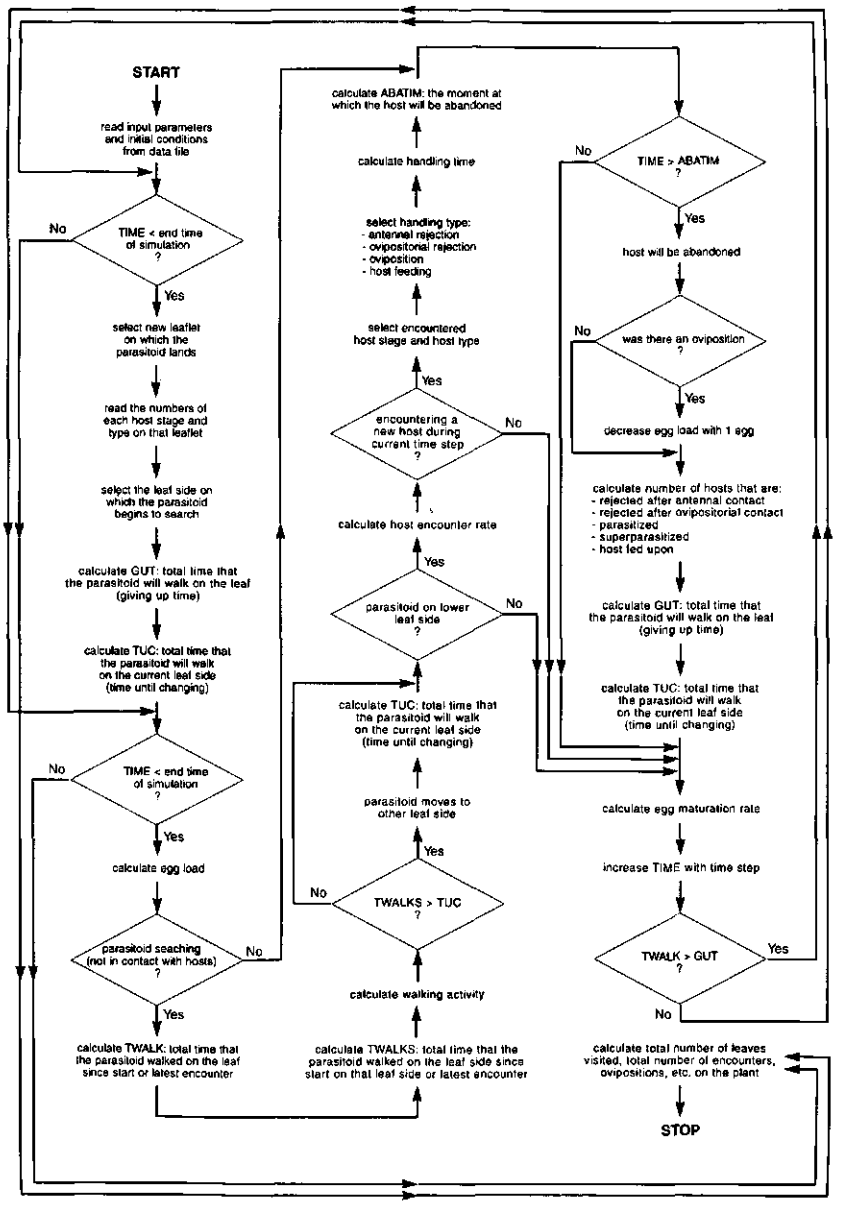


Figure 1. Flow diagram of the foraging behaviour of one *E. formosa* female on a plant.

where *E. formosa* is able to fly from leaflet to leaflet and where host densities are much lower.

The model presented here simulates the foraging behaviour of *E. formosa* on a tomato plant during a day. In order to understand quantitative effects of the parasitoids' foraging behaviour on whitefly populations in a crop, foraging behaviour is first studied at a smaller spatial scale. The parasitoid is able to fly from leaflet to leaflet and to move from one leaf side to the other. From the simulation results at different host densities, the number of encounters, ovipositions and host feedings in relationship to host density were generated. The shape of the curves helps to understand the host-parasitoid interaction at the population level (see introduction of Chapter 5). The importance of each input parameter of the model will be evaluated in a sensitivity analysis. The model will later be extended and used at a larger spatial and temporal scale, such as for a tomato crop during a growing season. The foraging behaviour will then be simulated during a parasitoids lifetime (Chapter 10).

THE SIMULATION MODEL

A stochastic Monte Carlo simulation model was developed for the foraging behaviour of the parasitoid on a tomato plant infested with hosts. The parasitoid is able to fly from leaflet to leaflet and to move from one leaf side to the other. The model for one parasitoid is presented in the flow diagram of Figure 1. A detailed description of the processes as simulated by the model and the input parameters can be found in Chapter 5. The model is initialized with the number of leaflets per plant, the number of infested leaflets and the number of each immature host stage per infested leaflet. The time step of simulation was taken 1.2 s, about one tenth of the smallest time coefficient in the model (handling time for rejection of a parasitized host), which is needed for accurate numerical integration. Accuracy was tested by comparing the simulation results with those obtained at a time step double or half in size. As *E. formosa* does not forage in the dark (Hoogcarspel & Jobsen, 1984), the time of simulation was set to a daylength of 16 h. Temperature was always 25°C. Number of replicates was 1000 at an uniform host distribution over leaflets and 5000 at a clustered distribution, except in the case of the sensitivity analysis at 24 clustered hosts per plant, where 10000 replicates were needed for a low standard error of the mean (SE<5%). Honeydew on the leaves was assumed to be absent. During the simulation, the initial condition of each replicate was taken the same. Therefore, morphological or physiological differences between parasitoids (i.e. in body size, number of ovarioles or relative egg maturation rate) were not taken into account.

In the model the tomato plant consisted of 120 leaflets, which is similar to a fully grown tomato plant with 17 leaves and 7 leaflets each. Foraging behaviour was simulated for two extreme host distributions: when all hosts were present on only one leaflet and the other 119 leaflets were clean (extremely clustered distribution) and when all hosts were divided equally over as many leaflets as possible (uniform distribution).

In the last situation host stages were separated in different leaf layers and if host density was lower than 120 per plant, not all leaflets were infested (with one host).

E. formosa does not distinguish between clean and infested leaves before landing. Noldus & van Lenteren (1990) and Sütterlin & van Lenteren (in prep.) did not observe differences in response to or number of landings on clean or infested leaves or plants for tomato, cucumber and gerbera. The same was found for leaves whether or not visited by parasitoids earlier. Therefore, in the model the tomato leaflets of the plant were visited randomly: the parasitoids made no distinction before landing between infested or clean leaflets, leaflets in different leaf layers, or leaflets that were visited earlier. Landing on the upper or lower leaf side occured at the same frequency.

RESULTS

Validation

Validation of the simulation results was very good for parasitoids foraging during a fixed time in an experimental arena (Chapter 5). Furthermore, the simulated residence times and number of encounters were similar to observations for parasitoids foraging on clean tomato leaflets and on leaflets with 77-200 black pupae (Chapter 6). Observations where the parasitoids are confined to a single plant are not available for validation or verification of the present model. Yano (1987) did release experiments on tomato in a small glasshouse. He found a maximum number of 10 ovipositions and about 2 host feedings per parasitoid per day when host densities were 400-600 per plant. These densities were similar to about 10 hosts per leaflet, because the tomato plants were only 0.5 m in height (about 50 fully grown leaflets) and such high host numbers must have been distributed quite uniformly over the plants, as the infestation was achieved by release of many whiteflies on small plants during a short time. At the same host density and a uniform host distribution, the model simulated 36.1 encounters, 9.7 ovipositions and 2.2 host feedings per parasitoid after a daylength of 16 h at 25°C.

Simulation results

A parasitoid searching on a tomato plant with 120 leaflets during 16 h was simulated. The host stages L1, L2, L3, L4, prepupa (PP) and pupa (PU) were always equally available, either on one leaflet (extremely clustered distribution) or on as many leaflets as possible (uniform distribution). Temperature was always 25°C and the tomato leaflet size was 22 cm^2 (one-side).

The percentage of parasitoids with no encounter (non-finders) during the day is given in Figure 2. This percentage rapidly declined with host density at the uniform host distribution. All parasitoids discovered hosts when the plant was infested with at least 1 host per leaflet. However, when the host distribution was extremely clustered, 80% of the parasitoids did not discover the infested leaflet during the day.

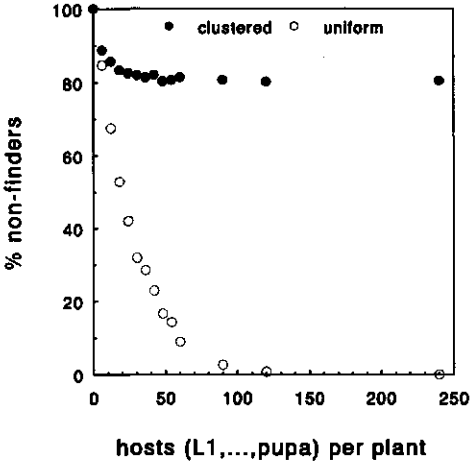


Figure 2. Simulated percentage of *E. formosa* parasitoids with no host encounter (non-finders) on a tomato plant during a day of 16 h. The host distribution over leaflets was clustered or uniform.

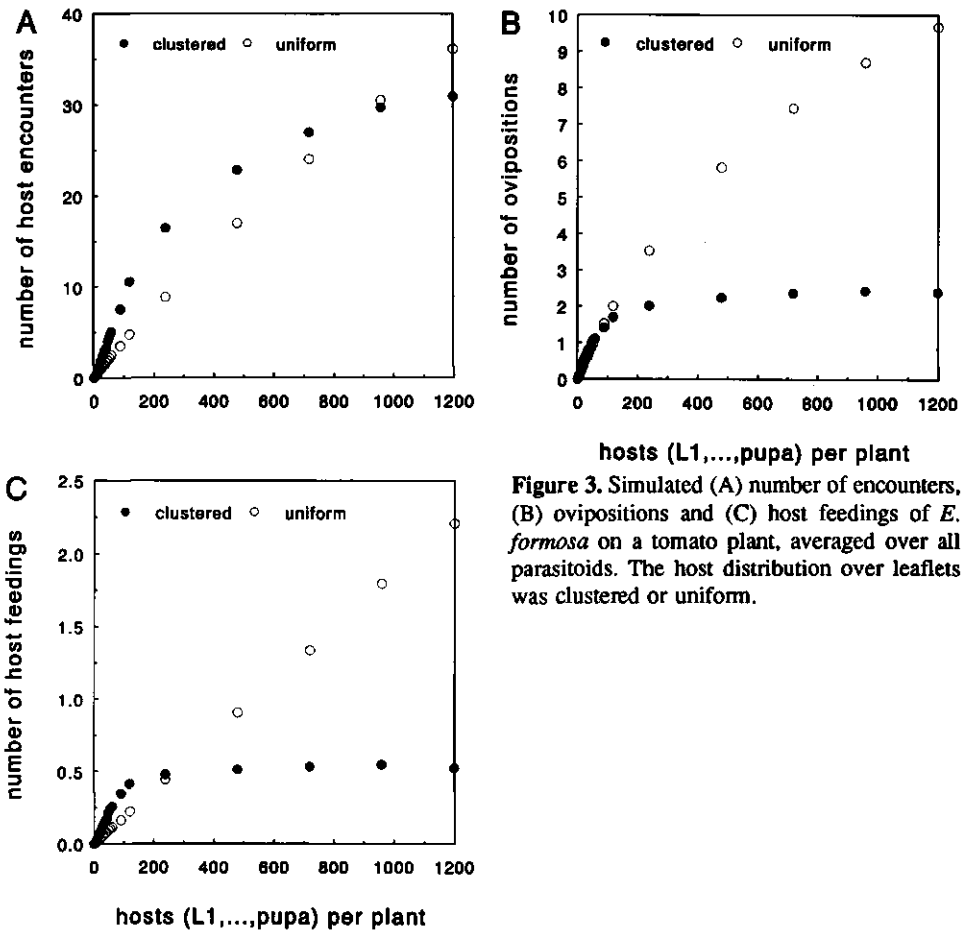


Figure 3. Simulated (A) number of encounters, (B) ovipositions and (C) host feedings of *E. formosa* on a tomato plant, averaged over all parasitoids. The host distribution over leaflets was clustered or uniform.

The mean number of encounters, ovipositions and host feedings increased with host density to a maximum of 272 encounters, 17.4 ovipositions and 3.0 host feedings in case of a uniform host distribution (Figure 3A-C). At the clustered distribution, the maximum levels were much lower (33 encounters, 2.5 ovipositions and 0.56 host feedings), because only 20% of the parasitoids discovered the infested leaflet (finders). The ratio between finders and non-finders caused large standard deviations which are not given in the figures. These successful parasitoids had maximum numbers of 163 encounters, 12.3 ovipositions and 2.7 host feedings (Figure 4). Variation between parasitoids resulted from the random visit of leaflets, the random landing on the upper or lower leaf side, the random encounter of hosts, the variable walking activity, the variable handling behaviour of an encountered host, the variable handling times and

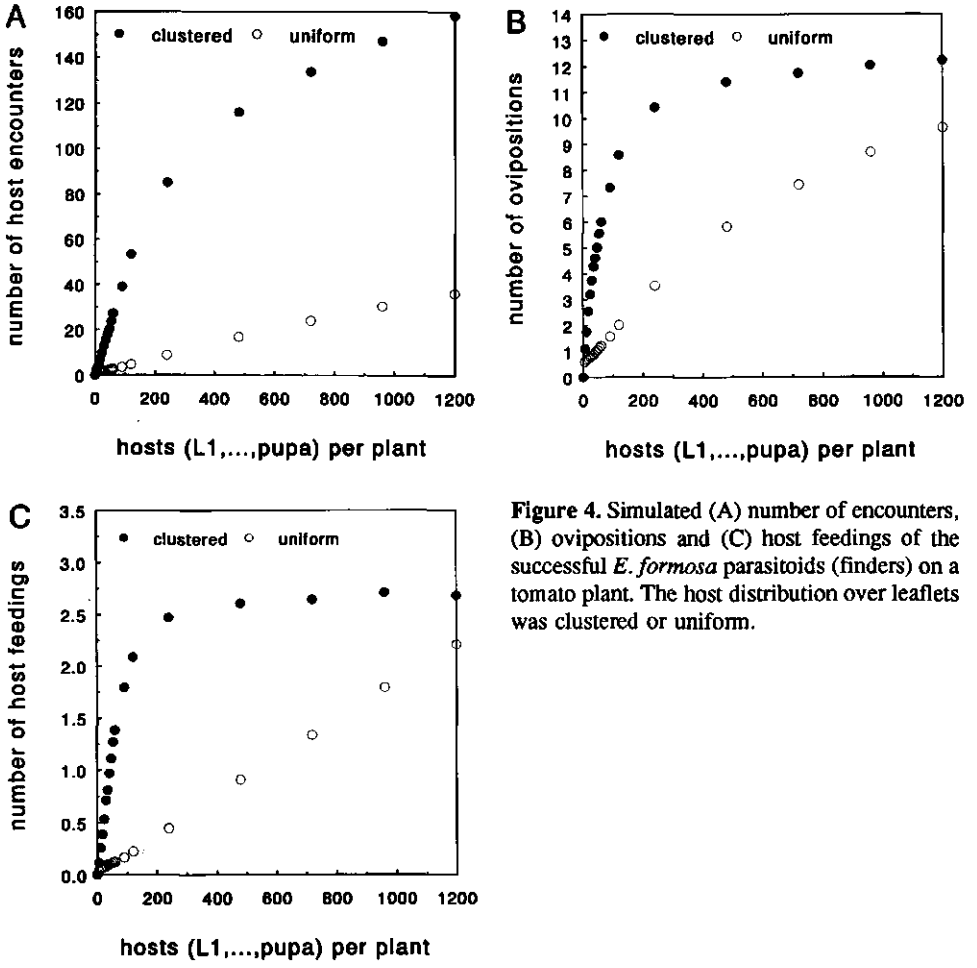


Figure 4. Simulated (A) number of encounters, (B) ovipositions and (C) host feedings of the successful *E. formosa* parasitoids (finders) on a tomato plant. The host distribution over leaflets was clustered or uniform.

from variation in the giving up time (GUT) and the time that the parasitoid searches on a particular leaf side (TUC). The coefficient of variation (SD/mean) for the number of encounters and ovipositions was 17.3 and 15.2% respectively, when all leaflets were infested with 15 hosts. This was six times lower than the variation on individual leaflets with the same host density (Chapter 6).

The shape of the curves of Figures 3 and 4 resembles a Type II response. At low host densities, a linear increase was simulated. Despite more than 80% non-finders, the overall mean number of encounters, ovipositions and host feedings were always higher when hosts were clustered than when uniformly distributed. At a density of only 1 L3 larva per plant, 3.4% of all parasitoids discovered the larva during the day, 2.4% had a successful parasitization and 0.10% used the larva for host feeding. Thus, the probability for the larva of being killed by one *E. formosa* per plant was 2.5% per day. When the host stages are equally available at 24 clustered hosts per plant, the probabilities of being killed were 0.9% for L1, 1.9% for L2, 3.0% for L3, 3.6% for L4, 3.4% for the prepupa and 2.4% for the pupa per day. These probabilities hardly changed with increasing host density until about 90 hosts per plant, due to the initial linear increase of the number of ovipositions and host feedings with host density. At a uniform host distribution, these probabilities of being killed were slightly lower (0.7-2.9%). The oviposition-host feeding ratio was initially 10:1 and dropped to 4.5:1 at higher densities.

Figure 5 shows the simulated number of visits the parasitoid made to leaflets. From 33 visits on average on clean plants, it decreased with host density due to the arrestment effect of the parasitoid on infested leaflets. When hosts were clustered on the plant, still 30 leaflets were visited at high host densities. This average is high compared to a uniform distribution, due to the 80% non-finders which visited 33 leaflets. The 20% finders visited on average 16 leaflets.

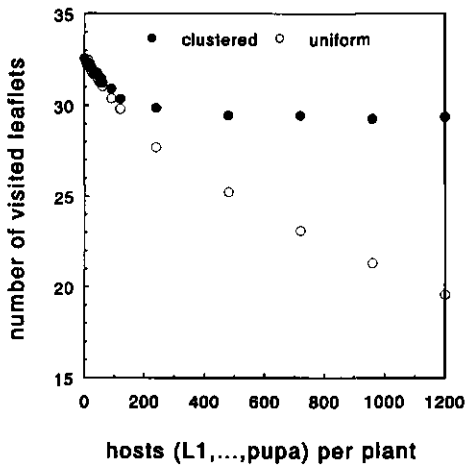


Figure 5. Simulated number of visited leaflets of *E. formosa* on a tomato plant, averaged over all parasitoids. The host distribution over leaflets was clustered or uniform.

The distribution of encounters over different host stages is given in Figure 6A for 1200 hosts per plant. They were calculated as percentages of the total number of encounters for all stages together. The same was done for the number of ovipositions and host feedings (Figures 6B-C). Host density did not affect the distribution of encounters. As the initial number of each host stage was equal, the distribution of encounters was only determined by host size (see equation of Skellam, 1958). At the uniform host distribution, the distribution of encounters shifted slightly to the most preferred stages L3, L4 and prepupa (Figure 6A). This was caused by the separation of the host stages on different leaf layers and not by the uniform host distribution itself. On leaflets with the preferred host stage ovipositions occurred earlier, thus

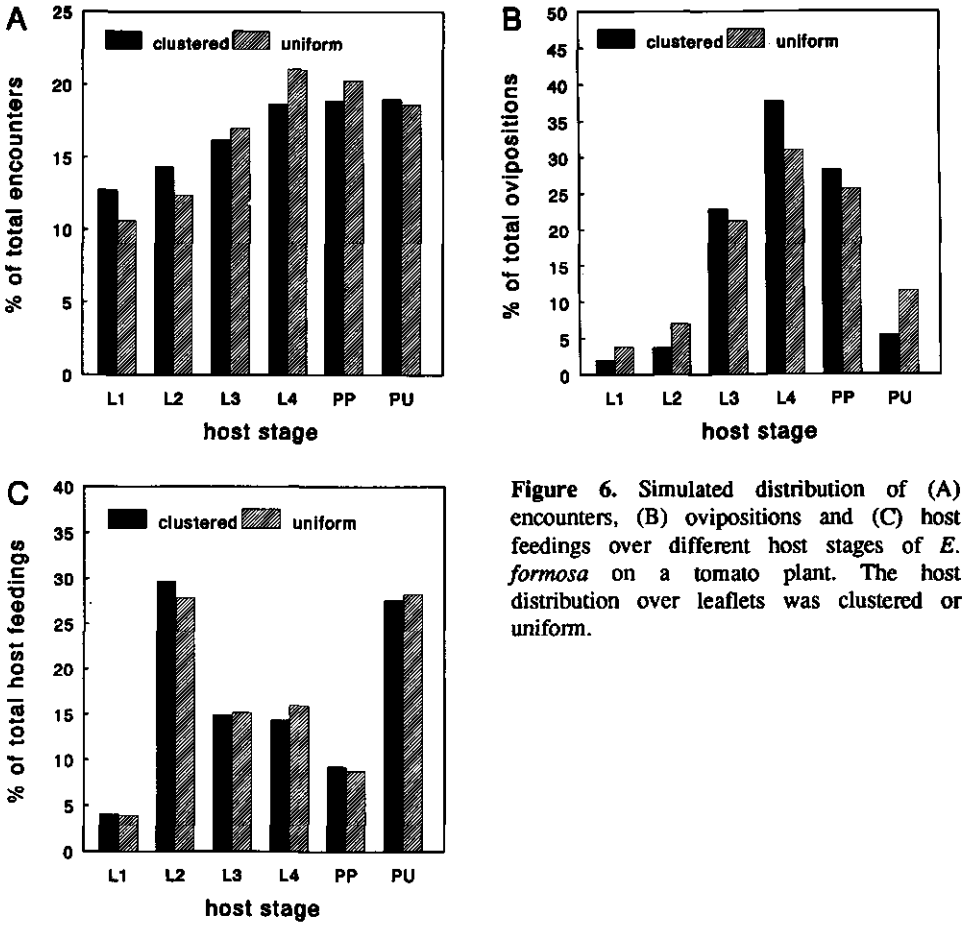


Figure 6. Simulated distribution of (A) encounters, (B) ovipositions and (C) host feedings over different host stages of *E. formosa* on a tomato plant. The host distribution over leaflets was clustered or uniform.

increasing the average residence time on such leaflets, so more hosts of that stage were encountered.

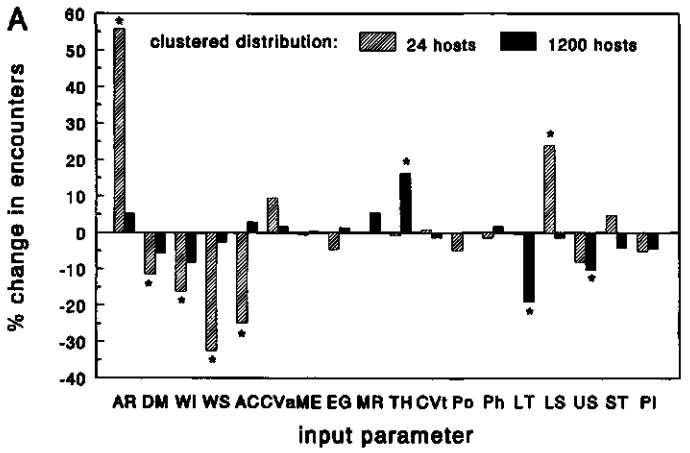
The distribution of ovipositions and host feedings over different host stages was determined by a combination of hosts being encountered (size) and the probability of an oviposition (success ratio) or a host feeding after encountering a host, of which the latter played the most important role. When hosts were clustered, the distribution of ovipositions shifted to the most preferred host stages. This effect was also found at higher host densities. The successful parasitoids laid more eggs and thus had a lower egg load on average than when hosts were uniformly distributed or at lower densities (see also Figure 4B). The shift is the result of a decreasing success ratio when egg load decreases (Chapter 5). In the model, this decrease was taken linear with equal slope for all stages, so the success ratio of the most preferred stages become relatively higher at a lower egg load.

Sensitivity analysis

The *change* in the number of encounters and ovipositions were simulated, based on a decrease of 25% in the value for one particular parameter, compared to a 'standard run'. This was done for 18 parameters at 24 and 1200 hosts per plant, when hosts were clustered or uniformly distributed. These densities correspond to a low and high number of ovipositions respectively (see also Figure 3B). SE/mean of the standard run varied between 0.57-3.63% for the number of encounters and between 0.58-4.43% for the number of ovipositions. Results are shown in Figure 7, in which parameters resulting in long bars are the most essential in determining the output under study.

As in greenhouses whiteflies show a strongly clustered distribution over plants and leaflets (Eggenkamp-Rotteveel Mansveld et al., 1982a,b), attention is focused on this situation. At a high host density the number of encounters was most sensitive to the parasitoids' leaving tendency (LT) and the handling time (TH) (Figure 7A). At a low density, the parameters used in the equation of Skellam (1958) were most important: the leaf area (AR), the walking speed (WS), the walking activity (AC), the width of the parasitoids' searching path (WI) and the size of the hosts (DM), plus the parasitoids' tendency of changing from the lower to the upper leaf side (LS). A change of both tendencies of changing leaf sides (ST), changing the *frequency* with which the parasitoids shifted from one leaf side to the other did not have an effect. The probability of landing on the lower leaf side where hosts can be found compared to the upper side (Pl) was not important for the number of encounters. This was caused by the frequent shifts *E. formosa* made on tomato leaflets.

The number of ovipositions at a high density was strongly affected by the maximum egg load (ME) and the leaving tendency (LT) (Figure 7B). These parameters were not important anymore at a low density. The number of ovipositions was then most sensitive to the same parameters as the number of encounters, plus the initial egg load (EG) and the success ratio (Po). Only the last two changed the number of ovipositions without affecting the number of encounters. The effect of a decreasing egg load is caused by a strong decrease in the success ratio (Chapter 5).


A
clustered distribution:
24 hosts
1200 hosts
% change in encounters
60
50
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AR DM WI WS ACCVaME EG MR TH CVt Po Ph LT LS US ST PI
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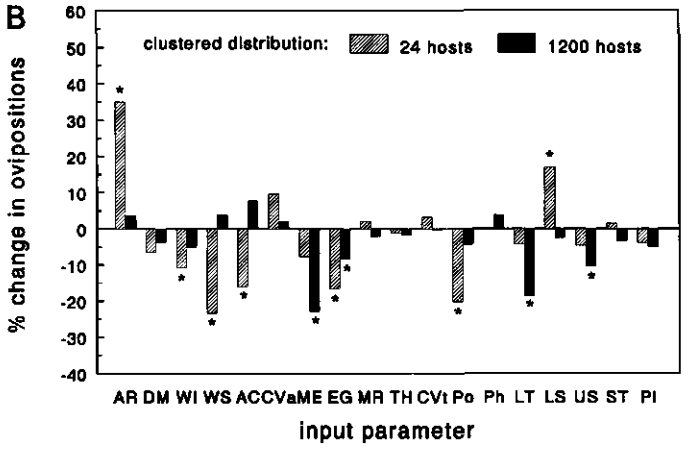
B
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24 hosts
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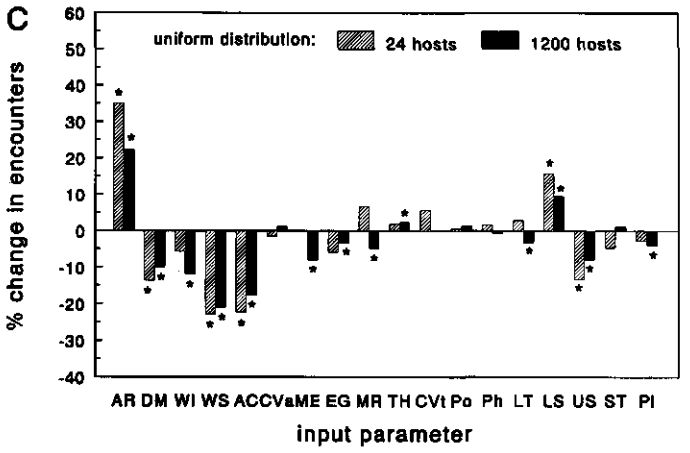
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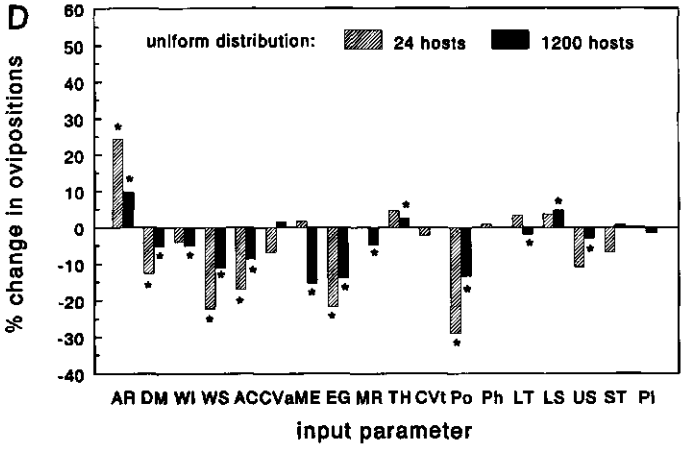

Figure 7. Change (%) in number of encounters and ovipositions of *E. formosa* on a tomato plant during a day of 16 h, when the value of one particular input parameter was decreased with 25%. The host distribution over leaflets was clustered (A, B) or uniform (C, D), and host numbers were 24 or 1200 per plant. Input parameters are leaf area (AR), diameter of host stages (DM), width of the parasitoids' searching path (WI), walking speed (WS), walking activity (AC), coefficient of variation of walking activity (CVa), maximum egg load (ME), initial egg load (EG), egg maturation rate (MR), host handling time (TH), coefficient of variation of handling time (CVt), probability of oviposition after encountering a host (success ratio, Po), probability of host feeding after encountering a host (Po), leaving tendency (LT), tendency of changing from the lower leaf side to the upper (LS), tendency of changing from the upper leaf side to the lower (US), both tendencies of changing from one leaf side to the other (ST), and the probability of landing on the lower leaf side compared to the upper side. Bars marked with * are significantly different from 0 (Student t-test on population mean; α=0.05).

Figures 7C-D show the results at a uniform host distribution. Bars were shorter than when hosts were clustered, but they were more often significantly different from zero, because variation in number of encounters and ovipositions between parasitoids was smaller when hosts were uniformly distributed. When host density was low, the same parameters were important at the two host distributions. At a high density, results were similar to those obtained at a low number of clustered hosts.

The influence of temperature is shown in Figure 8. At 18°C parasitoids were assumed not to fly and the walking activity was very low, as was observed in experiments (Chapter 4). At 20°C the number of encounters and ovipositions were always significantly lower than at 25°C. The relative differences were highest at 24 hosts per plant: a reduction of 40 and 34% respectively was simulated compared to 25°C at both host distributions. These reductions were caused by a reduction in walking speed of 39.2% and by a reduction in the relative egg maturation rate of 25.1% at 20 °C compared to 25°C (Chapter 5), of which the walking speed played the crucial role according to Figures 7A-B. Differences at 30°C compared to 25°C were never significant at 24 hosts per plant. At 1200 hosts per plant, a significant increase of 5-8%

in number of ovipositions was simulated. This was due to an increase in the relative egg maturation rate of 25.1% at 30°C compared to 25°C.

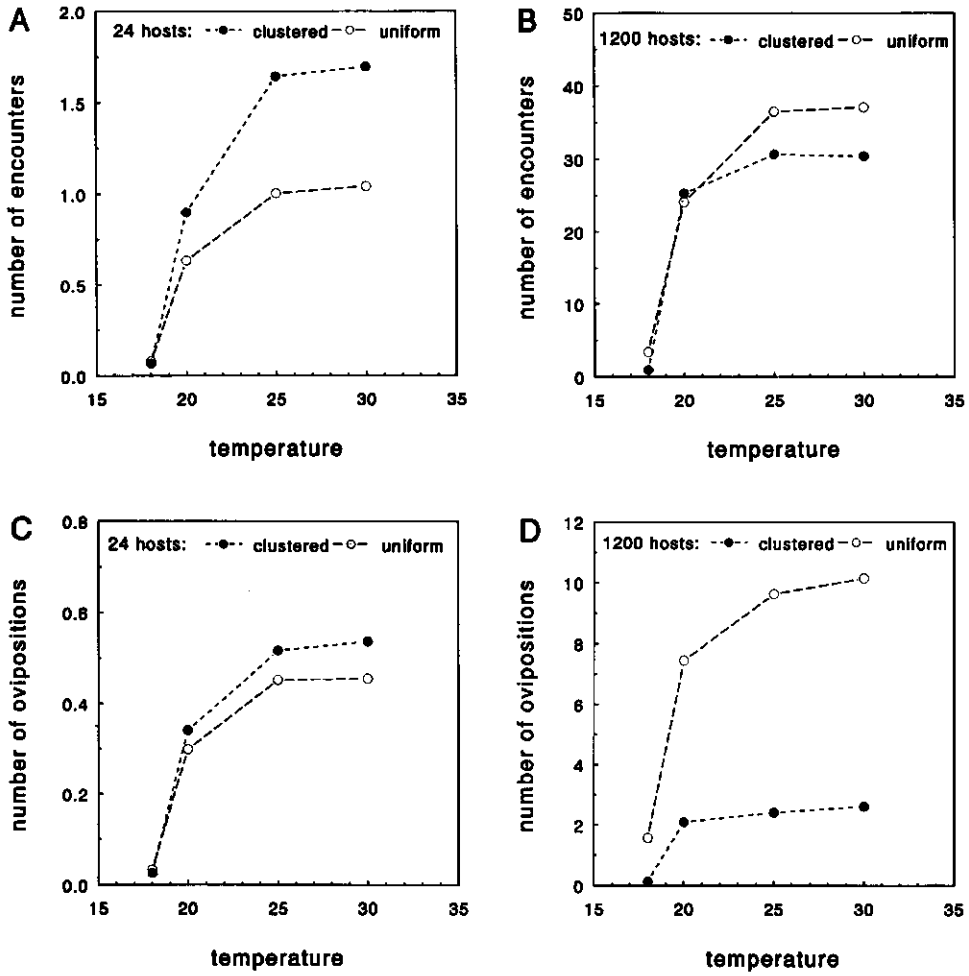

Figure 8. Simulated number of encounters and ovipositions of *E. formosa* on a tomato plant at different temperatures. The host distribution over leaflets was clustered or uniform, and host numbers were 24 (A, C) or 1200 (B, D) per plant.

DISCUSSION

Validation of the simulation results was very good for parasitoids foraging during a fixed time in an experimental arena (Chapter 5). Verification of the simulated residence time and number of encounters was also good for parasitoids foraging on clean tomato leaflets or on leaflets with high numbers of black pupae (Chapter 6). On tomato plants with 400-600 hosts, the simulated number of ovipositions and host feedings agreed well with observations of Yano (1987). Experiments at a low host density were not available.

According to the model, at most 20% of the parasitoids discovered hosts (finders) on a tomato plant with 120 leaflets during 16 h, if the host distribution over leaflets was extremely clustered. The other 80% searched on clean leaflets and were time-limited during the day. The finders laid on average 12 eggs at high host densities and soon became egg-limited. They visited on average 15 clean leaflets before discovering the infested leaflet, which reduced the time available for parasitization during the day. On a single leaflet a maximum number of 16 ovipositions was found, when the parasitoids were immediately placed on the infested leaflet (Chapter 6). The percentage finders will increase during the following days, due to the arrestment effect of parasitoids on leaflets with high host numbers.

The probability for the whitefly immatures (L1, L2,..., pupa) of being killed by *E. formosa* is 0.9-3.6% per day during the first day after release of one parasitoid per tomato plant at 25°C. This probability hardly changed with increasing host density until about 90 hosts per plant. The natural mortality is 0.9% per day averaged over all stages on the same host plant (Chapter 8). Thus, the mortality for each whitefly immature is increased 2-5 times when one parasitoid searches randomly on a plant. This is even a conservative estimate. It will increase during the days following the release, because of the arrestment effect of the parasitoid on infested leaflets. Inflow of other parasitoids from clean plants will increase the percentage finders. Furthermore, as the majority of killed hosts yields new parasitoids, the numerical response plays a role after a time period equal to the development duration.

In this study, *mechanistic* explanations were examined for the parasitoids' host encounters and ovipositions on the plant. They explain *how*, in terms of searching efficiency, the allocation of searching time, host handling and available eggs, the observed level of parasitism is realized. Mechanistic explanations can help to understand failure or success of biological control in practice. They do not explain *why* the parasitoids choose to behave in this way, in terms of selection pressure acting on them. They thus do not provide a *functional* explanation of the observed behaviour. Whether selection on parasitoid searching behaviour leads to direct, inverse, or no density dependence in parasitism across patches, is studied by Lessels (1985) for a population of parasitoids.

Most essential parameters for the number of encounters on a plant were these used in the equation of Skellam (1958), especially the leaf area, the parasitoids' walking speed and the walking activity. They determine the host density, the net

displacement of the parasitoid and the width of the encounter path. This was also found for individual leaflets (Chapter 6). The ratio of the parasitoids' time until changing from one leaf side to the other (TUC) on the lower leaf side compared to the upper side also played an important role. The number of encounters increased if TUC was highest on the lower leaf side where hosts can be found. However, for *E. formosa* TUC's were the same on both leaf sides (Chapters 2 and 3). At low host densities, the average giving up time (GUT) of the parasitoid was not important for the number of encounters on a plant, whereas it was very important on individual leaflets (Chapter 6). Only at high host densities and a clustered host distribution over leaflets, a lower GUT increased the number of encounters on the plant through a higher percentage of parasitoids discovering hosts (finders). The parasitoids then found the heavily infested leaflets sooner, without wasting much time on clean leaflets.

The number of ovipositions at low densities was determined by the same parameters as the number of encounters, plus the initial egg load and the success ratio. The egg maturation rate was not important during the day. However, the effect may be obscured, because egg maturation during the night affects the initial egg load of the parasitoids the next morning, which is important according to the model. The egg storage capacity of the parasitoid was not important at low host densities. The number of encounters and ovipositions on the plant were determined by almost the same parameters as on the leaf during shorter exposure times (Chapter 6).

When comparing the parasitization efficiency of *E. formosa* on different host plants, at different temperatures, or with other parasitoid strains or species with a comparable behaviour (synovigenic, solitary parasitoids with random search), attention should be focused on the parameters determining the ovipositions at low host density: the walking speed, the walking activity, the succes ratio, the initial egg load and the ratio of search times on both leaf sides. However, whether these parameters are also crucial for biological control in a tomato crop during a growing season remains to be investigated. As mass rearing of natural enemies is done at high host densities, the selection pressure may shift to egg storage capacity and egg maturation and care should be taken. Quality control of natural enemies is important in this respect.

The walking speed can be manipulated by temperature and leaf structure. Between 15 and 25°C, walking speed increased 2.8 times on tomato leaflets (Chapter 4). On smooth leaves like sweet pepper, walking speed was 2.7 times higher than on tomato leaves at 24°C (Hulspas-Jordaan & van Lenteren, 1978). The walking activity varied less and was 60-75% on gerbera, cucumber and tomato and constant above 18°C (Chapter 4). The success ratio can depend on the host insect on which the parasitoid was reared, as was shown for *E. formosa* with *Bemisia tabaci* as host (Henter et al., 1993). The initial egg load can in principle be manipulated by the night temperature, when parasitoids are not searching and new eggs mature. However, after a night of 8 h following a day on which all eggs have been laid, a temperature change from 15 to 20°C increased the initial egg load from 2.4 to only 3.4 according to the model.

The shape of the functional response on the plant resembles a Type II curve. At low host densities, the increase was initially linear. This response agrees with that

found by Yano (1987) for *E. formosa* on tomato plants in a glasshouse experiment during a day. According to van Lenteren & Bakker (1978), S-shaped Type III responses may be obscured by the 'experimental' procedure that was followed. They mention two possibilities: (1) if the parasitoid cannot leave the experimental arena, this increases the probability to detect hosts at a low density and (2) if the arena or leaf is small, this causes even the lowest host densities to be too high to detect the increasing attack rate. Chapter 6 showed that the first possibility can be excluded for *E. formosa*, because an S-shaped oviposition curve was not found on tomato leaflets either, when parasitoids were able to leave. However, the lowest density of one host per leaflet was still high compared to the situation in the field. The present study shows that also the second possibility can be excluded for *E. formosa*: even at low densities starting from one host per plant, an accelerating increase was not found. The number of encounters, ovipositions and host feedings of *E. formosa* increased with host density according to a Type II response at all spatial scales tested. The decreasing walking activity and success ratio with decreasing egg load is predominant at all levels, and even a change in GUT from 18.6 to 40.0 min after the first oviposition on the leaf does not show an effect.

A Type II response was also found for *Trichogramma pretiosum* on cotton plants or in a patchy environment, caused by egg limitation of the parasitoid (Allen & Gonzalez, 1975; Hassell, 1982). Mitchell Rohlfs & Mack (1984) found the same response for the parasitoid *Ophion flavidus* in plant cages. Weis (1983) found a Type II response per patch for the parasitoid *Torymus capite* in a patchy environment. The parasitoid *Catolaccus grandis* showed a Type I response in plant cages (Morales-Ramos & Cate, 1992). The same was found for the parasitoid *Cotesia flavipes* in field cages at low host densities, but a Type II response was found in experiments at higher densities (Wiedenmann & Smith, 1993). Care should be taken by comparing density dependence of different studies, as in many experiments not one but a population of parasitoids were released. The observed result might be caused by a combination of the functional response of one parasitoid and a possible aggregated response of parasitoids in high density patches, such as the examples of field studies of Hassell & Pacala (1990).

The shape of the curve helps to understand the dynamics of the host-parasitoid interaction at the population level. In case of a Type II response, percentage parasitism is inversely density-dependent. A high host density thus 'dilutes' the per capita parasitization pressure caused by one parasitoid. According to theory, this will have a destabilizing effect on the dynamics of host and parasitoid (see e.g. Murdoch & Oaten, 1975; Oaten & Murdoch, 1975). However, functional responses are only one factor in determining the dynamics at the population level. For *E. formosa*, the effect on the population level might depend on the balance between the 'dilution' effect of the per capita parasitization pressure and, for instance, arrestment and subsequent aggregation of parasitoids on leaves.

Many parasitoid species stay longer in high-density patches and field studies suggest that many parasitoids do tend to aggregate (reviews in Walde & Murdoch,

1988; Godfray, 1994). Summy et al. (1985) found that the parasitoid *Encarsia opulenta* aggregates in high-density patches of citrus blackfly and percentage parasitism in the field is density dependent. Parasitism of *Aphytis melinus* is independent of or inversily dependent on host density, whereas California red scale populations are well-regulated (Reeve & Murdoch, 1985). Other mechanisms play a role, and a spatial refuge for hosts has been found in the field. However, Murdoch (1994) tested and failed to find evidence for eight hypotheses that might account for the system's stability, including a refuge. Sabelis (1981, 1986) found a Type II functional response for the predatory mite, *Phytoseiulus persimilis* in prey patches, and the metapopulation dynamics were stabilized by factors contributing to the start of new prey patches and the asynchronization of local predator-prey cycles (Sabelis & Laane, 1986; Sabelis et al., 1991).

In a next study, the simulation model of the foraging behaviour of the parasitoid will be coupled with a model of the population dynamics of the greenhouse whitefly and *E. formosa* during a growing season on a crop (Chapter 10). The foraging behaviour will then be simulated during a parasitoids lifetime. This model can help to explain failure or success of biological control in the field.

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Chapter 8

Life-history parameters of greenhouse whitefly, *Trialeurodes vaporariorum* as a function of host plant and temperature

ABSTRACT

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

INTRODUCTION

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), is a well known, highly polyphagous pest insect. Recently, van Lenteren & Noldus (1990) reviewed whitefly-plant relationships. Adults and immatures feed on phloem sap and produce large amounts of honeydew, on which occasionally black moulds develop. As a result, crop yield is reduced (Lindquist et al., 1972). More important is the economic damage on fruits and ornamentals due to the residue of sticky honeydew. Hussey et al. (1958) measured significant yield reduction on tomato at an average pest density (between start of pest and final picking of fruits) of 22 scales/cm^2 leaf or more, and an economic yield reduction at 6 scales/cm^2 or more. According to Helgesen & Tauber (1974), a much lower density of 0.3-0.7 scales/cm^2 leaf is commercially acceptable on poinsettia.

Despite available insecticides, whiteflies are still a major economic problem in greenhouse crop production. Other control methods have been studied, such as resistance breeding (de Ponti et al., 1990) and biological control (Noldus & van Lenteren, 1990). Introduction of the parasitoid *Encarsia formosa* has proven to be commercially successful. In the Netherlands, about 90 percent of the tomato acreage is under biological control and the parasitoid has been introduced in many other countries (van Lenteren & Woets, 1988). As yet there is no satisfactory explanation as to why the parasitoid cannot be applied successfully on some other crops.

A simulation model based on developmental and behavioural aspects of individuals in relationship to host plant and environment is being developed to find out more about the tritrophic system host plant- greenhouse whitefly- *Encarsia formosa* in order to understand failure or success of biological control.

The simulation model consists of several submodels each simulating a certain subprocess, for example the population dynamics of the greenhouse whitefly, which depends on the host plant species and the environment. Inputs in this submodel are life-history parameters, such as immature development, immature mortality, adult longevity, sex ratio and fecundity or oviposition frequency. These life-history parameters have been reviewed to some extent by Vet et al. (1980), van Lenteren & Hulspas-Jordaan (1983) and Hulspas-Jordaan & van Lenteren (1989). In this article a more comprehensive review has been given and the relationship between life-history parameters and temperature has been estimated for each host plant by non-linear regression.

MATERIAL & METHODS

Between 1915 and 1990, about 100 studies were done on life-history parameters of the greenhouse whitefly. Data were selected on development rate of each immature stage, percentage mortality of each immature stage, sex ratio, longevity, pre-oviposition period, fecundity, oviposition frequency and period of increase of daily oviposition on several host plants, such as bean (*Phaseolus vulgaris* L.), cucumber (*Cucumis sativus* L.), eggplant (*Solanum melongena* L.), gerbera (*Gerbera jamesonii* Hook.), tobacco (*Nicotiana tabacum* L.), tomato (*Lycopersicon esculentum* Miller) and sweet pepper (*Capsicum annuum* L.). Data sets are incomplete for garden chrysanthemums (*Dendranthema* cvs), gherkin (*Cucumis sativus* L.), hibiscus (*Hibiscus rosa-sinensis* L.), melon (*Cucumis melo* L.), potato (*Solanum tuberosum* L.), one of the wild potatoes (*Solanum berthaultii* Hawkes) and tree tobacco (*Nicotiana glauca* Grah.). Sometimes a distinction was made between East European (Hungarian, Bulgarian, Russian) and West European whitefly. As van Lenteren et al. (1989) clearly showed, there is a difference in whitefly strains. Most experiments have focused on the effect of temperature on these parameters with little attention to other environmental factors such as humidity and light. All collected data are given in the appendices of van Roermund & van Lenteren (1992), in which the number of decimals have been copied from the original studies. Small experiments (with a low number of whiteflies) of one study were sometimes combined and the (weighted) average is given in these appendices.

Host plant and temperature are the most important factors influencing life-history parameters for many insect species. The relationship between life-history parameters and temperature was determined for each host plant by non-linear regression based on a least squares method of Marquard (Statgraphics User's Manual, version 4.0, 1989). For each life-history parameter, several mathematical 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):
$$Y = a * \{ \exp(b*(X-d)) - \exp(b*(e-d)-(e-X)/c) \}$$

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

The first three models are well known, the last two need some explanation. According to the Logan model (Figure 1), Y increases exponentially from the value *a* at the lower threshold temperature *d* to an optimum temperature with a relative increase of *b*, whereafter Y declines sharply until the upper lethal temperature *e* has been reached. If the lower threshold and upper lethal temperature are known, only three coefficients have to be estimated. The Weibull model of Figure 10 describes an exponential increase from the lower lethal temperature *a* to an optimum temperature, whereafter Y decreases exponentially. The scale parameter *b* is inversely related to the rate of increase, the shape parameter *c* controls the skewness of the curve and the coefficient *d* is the area under the curve. Other shapes are also possible, depending on the values of the coefficients. When the lower lethal temperature is known, three coefficients have to be estimated.

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

RESULTS

LIFE-HISTORY PARAMETERS

Whiteflies feed on phloem sap and produce large amounts of honeydew. The adults can migrate to other leaves or plants. The females lay their white eggs on the underside of the plant leaves. After a few days the eggs turn purple or black. The first instar larva (L1) is initially mobile and after a few hours it settles down and inserts its mouth parts into the leaf. Subsequently, the larva moults into the second (L2) and third (L3) instar,

which differ in size (for sizes, see Hulspas-Jordaan and van Lenteren, 1989). The next moult results in the last instar, which is initially flat and translucent, like the previous instars. As the last instar larva develops, it thickens and becomes white-coloured with waxy spines. During the last phase of its development the red pigmented eyes of the adult can be seen. Many studies do not distinguish the three phases of the last instar or they use different terms to describe these phases (Table 1). Because the parasitoid *Encarsia formosa* makes a significant difference in accepting the phases of the last instar (Nell et al., 1976), these phases have been distinguished as follows: fourth instar larva (L4), prepupa (PP) and pupa (PU). Development rate and mortality have been calculated for each of the three last phases separately (L4, PP, PU) and for the total last instar (L4+PP+PU).

Table 1. Terms used to describe the last immature instar of the greenhouse whitefly.

Author	First phase	Second phase	Third phase
This article	L4	prepupa	pupa
Hargreaves, 1915	L4	L4	L4
Weber, 1931	L4	L4	L4
Burnett, 1949	L4	pupa	pupa
Hussey & Gurney, 1957	pupa	pupa	pupa
Eijsackers, 1969	L4	L4	pupa
Kraayenbrink, 1972	L4	L4	L4
Veerkamp, 1975	L4	L4	pupa
van Bruggen, 1975	L4	L4	pupa
van Lenteren et al., 1976	L4	prepupa	pupa
Di Pietro, 1977	L4	pupa	pupa
Nechols & Tauber, 1977a and b	early 4th	Transitional	Pharate adult
Hulspas, 1978	L4	L4	pupa
van de Merendonk, 1978	L4	pupa	pupa
Zebitz, 1978	L4	L4	L4
Madueke, 1979	L4	L4	pupa
Li et al, 1980	pseudopupa	pseudopupa	pseudopupa
Christochowitz & van der Fluit, 1981	L4	prepupa	pupa
Agekyan, 1981	pupa	pupa	pupa
Arakawa, 1982	L4	prepupa	pupa
Kajita, 1982	L4	pupa	pupa
van Evert & Schutte, 1983	L4	prepupa	pupa
Burggraaf & van der Laan, 1983	L4	prepupa	pupa
Fransen & van Montfort, 1987	L4	prepupa	pupa
Yano, 1988	early L4	late L4	late L4
Kajita, 1989	L4	pupa	pupa
Dorsman & van der Vrie (unpubl.)	pupa	pupa	pupa

Immature development rate

The development rate of each immature stage was calculated as the reciprocal of its duration. Weber (1931) found a lower threshold temperature for development of eggs and the first three larval instars of 8°C on tobacco and for L4 larvae a few degrees lower. Van Evert & Schutte (1983) did experiments on tomato at 7°C and found hardly any development of all immature stages. Therefore a lower threshold temperature of 8°C was taken in the regression procedure. Osborne (1982) estimated a lower threshold temperature of 8.3°C by linear regression using data of Stenseth (1971), whereas Madueke & Coaker (1984), using their own data estimated the threshold temperature at 7.0-11.5°C.

Weber (1931) found an upper lethal temperature of 35°C for egg development and a somewhat higher temperature for the other immature stages. Van Evert & Schutte (1983) still found larval development at 35°C. Thus 35°C was taken as the upper lethal temperature for egg development and 38°C for other immature stages in the regression procedure. It was assumed that the lower threshold and upper lethal temperature for development were the same on all host plants. The Logan model yielded the highest coefficients of determination (r^2). This model was also used by Gerling et al. (1986) for immature development of the cotton whitefly, *Bemisia tabaci*. The relationships between development rate of the immature whitefly stages and temperature on eight host plants are shown in Tables 2-10 and presented in Figures 1-9 for tomato. Data on tobacco and tree tobacco were combined because no difference was observed.

Exceptional data points were excluded (n_e) from the regression, such as Eijsackers (1969; L1, L2, L3, pupa, L4+prepupa+pupa and total development on tomato at 30°C); van de Merendonk (1978; L4 on tomato at 24°C); Huang (1988; pupa on tomato at 25°C); Collman & All (1980; L2 on bean at 26°C); Hooy (1984; L1 on cucumber at 25°C); van Sas (1978; total development on cucumber and eggplant at 25°C); Di Pietro (1977; L1 at 22°C and L4+prepupa+pupa at 27°C on tobacco); Mulock Houwer (1977; L2 at 21°C, L3 at 25°C and total development at 25°C on gerbera). Huang (1988) used old plants, and Mulock Houwer (1977) used leaves that had been removed from the plant. The reasons for the exceptional development rates could not be ascertained from the other studies. All data points are presented in the relevant figures and in the appendices of van Roermund & van Lenteren (1992).

Table 2. Relationship between the development rate of eggs 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 (8 and 35°C respectively), r^2 is the coefficient of determination, and n_i and n_e are the number of data points included and excluded respectively.

Host plant	*a*	*b*	*c*	r^2	n_i	n_e
Tomato	0.0464	0.0767	2.56	0.733	19	0
Bean	0.0265	0.108	3.09	0.913	18	0
Cucumber	0.0303	0.115	4.09	0.865	7	0
Eggplant	-	-	-	-	2	0
(Tree)Tobacco	0.0409	0.0796	1.83	0.920	9	0
Gerbera	0.0320	0.103	3.67	0.947	9	0
Sweet pepper	-	-	-	-	4	0
Chrysanthemum	0.0444	0.0647	4.15	0.911	4	0

Table 3. Relationship between the development rate of L1 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 (8 and 38°C respectively), r^2 is the coefficient of determination, and n_i and n_e are the number of data points included and excluded respectively.

Host plant	*a*	*b*	*c*	r^2	n_i	n_e
Tomato	0.0612	0.101	3.21	0.726	14	1
Bean	0.0614	0.146	5.39	0.874	17	0
Cucumber	0.120	0.0581	1.19	0.617	6	1
Eggplant	-	-	-	-	2	0
(Tree)Tobacco	0.118	0.130	6.70	0.830	6	1
Gerbera	0.0749	0.0813	4.19	0.869	9	0
Sweet pepper	-	-	-	-	4	0
Chrysanthemum	0.0467	0.0515	2.08	0.975	4	0

Table 4. Relationship between the development rate of L2 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 (8 and 38°C respectively), r^2 is the coefficient of determination, and n_i and n_e are the number of data points included and excluded respectively.

Host plant	*a*	*b*	*c*	r^2	n_i	n_e
Tomato	0.100	0.0848	1.71	0.801	14	1
Bean	0.0704	0.0914	0.539	0.537	10	1
Cucumber	0.142	0.0712	0.886	0.762	7	0
Eggplant	-	-	-	-	2	0
(Tree)Tobacco	0.323	0.115	7.58	0.933	6	0
Gerbera	0.284	0.0957	8.16	0.581	8	1
Sweet pepper	-	-	-	-	4	0
Chrysanthemum	0.318	0.0441	15.0	0.593	4	0

Table 5. Relationship between the development rate of L3 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 (8 and 38°C respectively), r^2 is the coefficient of determination, and n_i and n_e are the number of data points included and excluded respectively.

Host plant	*a*	*b*	*c*	r^2	n_i	n_e
Tomato	0.123	0.0644	2.09	0.868	13	2
Bean	0.0835	0.0837	0.895	0.770	11	0
Cucumber	0.0874	0.120	4.60	0.876	7	0
Eggplant	-	-	-	-	2	0
(Tree)Tobacco	0.141	0.119	6.76	0.923	6	0
Gerbera	0.237	0.0918	8.44	0.822	8	1
Sweet pepper	-	-	-	-	4	0
Chrysanthemum	-	-	-	-	4	0

Table 6. Relationship between the development rate of L4 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 (8 and 38°C respectively), r^2 is the coefficient of determination, and n_i and n_e are the number of data points included and excluded respectively.

Host plant	*a*	*b*	*c*	r^2	n_i	n_e
Tomato	0.124	0.0774	0.236	0.989	5	1
Bean	-	-	-	-	2	0
Cucumber	0.148	0.112	6.09	0.804	3	0
Eggplant	-	-	-	-	1	0
(Tree)Tobacco	0.053	0.208	4.52	0.874	3	0
Gerbera	0.180	0.0768	8.23	0.528	5	0
Sweet pepper	-	-	-	-	3	0
Chrysanthemum	-	-	-	-	0	0

Table 7. Relationship between the development rate of the prepupa 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 (8 and 38°C respectively), r^2 is the coefficient of determination, and n_i and n_e are the number of data points included and excluded respectively.

Host plant	*a*	*b*	*c*	r^2	n_i	n_e
Tomato	0.331	0.0882	9.40	0.929	3	0
Bean	-	-	-	-	1	0
Cucumber	-	-	-	-	2	0
Eggplant	-	-	-	-	0	0
(Tree)Tobacco	-	-	-	-	1	0
Gerbera	0.338	0.106	7.60	0.918	5	0
Sweet pepper	-	-	-	-	0	0
Chrysanthemum	-	-	-	-	0	0

Table 8. Relationship between the development rate of the pupa 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 (8 and 38°C respectively), r^2 is the coefficient of determination, and n_i and n_e are the number of data points included and excluded respectively.

Host plant	*a*	*b*	*c*	r^2	n_i	n_e
Tomato	0.125	0.115	6.43	0.780	6	2
Bean	0.0743	0.0933	4.06	0.967	4	0
Cucumber	0.0585	0.108	1.20	0.416	3	0
Eggplant	-	-	-	-	1	0
(Tree)Tobacco	-	-	-	-	1	0
Gerbera	0.121	0.0955	6.82	0.685	5	0
Sweet pepper	-	-	-	-	1	0
Chrysanthemum	-	-	-	-	0	0

Table 9. Relationship between the development rate of L4+prepupa+pupa 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 (8 and 38°C respectively), r^2 is the coefficient of determination, and n_i and n_e are the number of data points included and excluded respectively.

Host plant	*a*	*b*	*c*	r^2	n_i	n_e
Tomato	0.0377	0.104	5.12	0.764	15	1
Bean	0.0635	0.116	7.16	0.846	17	0
Cucumber	0.0415	0.127	6.05	0.851	7	0
Eggplant	-	-	-	-	2	0
(Tree)Tobacco	0.0628	0.139	6.35	0.895	10	1
Gerbera	0.0911	0.0962	8.45	0.639	9	0
Sweet pepper	-	-	-	-	4	0
Chrysanthemum	0.0563	0.0165	4.30	0.114	4	0

Table 10. Relationship between the total immature development rate 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 (8 and 35°C respectively), r^2 is the coefficient of determination, and n_i and n_e are the number of data points included and excluded respectively.

Host plant	*a*	*b*	*c*	r^2	n_i	n_e
Tomato	0.0109	0.0838	2.13	0.739	29	1
Bean	0.00915	0.109	4.21	0.929	28	0
Cucumber	0.0153	0.148	5.65	0.960	12	1
Eggplant	0.00906	0.167	4.89	0.891	14	1
(Tree)Tobacco	0.0220	0.123	6.74	0.771	11	0
Gerbera	0.0316	0.146	6.33	0.953	21	1
Sweet pepper	0.0151	0.0928	6.37	0.344	14	0
---East European whitefly	-	-	-	-	5	0
---West European whitefly	0.00777	0.138	5.05	0.730	9	0
Chrysanthemum	0.0143	0.0294	2.62	0.983	4	0

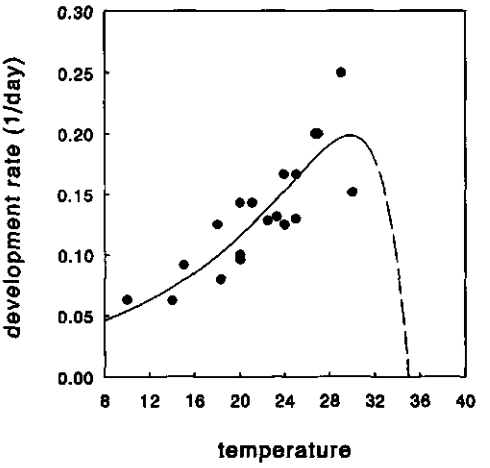

Figure 1. Relationship between the development rate (1/day) of the egg stage and temperature on tomato.

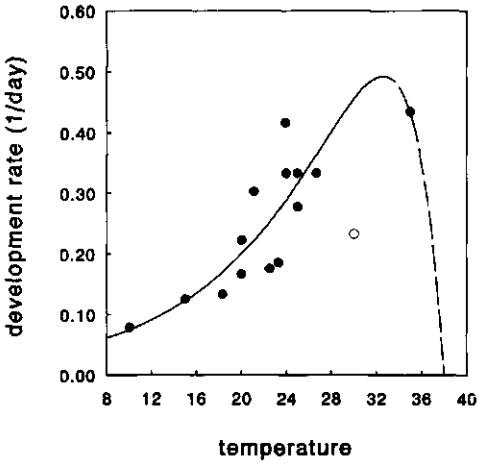

Figure 2. Relationship between the development rate (1/day) of L1 and temperature on tomato. Open dots represent data points excluded from the regression.

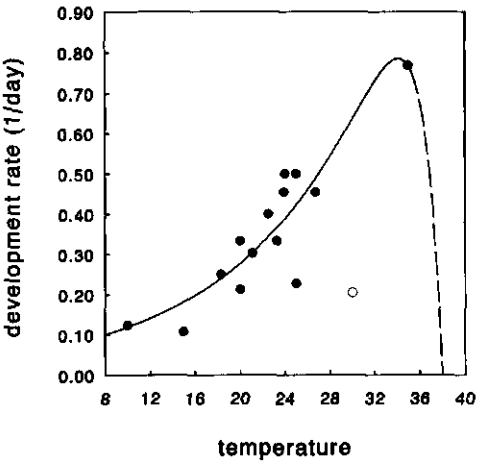

Figure 3. Relationship between the development rate (1/day) of L2 and temperature on tomato. Open dots represent data points excluded from the regression.

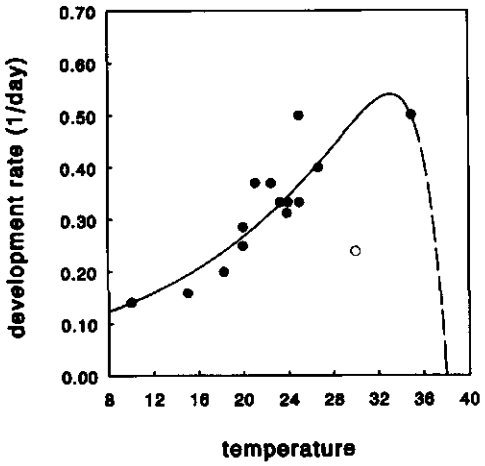

Figure 4. Relationship between the development rate (1/day) of L3 and temperature on tomato. Open dots represent data points excluded from the regression.

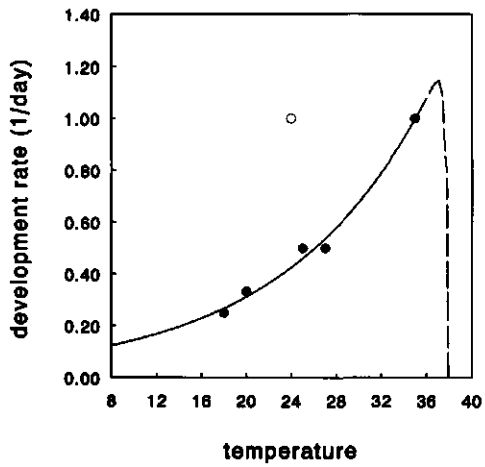

Figure 5. Relationship between the development rate (1/day) of L4 and temperature on tomato. Open dots represent data points excluded from the regression.

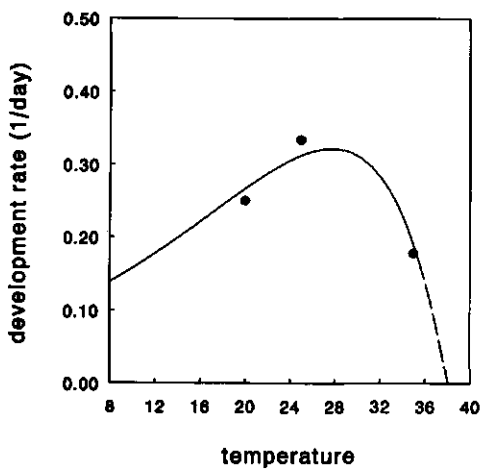

Figure 6. Relationship between the development rate (1/day) of the prepupa and temperature on tomato.

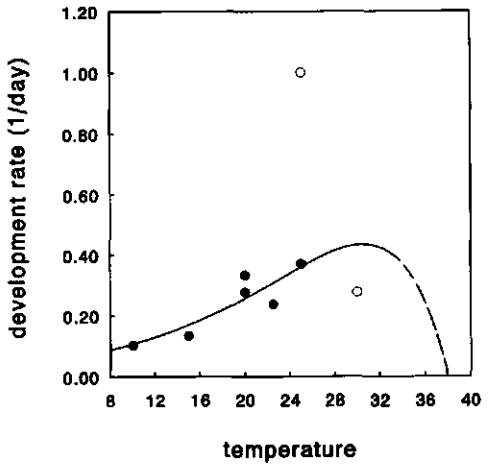

Figure 7. Relationship between the development rate (1/day) of the pupa and temperature on tomato. Open dots represent data points excluded from the regression.

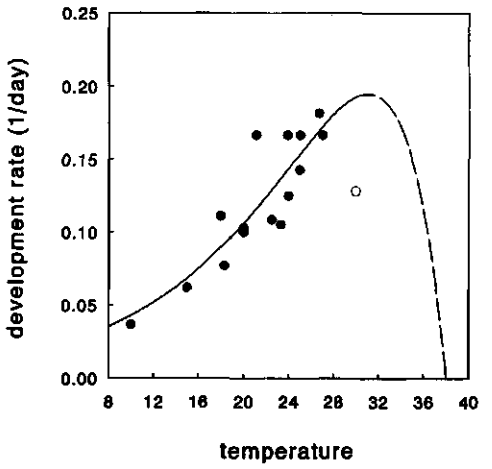

Figure 8. Relationship between the development rate (1/day) of L4+prepupa+pupa and temperature on tomato. Open dots represent data points excluded from the regression.

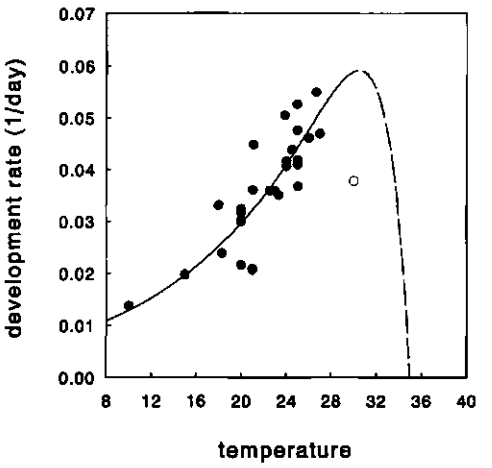

Figure 9. Relationship between the total immature development rate (1/day) and temperature on tomato. Open dots represent data points excluded from the regression.

Relative development duration

The development duration of a development stage can also be expressed as a proportion of the total immature development duration. As shown in Table 10, the curves for total immature development rate are often based on more data points and show a higher r^2 than the curves for development rate of individual stages. Curves for the L4, prepupa and pupa stages especially are sometimes based on a few data points only. If the proportion is independant of temperature, that is development duration of all stages change in the same way with temperature, data points measured at fluctuating temperature can also be included to produce a more reliable estimate.

For all host plants, the relationship between the duration of each stage expressed as a proportion of the total length of all immature stages and temperature was examined for data points obtained at a constant temperature. After visual inspection of the data, it was concluded that only the linear model should be tested. In this way, 46 linear regressions could be made. In 42 cases, the regression was not significant (α=0.05; data not shown), while in three cases the slope was significantly negative, and in one case significantly positive. Therefore, it was concluded that there is no relationship between the proportion of total immature duration and temperature. This means that data points obtained at fluctuating temperature can also be included to calculate the mean proportion.

Results are shown in Tables 11-21. As a measure of variation among data, the coefficient of variation (*cv*) was calculated, which is the standard deviation divided by the overall mean (sd_{n-1}/mean). No data points were excluded (n_e=0). Where estimation of the Logan model was not possible in Tables 2-9, the development rate can be estimated by calculating total immature development rate (Table 10) and then dividing this figure by the proportion in Tables 11-18.

The sum of the proportions of all immature stages of Tables 11-18 for one host plant is not exactly 1.000, because the studies or number of data points were not the same for all stages. Proportions can be rounded off for this purpose.

Data were analysed for host plant effects by a Kruskal-Wallis test, although differences among host plants can also be caused by differences in experimental conditions and in whitefly strains. The proportion of the duration of the short stages L1, L2 and L3 compared to total immature duration does not vary significantly among host plants (Kruskal-Wallis test, α=0.05). It is possible that this is caused by inaccuracies during observation. Usually in development experiments, immature stages are checked once a day, which is not frequent enough for measurement of the short stages. This effect is also shown by the higher *cv* values for short stages.

Table 11. Development duration of the eggs expressed as proportion of the total immature development duration, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.295	0.155	27
Bean	0.302	0.154	22
Cucumber	0.312	0.0535	10
Eggplant	0.324	0.00648	2
Tobacco	0.266	0.0286	6
Tree tobacco	0.289	0.172	3
Gerbera	0.289	0.115	12
Sweet pepper	0.291	0.128	4
Chrysanthemum	0.224	0.130	4
Hibiscus	0.270	-	1
All host plants	0.291	0.156	93

Kruskal-Wallis test, P=0.0439, n=93.

Table 12. Development duration of L1 expressed as proportion of the total immature development duration, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.161	0.172	23
Bean	0.158	0.167	17
Cucumber	0.136	0.136	10
Eggplant	0.146	0.0663	2
Tobacco	0.186	-	1
Tree tobacco	0.142	0.296	3
Gerbera	0.153	0.187	12
Sweet pepper	0.186	0.277	4
Chrysanthemum	0.215	0.213	4
Hibiscus	0.154	-	1
All host plants	0.158	0.208	79

Kruskal-Wallis test, P=0.0698, n=79.

Table 13. Development duration of L2 expressed as proportion of the total immature development duration, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.114	0.285	24
Bean	0.123	0.322	11
Cucumber	0.0988	0.0931	10
Eggplant	0.0808	0.214	2
Tobacco	0.0873	-	1
Tree tobacco	0.0933	0.046	3
Gerbera	0.105	0.179	12
Sweet pepper	0.113	0.264	11
Chrysanthemum	0.130	0.243	4
Hibiscus	0.100	-	1
All host plants	0.111	0.268	81

Kruskal-Wallis test, P=0.370, n=81.

Table 14. Development duration of L3 expressed as proportion of the total immature development duration, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.127	0.236	24
Bean	0.122	0.177	11
Cucumber	0.106	0.0840	10
Eggplant	0.103	0.137	2
Tobacco	0.117	-	1
Tree tobacco	0.122	0.0181	3
Gerbera	0.125	0.252	12
Sweet pepper	0.121	0.213	11
Chrysanthemum	0.112	0.264	4
Hibiscus	0.120	-	1
All host plants	0.122	0.217	81

Kruskal-Wallis test, P=0.401, n=81.

Table 15. Development duration of L4 expressed as proportion of the total immature development duration, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.0816	0.360	8
Bean	0.140	0.225	2
Cucumber	0.0977	0.0972	4
Eggplant	0.0930	-	1
Tobacco	0.135	-	1
Tree tobacco	0.208	0.0866	2
Gerbera	0.136	0.181	8
Sweet pepper	0.115	0.196	10
Chrysanthemum	-	-	0
Hibiscus	0.136	-	1
All host plants	0.118	0.314	38

Kruskal-Wallis test, P=0.00850, n=38.

Table 16. Development duration of the prepupa expressed as proportion of the total immature development duration, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.128	0.184	5
Bean	0.0880	-	1
Cucumber	0.117	0.0849	3
Eggplant	-	-	0
Tobacco	-	-	0
Tree tobacco	0.0751	-	1
Gerbera	0.0696	0.0862	5
Sweet pepper	0.0925	0.186	5
Chrysanthemum	-	-	0
Hibiscus	0.108	-	1
All host plants	0.0960	0.301	22

Kruskal-Wallis test, P=0.0141, n=22.

Table 17. Development duration of the pupa expressed as proportion of the total immature development duration, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.120	0.238	11
Bean	0.129	0.0241	4
Cucumber	0.150	0.281	4
Eggplant	0.202	-	1
Tobacco	0.117	-	1
Tree tobacco	-	-	0
Gerbera	0.137	0.0884	5
Sweet pepper	0.0949	0.314	6
Chrysanthemum	-	-	0
Hibiscus	0.112	-	1
All host plants	0.126	0.258	34

Kruskal-Wallis test, P=0.0392, n=34.

Table 18. Development duration of L4+prepupa+pupa expressed as proportion of the total immature development duration, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.307	0.0812	26
Bean	0.332	0.145	19
Cucumber	0.347	0.0706	10
Eggplant	0.352	0.0119	2
Tobacco	0.332	0.0169	6
Tree tobacco	0.369	0.100	3
Gerbera	0.331	0.109	12
Sweet pepper	0.314	0.133	11
Chrysanthemum	0.319	0.187	4
Hibiscus	0.359	-	1
All host plants	0.327	0.117	96

Kruskal-Wallis test, P=0.0117, n=96.

Table 19. Development duration of L4 expressed as proportion of the development duration of L4+prepupa+pupa, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.269	0.383	8
Bean	0.400	0.163	2
Cucumber	0.290	0.0765	4
Eggplant	0.267	-	1
Tobacco	0.413	-	1
Tree tobacco	0.598	0.128	2
Gerbera	0.420	0.170	8
Sweet pepper	0.357	0.123	10
Chrysanthemum	-	-	0
Hibiscus	0.379	-	1
All host plants	0.361	0.284	38

Kruskal-Wallis test, P=0.00663, n=38.

Table 20. Development duration of the prepupa expressed as proportion of the development duration of L4+prepupa+pupa, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.412	0.133	5
Bean	0.266	-	1
Cucumber	0.335	0.0686	3
Eggplant	-	-	0
Tobacco	0.230	-	1
Tree tobacco	-	-	0
Gerbera	0.206	0.132	5
Sweet pepper	0.303	0.299	5
Chrysanthemum	-	-	0
Hibiscus	0.302	-	1
All host plants	0.296	0.330	22

Kruskal-Wallis test, P=0.0127, n=22.

Table 21. Development duration of the pupa expressed as proportion of the development duration of L4+prepupa+pupa, *cv* is the coefficient of variation and n_i is the number of data points.

Host plant	Mean	*cv*	n_i
Tomato	0.383	0.228	11
Bean	0.393	0.0326	4
Cucumber	0.429	0.274	4
Eggplant	0.568	-	1
Tobacco	0.357	-	1
Tree tobacco	-	-	0
Gerbera	0.403	0.0796	5
Sweet pepper	0.310	0.254	6
Chrysanthemum	-	-	0
Hibiscus	0.312	-	1
All host plants	0.384	0.222	34

Kruskal-Wallis test, P=0.122, n=34.

Immature mortality

Immature mortality of each stage was expressed as a percentage of the number of individuals entering that stage. The relationship between percentage mortality and temperature on each host plant was examined by using data points obtained at a constant temperature. From visual inspection of the data, it was concluded that only the linear model should be tested. In this way, 46 linear regressions were done, from which only eight were significant (α=0.05; data not shown). Of these eight significant regressions, the slope was negative in two cases, 0 in three cases and positive in three cases. Therefore, it was concluded that there is no relationship between percentage mortality and temperature. Thus, experiments done at fluctuating temperature could also be used to calculate the mean percentage mortality for each immature stage on each host plant.

Yano (1981) found higher mortality at low temperatures (around 15°C) on tobacco, but these results were not confirmed by other studies (Dorsman & van der Vrie, unpubl. on gerbera; Weber, 1931 on tobacco). At high temperatures (30°C or more) mortality of egg, prepupa and pupa was usually higher (van Evert & Schutte, 1983; Weber, 1931). This resulted in a higher total immature mortality (van Evert & Schutte, 1983; Weber, 1931; Yano, 1981). However, high mortality was only observed when temperature was constantly high. At fluctuating temperatures with peaks of 30°C or more, which is usually the case in greenhouses, higher mortality was not observed (van Evert & Schutte, 1983; Kajita, 1982; Yano, 1988; van Vianen et al., 1987, also in van Lenteren et al., 1989; Meyer, 1990, also in Meyer et al., 1990). Even if eggs, prepupae and pupae remained for as long as five hours at temperatures between 30 and 35°C, mortality was not higher than at lower temperatures (van Evert & Schutte, 1983). This means that at high temperatures the duration of exposition is important. Because in greenhouses temperatures do not often exceed 30°C for more than 5 hours, this effect was not included in the tables below.

The percentage mortality was calculated using data obtained at an average temperature not exceeding 30°C. Exceptionally high mortalities were excluded, such as observed by Oostenbrug (1988; also in van Lenteren et al., 1989; egg, L1, L2, L3, L4, prepupa, pupa, L4+prepupa+pupa and total mortality on tomato at 22.9°C); Kusters (1990; egg, L1, L2, L3, L4, prepupa, pupa, L4+prepupa+pupa and total mortality on gerbera at 22°C); Schönherr (1988; egg, L1, L2, L3, L4, L4+prepupa+pupa and total mortality on gerbera at 23.5°C (three times)); Nechols & Tauber (1977a; L1, L2, L3, and L4 mortality on tobacco at 25°C); Yano (1981; L1, L3 and total mortality on tobacco at 15°C); Yano (1988; L2 and total mortality on tomato at 20°C); van de Merendonk (1978; L1 mortality on sweet pepper at 24°C); Kraayenbrink (1972; L1 mortality on sweet pepper at 23.3°C); Zebitz (1978; L2, L3, L4+prepupa+pupa and total (twice) mortality on tobacco at 25°C, and total mortality at 20.5°C); Li & Li (1983; L4+prepupa+pupa and total mortality on cucumber at 17.8°C); Huang (1988; total mortality on tomato at 20°C); Laska (1986; total mortality on bean at 20°C); Malausa et al. (1984; total mortality on eggplant at 22°C (twice)); van Sas (1978; total mortality on gerbera at 25°C); Mulock Houwer (1977; total mortality on gerbera at 21°C).

The reasons for the high mortalities could not always be ascertained. Kusters (1990) and Schönherr (1988) used whitefly not originating from gerbera. Nechols & Tauber (1977a) and Zebitz (1978) used host varieties not used in any other experiments. Mulock Houwer (1977) used leaves that had been removed from the plant.

Results are shown in Tables 22-30. Host plant effects were not tested statistically, because differences in mortality among host plants were obvious. The high variation in percentage mortality among different experiments is expressed by the high *cv* values.

Table 22. Mean egg mortality 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.

Host plant	Mean	*cv*	n_i	n_e
Tomato	3.7	0.885	15	1
Bean	1.6	0.713	7	0
Cucumber	5.6	0.959	9	0
Eggplant	4.1	-	1	0
Tobacco	2.8	0.991	5	0
Tree tobacco	3.4	0.518	3	0
Gerbera	1.5	0.551	3	4
Sweet pepper	12.5	0.802	10	0
---West European whitefly	10.6	0.797	4	0
---East European whitefly	13.7	0.839	6	0

Table 23. Mean L1 mortality 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.

Host plant	Mean	*cv*	n_i	n_e
Tomato	4.2	0.632	11	1
Bean	5.7	0.071	3	0
Cucumber	2.2	1.307	8	0
Eggplant	1.2	1.175	2	0
Tobacco	12.2	1.121	4	2
Tree tobacco	18.8	0.515	3	0
Gerbera	4.3	0.893	3	4
Sweet pepper	31.8	0.660	11	0
---West European whitefly	30.3	0.188	5	2
---East European whitefly	14.6	0.431	4	0

Table 24. Mean L2 mortality 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.

Host plant	Mean	*cv*	n_i	n_e
Tomato	2.6	0.814	10	2
Bean	1.8	1.051	3	0
Cucumber	2.7	1.121	8	0
Eggplant	0.1	1.400	2	0
Tobacco	0.9	1.029	5	2
Tree tobacco	3.4	0.642	3	0
Gerbera	2.0	0.435	3	4
Sweet pepper	24.0	0.523	11	0
---West European whitefly	31.4	0.348	4	0
---East European whitefly	19.7	0.610	7	0

Table 25. Mean L3 mortality 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.

Host plant	Mean	*cv*	n_i	n_e
Tomato	3.7	0.812	11	1
Bean	0.0	0.000	3	0
Cucumber	3.2	1.514	8	0
Eggplant	0.1	1.400	2	0
Tobacco	7.2	1.359	4	3
Tree tobacco	2.9	1.050	3	0
Gerbera	1.3	0.953	3	4
Sweet pepper	27.2	0.769	11	0
---West European whitefly	25.5	0.255	4	0
---East European whitefly	28.1	0.943	7	0

Table 26. Mean L4 mortality 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.

Host plant	Mean	*cv*	n_i	n_e
Tomato	3.4	1.273	3	1
Bean	0.0	0.000	3	0
Cucumber	0.3	0.967	4	0
Eggplant	0.0	-	1	0
Tobacco	-	-	0	1
Tree tobacco	1.0	0.671	2	0
Gerbera	0.0	0.000	3	4
Sweet pepper	22.9	0.899	10	0
---West European whitefly	13.4	0.767	3	0
---East European whitefly	27.0	0.858	7	0

Table 27. Mean prepupa mortality 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.

Host plant	Mean	*cv*	n_i	n_e
Tomato	3.8	-	1	1
Bean	0.0	0.000	3	0
Cucumber	-	-	0	0
Eggplant	-	-	0	0
Tobacco	1.3	-	1	0
Tree tobacco	-	-	0	0
Gerbera	0.0	0.000	3	1
Sweet pepper	1.6	0.722	5	0
---West European whitefly	1.5	0.093	2	0
---East European whitefly	1.6	0.982	3	0

Table 28. Mean pupa mortality 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.

Host plant	Mean	*cv*	n_i	n_e
Tomato	2.6	0.327	2	1
Bean	1.3	0.864	3	0
Cucumber	0.4	-	1	0
Eggplant	1.1	-	1	0
Tobacco	-	-	0	0
Tree tobacco	-	-	0	0
Gerbera	0.7	1.716	3	1
Sweet pepper	8.0	0.759	6	0
---West European whitefly	11.3	0.673	3	0
---East European whitefly	4.7	0.253	3	0

Table 29. Mean mortality of L4+prepupa+pupa 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.

Host plant	Mean	*cv*	n_i	n_e
Tomato	7.3	0.655	9	1
Bean	1.3	0.864	3	0
Cucumber	3.8	1.579	6	1
Eggplant	2.8	-	1	0
Tobacco	18.4	0.682	11	1
Tree tobacco	1.8	0.733	3	0
Gerbera	0.6	1.746	3	4
Sweet pepper	32.8	0.664	7	0
---West European whitefly	22.0	0.119	3	0
---East European whitefly	40.8	0.666	4	0

Table 30. Mean total immature mortality expressed as the percentage of the number entering the egg stage, *cv* is the coefficient of variation, and n_i and n_e are the number of data points included and excluded.

Host plant	Mean	*cv*	n_i	n_e
Tomato	16.7	0.713	21	4
Bean	7.9	0.284	7	1
Cucumber	15.9	0.663	12	1
Eggplant	12.9	0.574	11	2
Tobacco	30.0	0.464	4	4
Tree tobacco	30.3	0.405	3	0
Gerbera	10.2	0.406	15	6
Sweet pepper	69.7	0.299	24	0
---West European whitefly	80.7	0.075	6	0
---East European whitefly	66.0	0.345	18	0

Sex ratio

The relationship between sex ratio (expressed as the proportion of females of total offspring) and temperature was studied for each host plant using data obtained at a constant temperature. From visual inspection of the data, it was concluded that only the linear model should be tested. The linear regression was not significant for tomato, bean and cucumber. Only for sweet pepper it was, but the data were for temperatures between 22 and 27°C, so the regression is not reliable. For all host plants together, the regression was not significant (P=0.253, n=43). Therefore it was concluded that sex ratio was not related to temperature. A Kruskal-Wallis test (α=0.05) showed no effect of host plant on sex ratio (see Table 31). Four data points of van Rongen (1979) on cucumber were excluded because of difficulties in interpreting the sampling method. Data points of Lloyd (1922) on various host plants were combined because of the small number of whiteflies used and were not included in the Kruskal-Wallis test.

Table 31. Sex ratio expressed as the proportion of females of total offspring, *cv* is the coefficient of variation and n_i and n_e are the number of data points included and excluded.

Host plant	Mean	*cv*	n_i	n_e
Tomato	0.483	0.063	5	0
Bean	0.553	0.166	12	0
Cucumber	0.543	0.146	5	4
Eggplant	0.440	-	1	0
Tobacco	-	-	0	0
Tree tobacco	0.514	0.018	2	0
Gerbera	0.525	0.176	3	0
Sweet pepper	0.525	0.090	9	0
Wild potato	0.732	-	1	0
Potato	0.700	-	1	0
Various	0.558	-	1	0
All host plants	0.538	0.149	40	4

Kruskal-Wallis test, P=0.219, n=39.

Longevity

As rough data indicated longevity was lower in males than in females, this life-history parameter was studied separately for the sexes. Data points obtained at constant temperatures were used to examine the relationship between female longevity and temperature. Weber (1931) did experiments at extreme temperatures and found longevities of 6.5 days at 0°C and 0.25 days at 36°C on tobacco. These data have been taken as the arbitrary lower and upper values for all host plants. The highest coefficients of determination (r^2) were obtained when the third degree polynomial and the Weibull model were used. On the basis of visual inspection of the curves, the Weibull model was chosen. The third degree polynomials yielded biologically unrealistic tails. Table 32 shows the results. The lower lethal temperature (coefficient a) is fixed at -10°C

according to Weber (1931). Figure 10 presents the relationship between female longevity and temperature on tomato.

The coefficients of determination on tomato and eggplant were low because of differences in host plant variety, as shown for tomato by an increase in r^2 when host plant varieties were analysed separately. High variation in longevity among eggplant varieties was shown by Malausa et al. (1984, 1988). The shape coefficient c for eggplant was fixed at 3.50 (average of host plants with high r^2) because data at low temperatures were missing. The great variation in longevity on sweet pepper, also shown by Zabudskaya (1989), was not caused by a difference in whitefly strains, because r^2 remained low when the West European and East European strain were analyzed separately. Data below 22°C were not available, which resulted in a shape coefficient of 10.9.

Table 32. Relationship between female longevity and temperature based on the Weibull model where b, c and d are coefficients, a is the lower lethal temperature of -10°C, r^2 is the coefficient of determination and n_i and n_e are the number of data points included and excluded.

Host plant	b	c	d	r^2	n_i	n_e
Tomato	29.6	4.68	723	0.609	22	2
---'Bonnie Best'	27.8	5.56	622	0.905	11	0
---'Moneymaker'+'Moneydor'	29.0	3.45	725	0.864	6	2
Bean	26.2	3.79	754	0.852	7	0
Cucumber	31.4	3.59	752	0.793	12	2
Eggplant	33.2	3.50[1)]	1570	0.486	20	0
Tobacco	30.1	3.06	833	0.716	11	0
Gerbera	29.1	3.43	1230	0.849	8	4
Sweet pepper	38.6	10.9	131	0.482	17	0
---West European whitefly	23.5	2.64	260	0.402	8	0
---East European whitefly	27.5	4.02	964	0.442	11	0

[1)] Fixed at 3.50

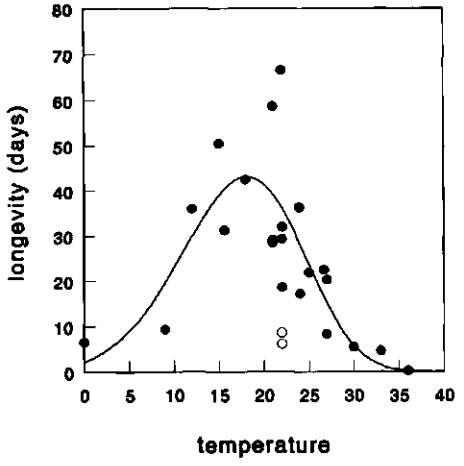

Figure 10. Relationship between the female longevity (day) and temperature on tomato. Open dots represent data points excluded from the regression.

Exceptional data points were excluded from the regression, such as van Boxtel (1980; twice on tomato cv. 'Moneymaker' and twice on cucumber) and Mulock Houwer (1977; four times on gerbera). Van Boxtel did these experiments in winter on poor quality host plants and as already mentioned, Mulock Houwer did experiments on leaves removed from the plant.

Not enough data were available to estimation the relationship between male longevity and temperature in the same way as for female longevity. However, it was possible to express male longevity as a proportion of female longevity because in many studies longevity was examined for both sexes under the same environmental conditions. According to the available data, there is no significant linear relationship between this proportion and temperature (P=0.167, n=28), so data were averaged (Table 33). Differences in the proportion among host plants were not significant (Kruskal-Wallis test, α=0.05).

Data points of Genchev (1986, on bean) and Lloyd (1922, twice on various host plants) were excluded, because the first study differed greatly from other studies and the second used a small number of whiteflies. Male longevity can easily be estimated by calculating female longevity from Table 32 and then multiplying this figure by the proportion given in Table 33.

Table 33. Male longevity expressed as the proportion of female longevity, *cv* is the coefficient of variation and n_i and n_e are the number of data points included and excluded.

Host plant	Mean	*cv*	n_i	n_e
Tomato	0.46	0.281	2	0
Bean	0.71	-	1	1
Cucumber	0.64	0.137	7	0
Eggplant	0.47	0.248	8	0
Sweet pepper	0.53	0.316	10	0
Various	-	-	0	2
All host plants	0.54	0.264	28	3

Kruskal-Wallis test, P=0.0787, n=28.

The survival pattern of adult whiteflies in relation to age has been studied by van Rongen (1979), van Sas (1978; also in van Sas et al., 1978), van Boxtel (1980; also in van Boxtel et al., 1978), Yano (1981, 1988, 1989), Burggraaf-van Nierop & van der Laan (1983; also in van der Laan et al., 1982), Dorsman & van der Vrie (1987) and Oostenbrug (1988; also in van Lenteren et al., 1989). The results are shown in graphs without fitting the data to a statistical distribution and without giving the original data. S-shaped or linear decline are mostly shown. An exponential decline was found for Dutch whiteflies on sweet pepper (Burggraaf-van Nierop & van der Laan, 1983; Oostenbrug, 1988). The survivalship curves of van Boxtel (1980) on eggplant and van Sas (1978) on tomato showed a tail to the right, indicating that some individuals reached a high age (more than twice the average). However, on 7 other host plants this was not clear and van Rongen (1979), Yano (1981, 1988, 1989) and

Dorsman & van der Vrie (1987) did not find this at all. Because adults of high age are not important for the population growth rate, as shown by Birch (1948), it is possible to describe the whitefly survivalship curve by a decreasing cumulative normal distribution, of which the S-shape depends on the variation in longevity. Maximum longevity can be calculated as the mean longevity plus three times the standard deviation to include 96 % of the adults.

Pre-oviposition period

The period between adult emergence and oviposition was measured only between temperatures of 17°C and 27°C. The exponential model described the best relationship between the pre-oviposition period and temperature, although r^2's were low. Differences among host plants were not clear. Extrapolation to temperatures below 17°C is very unreliable, because of a rapid increase of the pre-oviposition period according to the exponential model. For low temperatures, a pre-oviposition period the same as that at 17°C is a better estimate. Table 34 gives the results of the regression and Figure 11 shows the graph when all host plants were combined.

Table 34. Relationship between the 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.

Host plant	a	b	r^2	n_i	n_e
Tomato	0.558	-0.0213	0.014	4	0
Bean	1.94	-0.0765	0.380	6	0
Eggplant	3.97	-0.176	0.968	3	0
All host plants	2.17	-0.0901	0.328	13	0

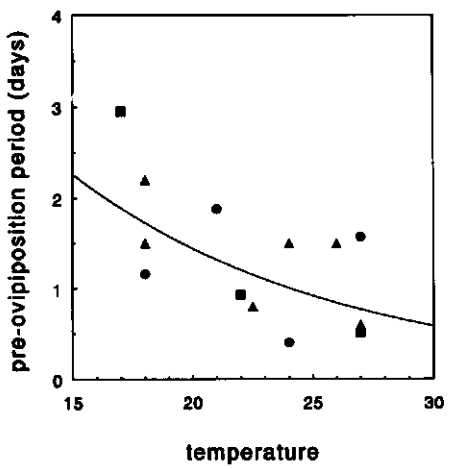

Figure 11. Relationship between the pre-oviposition period (day) and temperature. Circle: tomato; triangle: bean and square: eggplant.

Fecundity

Fecundity is the total number of eggs laid in a female's lifetime. Some of the variation in fecundity among females is caused by variation in longevity. Weber (1931) found a lower and upper threshold temperature for oviposition of 10 and 37°C on tobacco and a lower threshold temperature for egg maturation of 4°C. Pravisani (1981) studied fecundity at 2.5°C intervals on bean and found 7.5 and 37.5°C respectively. It is assumed that these lower and upper temperatures are the same on other host plants. When the relationship between fecundity and temperature was studied, the best fits were obtained with the Weibull model and resulted in the highest r^2 values and realistic tails of the curves. Table 35 presents the results for different host plants and Figure 12 for tomato. As for longevity, r^2 values were low for tomato, eggplant and sweet pepper, because of the differences in varieties of the tomato and eggplant. For cucumber a biological realistic fit was only possible when the shape coefficient c was fixed at the average value of 2.70 for the other host plants. Data for sweet pepper below 22°C were not available, which resulted in a shape coefficient of 7.55.

Exceptional data points were excluded from the regression, such as van Boxtel (1980; twice on tomato, twice on cucumber, once on sweet pepper at 22°C); Huang (1988; twice on tomato); Christochowitz & van der Fluit (1983; on tomato); Burnett (1949; on tomato at 18°C); Collman & All (1980; on bean at 26°C); Zabudskaya (1989; seven times on cucumber); Di Pietro (1977; on eggplant at 27°C) and Mulock Houwer (1977; four times on gerbera). Van Boxtel (1980) did these experiments in winter on poor quality host plants. Huang (1988) used old host plants, Christochowitz & van der Fluit (1983) studied fecundity over a period of 17 days only, Mulock Houwer (1977) used leaves removed from the plant. Low fecundities obtained by Zabudskaya (1989) may be due to the East European whitefly strain or to the cucumber variety. No clear explanation could be found for low data points of Collman & All (1980) and Di Pietro (1977) and for the very high data point of Burnett (1949).

Table 35. Relationship between fecundity and temperature based on the Weibull model where b, c and d are coefficients, a is the lower threshold temperature of 7.5°C, r^2 is the coefficient of determination and n_i and n_e are the number of data points included and excluded.

Host plant	b	c	d	r^2	n_i	n_e
Tomato	14.9	2.58	2350	0.481	25	6
---'Bonnie Best'	12.8	3.91	2430	0.921	10	0
---'Moneymaker'+'Moneydor'	12.8	2.23	2580	0.848	7	3
Bean	14.6	2.27	1840	0.998	5	1
Cucumber	17.9	2.70[1)]	3300	0.961	4	9
Eggplant	17.1	2.55	8940	0.618	18	1
Tobacco	17.2	3.64	3700	0.947	8	0
Gerbera	17.6	2.37	4190	0.787	17	4
Sweet pepper	22.8	7.55	736	0.277	15	1
---West European whitefly	14.0	7.55[1)]	60	0.173	6	1
---East European whitefly	22.9	7.55[1)]	757	0.187	11	0

[1)] Fixed at given value.

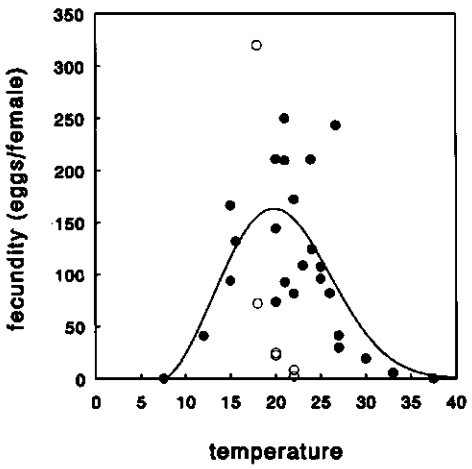

Figure 12. Relationship between the fecundity (egg/female) and temperature on tomato. Open dots represent data points excluded from the regression.

Oviposition frequency

Mean oviposition frequency can be calculated by dividing the fecundity of a female whitefly by her longevity. Oviposition frequency may be less variable than fecundity, because differences in longevity are accounted for.

Only 'whole lifetime' experiments done at a constant temperature were used to examine the relationship between oviposition frequency and temperature. Lower and upper threshold temperatures of 7.5 and 37.5°C observed by Pravisani (1981) were taken for all host plants. The Weibull model yielded the best fit, although the r^2 values of the third degree polynomials were very close. The tails of the third degree polynomials were not always realistic. The mean oviposition frequency is given in Table 36 and for tomato also in Figure 13. Data for sweet pepper below 20°C were not available, which resulted in a shape coefficient of 9.25.

Exceptional data points were excluded from the regression, such as van Boxtel (1980; twice on tomato, once on sweet pepper at 22°C); Hussey & Gurney (1957; on tomato at 26.7°C); Zabudskaya (1989; on tomato at 27°C); Castresana Estrada et al. (1982; on tomato at 22°C) and Mulock Houwer (1977; four times on gerbera). Data from van Boxtel (1980), Zabudskaya (1989), and Mulock Houwer (1977) were excluded for the same reasons that they were excluded from study on fecundity. The high oviposition frequency given by Hussey & Gurney (1957) and the low value of Castresana Estrada et al. (1982) could not be explained.

Table 36. Relationship between mean oviposition frequency during a lifetime and temperature based on the Weibull model where b, c and d are coefficients, a is the lower threshold temperature of 7.5°C, r^2 is the coefficient of determination and n_i and n_e are the number of data points included and excluded.

Host plant	b	c	d	r^2	n_i	n_e
Tomato	16.8	2.64	107	0.759	17	5
---'Bonnie Best'	16.7	3.01	119	0.922	10	0
---'Moneymaker'+'Moneydor'	16.4	2.57	76.7	0.985	5	2
Bean	15.8	3.33	56.2	0.971	6	0
Cucumber	16.8	4.12	87.8	0.988	7	0
Eggplant	17.6	2.76	170	0.937	12	0
Tobacco	19.4	3.14	156	0.958	8	0
Gerbera	20.6	3.36	105	0.897	8	4
Sweet pepper	18.7	9.25	27.6	0.404	19	1
---West European whitefly	21.0	6.45	40.8	0.550	8	1
---East European whitefly	18.4	4.57	53.1	0.376	13	0

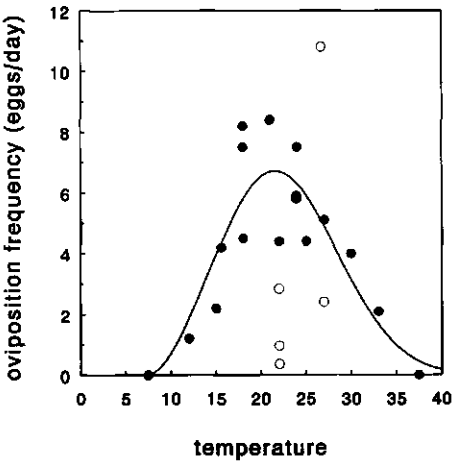

Figure 13. Relationship between the mean oviposition frequency during a lifetime (egg/female/day) and temperature on tomato. Open dots represent data points excluded from the regression.

Change in oviposition frequency during ageing

Oviposition frequency is not constant throughout the lifetime of a female. Van Sas (1978; also in van Sas et al., 1978), van Boxtel (1980; also in van Boxtel et al., 1978), Yano (1981, 1988, 1989), Burggraaf-van Nierop & van der Laan (1983; also in van der Laan et al. (1982), Steenhuis (unpubl.), Dorsman & van der Vrie (1987 and unpubl.) and Oostenbrug (1988; also in van Lenteren et al., 1989) have shown that oviposition frequency usually varied greatly from day to day. In all cases it increased in the first few days from zero to a maximum level. This maturation period, in which the pre-oviposition period is included, was estimated from these studies. The relationship between maturation period and temperature could be described well by the exponential

model (see Table 37). Hulspas-Jordaan & van Lenteren (1989) published slightly different data.

In some studies the oviposition frequency was found to be constant after the maturation period until the whiteflies died (van Boxtel (1980) on eggplant and tomato; Yano (1981, 1988, 1989); Oostenbrug (1988) for Hungarian whiteflies), but more often it remained constant for a period and then decreased almost linearly with age (van Boxtel (1980) on cucumber; van Sas (1978) on five host plants; Burggraaf-van Nierop & van der Laan (1983); Dorsman & van der Vrie (1987 and unpubl.); van Lenteren et al., 1989 for Dutch whiteflies).

In general, oviposition frequency during ageing increases linearly with maturation to a maximum. This level remains constant until mean longevity is attained and then decreases linearly to zero at maximum longevity. Maximum longevity can be estimated from the mean longevity plus three times the standard deviation. The maximum level of the oviposition frequency can be calulated by using the fecundity, the pre-oviposition period, the maturation period and the mean longevity.

Table 37. Relationship between the maturation period (pre-oviposition period included) 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.

Host plant	a	b	r^2	n_i	n_e
All host plants	2.82	-0.0568	0.953	5	0

VARIATION AMONG INDIVIDUALS

So far only mean values of the life-history parameters were used to relate the parameter to host plant and temperature. Variation among individuals within one experiment was also obtained in many studies. As a measure of this variation, the coefficient of variation (*cv*, also called relative dispersion) was calculated, that is the sample standard deviation divided by the overall mean (sd_{n-1}/mean). For data from different populations, the mean and standard deviation often tend to change together so that the *cv* is relatively stable. The *cv* values should be used as input parameters in simulation models when stochasticity is desired and normality can be assumed, as arises often during developmental dispersion (Goudriaan & van Roermund, 1989; Schaub & Baumgärtner, 1989).

Mean *cv* values were calculated for immature development duration, longevity, fecundity, oviposition frequency and pre-oviposition period. Two catagories of *cv* values were excluded: values of which the number of replicates (n) was lower than the total number of whiteflies (because then variation among n experiments was calculated instead of variation among individuals) and values of mean life-history parameters which were excluded from the regression in Tables 2-37 (referred to Tables 38-40 as the number of observations excluded, n_e). If variation was given without the number of replicates or whiteflies, it was assumed to be among individuals and was included.

Variation in immature development duration

Variation among individuals in development duration (which is almost equal to the variation in development rate) can be measured by following individual larvae separately through leaf mapping or calculated after linearization of the s-curve when populations were followed. The latter method was chosen by van Zoest (1987).

Only data obtained at a constant temperature were used when the relationship between *cv* and temperature was studied. From visual inspection it was concluded that only the linear model should be tested. No significant relationship could be found from 11 cases tested (α=0.05, results not shown), so *cv* values obtained at constant and fluctuating temperatures were combined. Table 38 shows the mean *cv* of development duration of each whitefly immature stage on each host plant. No observations were excluded (n_e = 0). Data on tobacco and tree tobacco were combined, because no difference was observed. According to Kruskal-Wallis tests, differences in *cv* among host plants were only significant for the egg stage (α=0.05). This is probably due to a high *cv* on sweet pepper. The *cv* of the development duration of the shorter stages (L2, L3, L4) is higher than that of the longer stages (egg- and total immature stage) and can be caused by inaccuracies during experimentation. In many studies individuals were checked once a day, which is not frequent enough for reliable estimation of the duration of stages of only a few days duration.

Sequential dependance of development 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 accurately if the development duration of each individual during each stage is known. This was done by Hulspas-Jordaan & van Lenteren (1989) using data of Christochowitz & van der Fluit (1981), showing no correlation between successive stages. If it occurs, the variance (sd^2) of the total immature development duration will be lower than when calculated from the variances of the separate stages. From data of Eijsackers (1969), Nechols & Tauber (1977b), Laska et al. (1980), Kusters (1990) and Dorsman & van der Vrie (unpubl.), the measured variance of the total immature development duration was compared to the calculated variance and no significant difference was found (Wilcoxon signed rank test, P=0.610, n=12 pairs). Thus sequential dependance appears to be absent.

Variation in longevity and pre-oviposition period

The relationship between *cv* and temperature was studied for each host plant separately. From visual inspection it was concluded that only the linear model should be tested. No significant regression was found in the six tested for longevity. For the pre-oviposition period, however, one significant relationship was found on bean in two tested (α=0.05), but the number of observations was very low (n=3, data not shown). Therefore, no relationship with temperature was assumed. Table 39 shows mean *cv* values on each of the seven host plants. Data on other host plants were also used but

Table 38. Mean coefficient of variation among individuals (*cv*) of immature development duration of each whitefly stage and number of observations included (n_i).

Host plant	Egg		L1		L2		L3		L4		Prepupa		Pupa		Total	
	cv	n_i	*cv*	n_i	*cv*	n_i	*cv*	n_i	*cv*	n_i	*cv*	n_i	*cv*	n_i	*cv*	n_i
Tomato	0.11	8	0.26	7	0.35	10	0.36	10	0.50	4	0.31	4	0.30	8	0.077	16
Bean	0.081	4	0.22	4	0.24	4	0.24	4	-	0	-	0	0.19	3	0.10	1
Cucumber	0.057	3	-	0	-	0	-	0	-	0	-	0	-	0	0.058	4
Eggplant	-	0	-	0	-	0	-	0	-	0	-	0	-	0	0.087	1
(Tree)Tobacco	0.029	4	0.35	1	0.29	1	0.22	1	0.39	1	0.42	1	0.16	1	0.076	11
Gerbera	0.065	5	0.24	5	0.28	5	0.28	5	0.24	5	0.52	1	0.25	1	0.072	17
Sweet pepper	0.16	2	-	0	0.46	9	0.44	10	0.53	9	0.38	5	0.46	5	0.14	6
Hibiscus	0.11	1	0.39	1	0.60	1	0.60	1	0.62	1	0.41	1	0.20	1	0.16	1
All host plants	0.083	27	0.25	19	0.36	31	0.36	31	0.45	20	0.37	12	0.31	19	0.084	59
Kruskal-Wallis test	P=0.0424, n=27		P=0.365, n=19		P=0.0875, n=31		P=0.0704, n=31		P=0.271, n=20		P=0.163, n=12		P=0.510, n=19		P=0.126, n=59	

are not given separately in the table. No significant host plant effect on the *cv* was found (Kruskal-Wallis test, α=0.05), although on poor host plants such as sweet pepper *cv* tends to be higher.

In some studies the longevity of males was compared to that of females under the same experimental conditions. From these 15 experiments the *cv* of male longevity tended to be higher than that of females (mean *cv* was 1.0 and 0.68 respectively), but no significant difference could be found (Wilcoxon signed rank test, P=0.0938, n=15 pairs).

Table 39. Mean coefficient of variation among individuals (*cv*) of female longevity and pre-oviposition period and number of observations included (n_i) and excluded (n_e).

	Female longevity			Pre-oviposition period		
Host plant	*cv*	n_i	n_e	*cv*	n_i	n_e
Tomato	0.54	21	2	-	0	0
Bean	0.41	4	0	0.92	3	0
Cucumber	0.48	4	2	-	0	0
Eggplant	0.45	7	0	0.83	3	0
Tobacco	0.39	6	0	-	0	0
Gerbera	0.55	9	4	-	0	0
Sweet pepper	0.76	14	0	-	0	0
All host plants	0.56	69	8	0.88	6	0
Kruskal-Wallis test	P=0.0640, n=69			P=0.827, n=6		

Variation in fecundity and oviposition frequency

The relationship between *cv* and temperature was studied for each host plant separately. From visual inspection of the data it was concluded that only the linear model should be tested. No significant regression was found for the *cv* of fecundity on four host plants (α=0.05). Of the four tested for mean oviposition frequency during a lifetime only on tomato *cv* increased linearly with temperature (α=0.05), but r^2 was very low (0.348, data not shown). Therefore it was concluded that a relationship with temperature was absent. Table 40 shows the results. Data on other host plants were also used but are not given separately in the table.

A significant host plant effect was found, due to the high *cv* on sweet pepper. The *cv* of fecundity is in general higher than that of oviposition frequency, because fecundity is a combination of oviposition frequency and longevity which both vary among individuals.

Table 40. Mean coefficient of variation among individuals (cv) of fecundity and mean oviposition frequency during a lifetime and number of observations included (n_i) and excluded (n_e).

	Fecundity			Oviposition frequency		
Host plant	cv	n_i	n_e	cv	n_i	n_e
Tomato	0.64	22	3	0.39	17	3
Bean	0.44	3	3	0.81	1	2
Cucumber	0.61	3	2	0.51	5	0
Eggplant	0.47	6	1	0.29	6	0
Tobacco	0.49	6	0	0.61	6	0
Gerbera	0.54	4	4	0.24	4	4
Sweet pepper	1.41	8	1	0.97	10	1
All host plants	0.71	55	15	0.52	52	9
Kruskal-Wallis test	P=0.00166, n=55			P=0.000231, n=52		

DISCUSSION

Most studies on life-history parameters of the greenhouse whitefly have focused on the relationship to temperature and host plants. Almost all experiments have been conducted at sub-optimal temperatures. Lower threshold and upper lethal temperatures were often obtained on one host plant species only. The same values were used for the other host plants in order to obtain realistic tails of the curves.

Few experiments have been done to study other factors, such as light intensity, air humidity or whitefly density. Weber (1931) studied the effect of humidity on immature mortality and found lowest mortality at 70-80 % R.H.. He also measured oviposition frequency in the dark, which was low compared to the oviposition frequency at daylight conditions. Hussey & Gurney (1959) did not find differences in oviposition at different light intensities or daylengths. Van Boxtel (1980; also in van Boxtel et al., 1978) noted a lower oviposition and longevity in winter than in spring, but also host plant quality played a role in his experiments. All these studies are qualitative and no attempt has been made to quantify the relationship between oviposition and light intensity.

The effect of whitefly density on immature mortality and oviposition frequency was studied by Xu Rumei (1983; also in Xu Rumei et al., 1984) and Yano (1988; also in Yano, 1989). High whitefly densities were shown to result in higher immature mortality and lower oviposition. Xu Rumei (1983) found an increase in mortality during the egg-L2 stage above densities of 8 eggs/cm^2, and during the L3-pupal stage between 0 and 3 (L3) larvae/cm^2 on bean. However, Yano (1988) did not find a significant increase of immature mortality up to a density of 30 eggs/cm^2 on tomato.

Xu Rumei (1983) found a decrease in oviposition frequency for densities above 3.6 adults/cm^2 on bean. However, Yano (1988) did not find a significant decrease below densities of 10 adults/cm^2 on tomato, despite a high variation in oviposition frequency at low densities. Such densities are only obtained well beyond the economic

damage threshold, and will not be found in the greenhouse because control measures will have been taken.

Not all studies on life-history parameters describe how these parameters and *cv* values were calculated. In a number of cases the original protocols of the experiments were available so that they could be (re)calculated according to the proper method. Information needs to be given on variation (minimum and maximum value, coefficient of variation) and number of replicates, as well as host plant variety and whitefly origin. This information is often lacking, thus making interpretation difficult (see appendices of van Roermund & van Lenteren, 1992).

From some studies it was not always clear whether mean longevity and development rate were calculated as arithmetic mean or 50 % point. Mean oviposition frequency during a lifetime was calculated by one of three methods: fecundity divided by longevity for each female and then averaged over all females; total number of eggs on a particular day divided by total number of still living females on that day and then averaged over all days (maximum longevity); and the sum of fecundity of all females divided by the sum of longevity. These three methods lead to the same result provided oviposition is constant during ageing. But if oviposition decreases during ageing, the first method overestimates and the second method underestimates mean oviposition frequency.

When multiplying the oviposition frequency of Table 36 with the longevity of Table 32, the result is usually higher than the fecundity of Table 35. The first method to calculate mean oviposition frequency was obviously more frequently used.

In studies on the change in oviposition during ageing, oviposition frequency was calculated per still living female or per introduced female. The disadvantage of the calculation per introduced female is that two life-history parameters, oviposition and longevity, are combined and can not be derived from these data anymore. The best method is to average the mean oviposition frequency over all still living females for each day. Variation among individuals has to be calculated for each day as well, because the number of replicates (whiteflies) decreases in time.

In studies on sex ratio, individuals have to be sexed just after emergence from pupa. In some studies, however, an adult population was sampled from host leaves, which is not satisfactory because more females will be sampled because longevity is higher in females than in males. In this way two life-history parameters, sex ratio and longevity, are mixed and can not be derived from such a sample separately. It is also possible that differences in behaviour between the sexes affect the sex ratio in the sample.

The coefficients which describe each life-history parameter in relation to temperature on a host plant will be used as inputs in a simulation model of the population dynamics of greenhouse whitefly. This model explains population dynamics and host plant performance by integration of individual life-history parameters. The effect of each life-history parameter will be evaluated and is of importance in plant resistance breeding. A preliminary version of the model was published by Hulspas-Jordaan & van Lenteren (1989) and Yano et al. (1989a and b).

The model will be used as a submodel in a simulation model of the tritrophic interaction between host plant, greenhouse whitefly and the parasitoid *Encarsia formosa* (Chapter 10). The model will help to gain better insight into the complex tritrophic system which is essential to understand whether biological control is feasible, particularly when new crops and other environmental factors are involved. The model will be used to evaluate timing and number of parasitoid release.

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Chapter 9

Life-history parameters of the greenhouse whitefly parasitoid *Encarsia formosa* as a function of host stage and temperature

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.

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. *E. 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 satisfactory 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 *E. 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 *E. 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.

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 *E. 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 the appendices of van Roermund & van Lenteren (1992), 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):
$$Y = a * \{ \exp(b*(X-d)) - \exp(b*(e-d)-(e-X)/c) \}$$

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

These models are described in Chapter 8. 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.

RESULTS

LIFE-HISTORY PARAMETERS

E. 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 Chapter 8. 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.

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 (Chapter 8).

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).

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

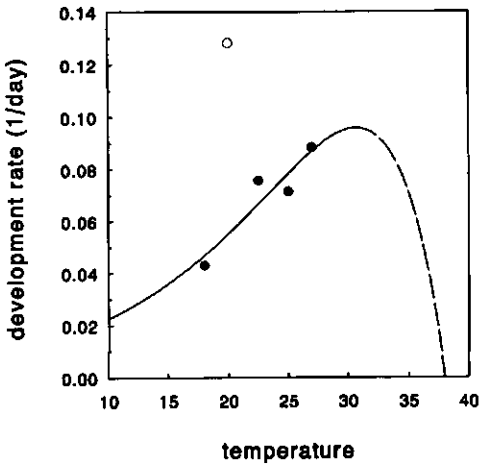

Figure 1. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the first larval stage of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

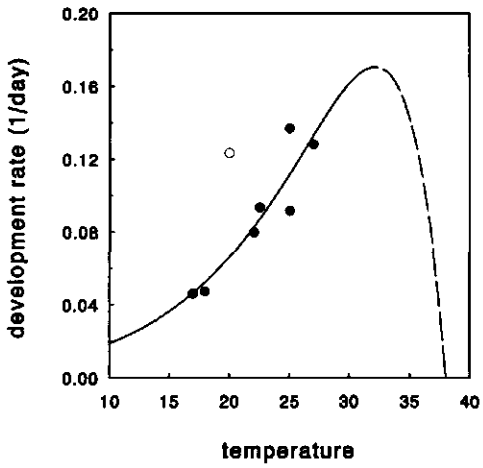

Figure 2. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the second larval stage of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

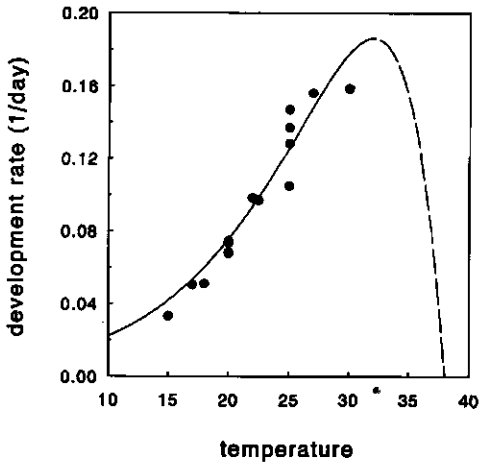

Figure 3. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the third larval stage of the greenhouse whitefly and temperature.

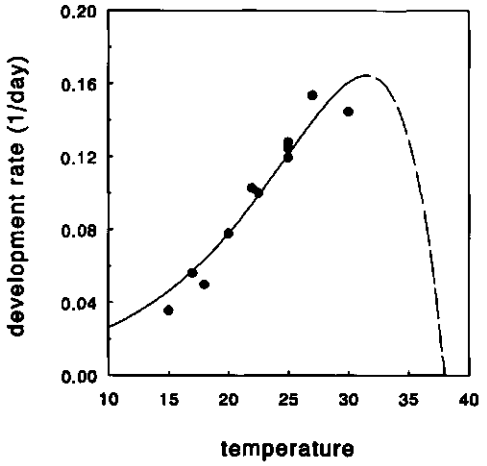

Figure 4. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the fourth larval stage and prepupa of the greenhouse whitefly and temperature.

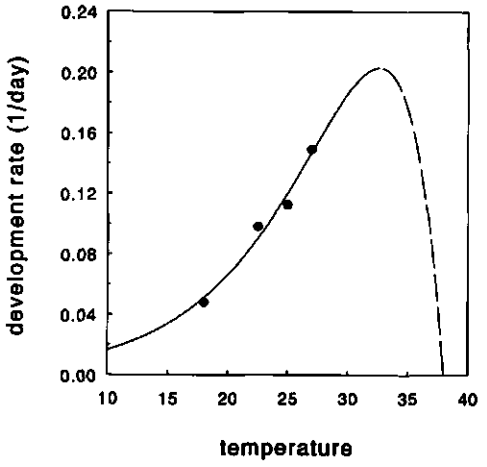

Figure 5. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in the pupa of the greenhouse whitefly and temperature.

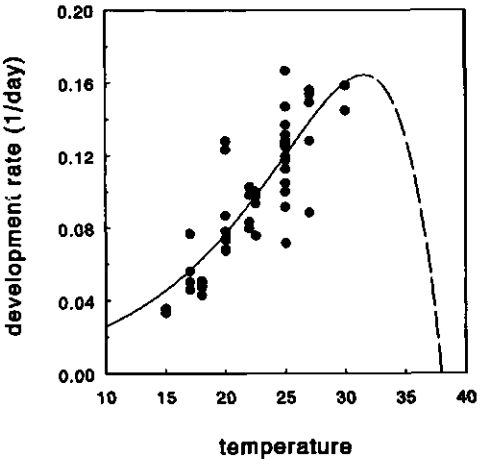

Figure 6. Relationship between the development rate (1/day) of the white stage of *Encarsia formosa* in all immature stages of the greenhouse whitefly and temperature.

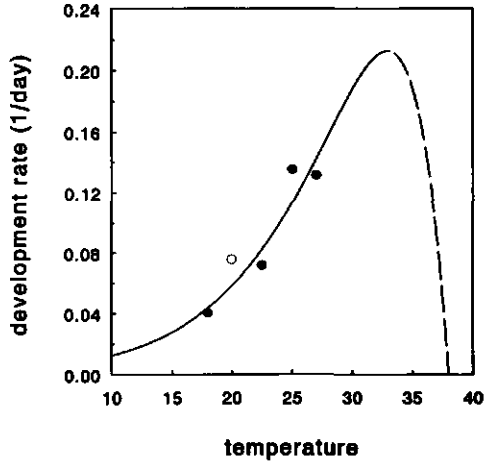

Figure 7. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the first larval stage of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

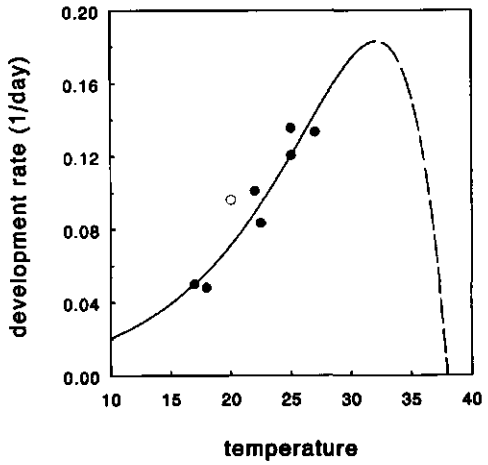

Figure 8. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the second larval stage of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

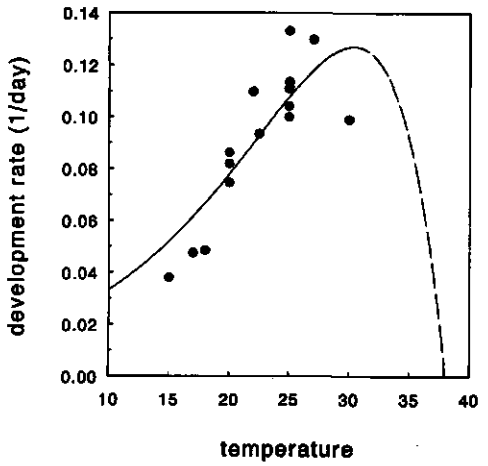

Figure 9. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the third larval stage of the greenhouse whitefly and temperature.

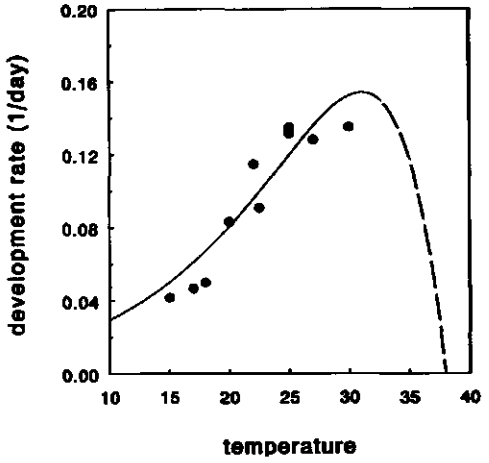

Figure 10. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the fourth larval stage and prepupa of the greenhouse whitefly and temperature.

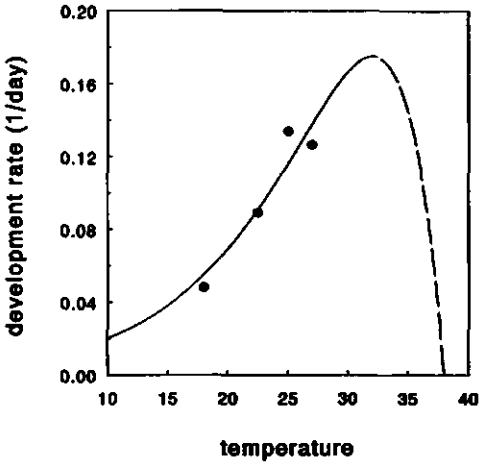

Figure 11. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in the pupa of the greenhouse whitefly and temperature.

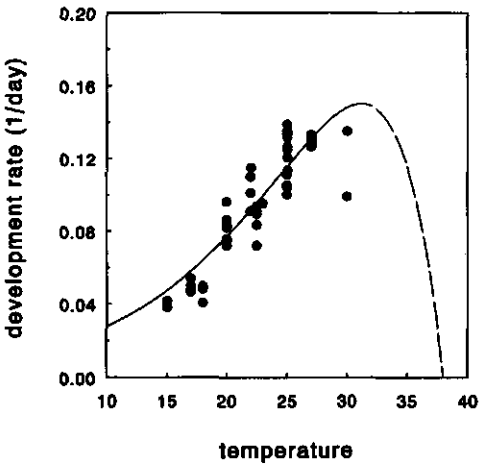

Figure 12. Relationship between the development rate (1/day) of the black stage of *Encarsia formosa* in all immature stages of the greenhouse whitefly and temperature.

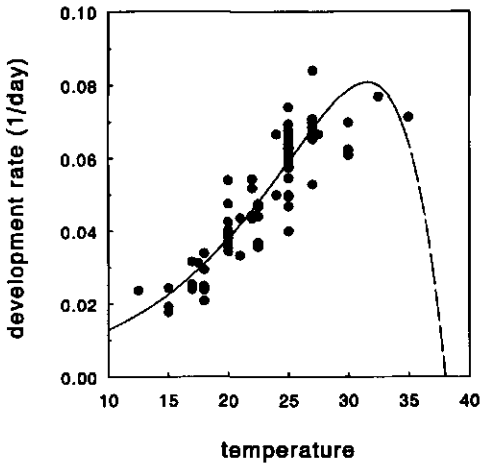

Figure 13. Relationship between the development rate (1/day) of the total immature stage of *Encarsia formosa* in all immature stages of the greenhouse whitefly and temperature.

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 1-3 and in Figures 1-13.

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.

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

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

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.

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).

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.

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.

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

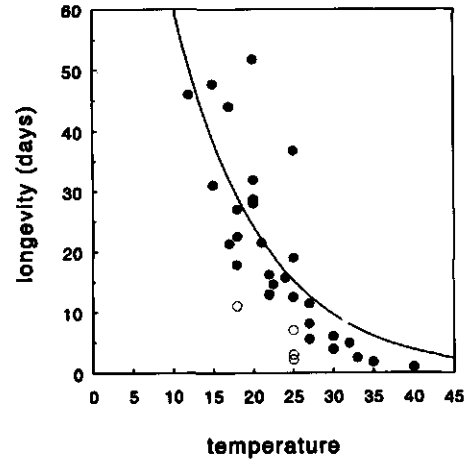

Figure 14. Relationship between the longevity (day) of *Encarsia formosa* and temperature in the presence of greenhouse whitefly immatures. Open dots represent data points excluded from the regression.

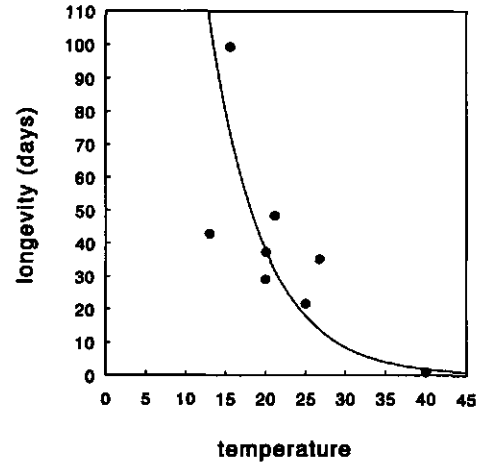

Figure 15. Relationship between the longevity (day) of *Encarsia formosa* and temperature in the absence of greenhouse whitefly immatures and in the presence of honey or honeydew.

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

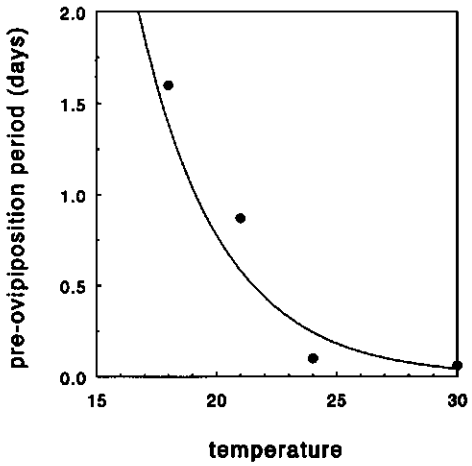

Figure 16. Relationship between the pre-oviposition period (day) of *Encarsia formosa* and temperature in the presence of greenhouse whitefly immatures on tomato.

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.

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

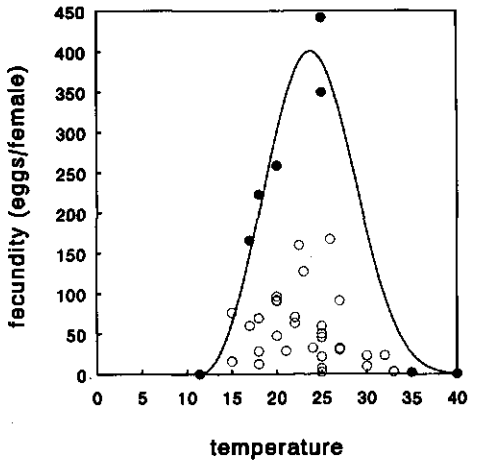

Figure 17. Relationship between the fecundity (egg/female) of *Encarsia formosa* in greenhouse whitefly immatures of third larval stage or up and temperature. Open dots represent data points excluded from the regression.

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*.

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

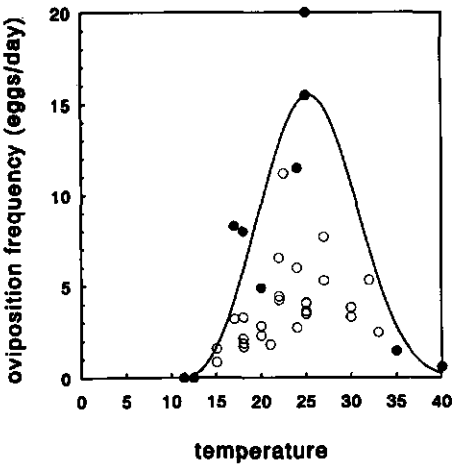

Figure 18. Relationship between the oviposition frequency (egg/female/day) of *Encarsia formosa* in all immature stages of the greenhouse whitefly and temperature. Open dots represent data points excluded from the regression.

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 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.

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.

Variation in 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 Kruskal-Wallis test (α=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 (α=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 (α=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* values 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 (Kruskal-Wallis test, α=0.05); the *cv* values are relatively low.

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.

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
Kruskal-Wallis test	P=0.953, *n*=27		P=0.446, *n*=6		P=0.973, *n*=43	

Variation in 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 (α=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 (Kruskal-Wallis test, α=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
Kruskal-Wallis test	P=0.798, *n*=25		

Variation in 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 (α=0.05) when data at temperatures below 35°C were included (α=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 (α=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 of Tables 9 and 10 were included except those of Kajita (1979) obtained at 35 and 40°C. Secondly, data not used in the regression were included 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 (Kruskal-Wallis test, α=0.05), the mean *cv* can be calculated from all the data.

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 Tables 9 and 10.

	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
Kruskal-Wallis test	P=0.0643, *n*=31		P=0.490, *n*=27	

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 parasitism 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 parasitism between shaded and unshaded plants. Burnett (1948) noted a higher dispersion in light.

As discussed for the greenhouse whitefly (Chapter 8), 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*. 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*, the oviposition rate will be 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 (Chapters 5, 6 and 7).

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 (Chapter 10). 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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Chapter 10

Biological control of greenhouse whitefly with the parasitoid *Encarsia formosa* on tomato: an individual-based simulation approach

ABSTRACT

Biological control strategies of greenhouse whitefly with the parasitoid *E. formosa* were studied with a simulation model of the parasitoid-host interaction in a crop. The model is based on developmental biology of both insect species and on the searching and parasitization behaviour of individual parasitoids, in relationship to host plant characteristics and greenhouse climate. The model includes stochasticity and spatial structure which is based on location coordinates of plants and leaves. The simulated population increase of greenhouse whitefly in the absence or presence of parasitoids agreed well with observed populations in a tomato crop. Whiteflies were suppressed rather than regulated by the parasitoids at extremely low densities (<0.3 unparasitized pupae per plant), but did not become extinct. Percentage black pupae fluctuated between 40 and 70%. According to the model, the parasitoid adults reached high densities of 7.4 per plant, but due to the low whitefly density not more than 1% of the parasitoids was searching on infested leaflets. The degree of whitefly control was strongly affected by variation in giving up time (GUT) of the parasitoids. When variation in GUT was excluded in the model, the whitefly population became almost extinct. Other important parameters of the parasitoid which strongly influenced the level of control were the walking speed and walking activity, the probability of oviposition after encountering a host, the ratio of search times on both leaf sides, and the longevity. The combined effect of these important attributes of a parasitoid can be tested with the model. When comparing success of *E. formosa* on different crops, attention should be focused on the same parameters, plus the whitefly development duration and the number, size and production of leaves in the canopy. The model can be used to evaluate a number of release strategies on several crops and under various greenhouse climate conditions.

INTRODUCTION

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae), is a very common, highly polyphagous pest insect. Adults and immatures are phloem feeders and can contribute to reduced productivity by directly consuming transportable carbohydrates, nitrogen and other nutrients. Furthermore, they produce large amounts of honeydew on the leaf, on which occasionally sooty moulds develop, thus reducing leaf photosynthesis (Byrne et al., 1990). Both damage components reduce crop yield, as observed for tomato by Lindquist et al. (1972). More important is the economic damage on fruits and ornamentals due to the residue of sticky honeydew. Hussey et al. (1958) measured significant yield reduction on tomato at an average pest density (between start of pest and final picking of fruits) of 22 scales/cm^2 leaf or more, and an economic damage at 6 scales/cm^2 or more. According to Helgesen & Tauber

(1974), a much lower density of 0.3-0.7 scales/cm^2 leaf is commercially acceptable on poinsettia.

Whiteflies are a major economic problem in greenhouse crop production. Non-chemical control methods have been studied, such as resistance breeding (de Ponti et al., 1990) and biological control (Noldus & van Lenteren, 1990). Biological control with the parasitoid *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) is now used commercially in 90% of the tomato growing areas in the Netherlands and in many other countries (van Lenteren & Woets, 1988). The parasitoid was already 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. In tomato greenhouses today, on average one *E. formosa* is released per plant at two-week intervals. When adult whiteflies are observed, release rates are increased to two per plant at one-week intervals until about 80% black pupae are observed. This usually takes three introductions (Koppert Biological Systems, pers. comm.).

As yet there is no satisfactory explanation as to why similar parasitoid introduction rates cannot be applied successfully on other important greenhouse crops, such as cucumber and gerbera. It is hypothesized that the following host plant differences might be responsable: (1) the quality of the host plant for the whitefly, which determines the population development of the pest and (2) the properties of the host plant for the parasitoid, which influence the searching behaviour and the parasitization efficiency. Which of these effects is most important on a greenhouse scale can only be evaluated after integration of all relevant processes.

The present study aims at integrating existing knowledge on the major processes known to affect the whitefly-parasitoid interaction in a crop by means of a simulation model. The goal is to better understand the tritrophic system host plant- greenhouse whitefly- *E. formosa* which can help to explain failure or success of biological control. The model is based on developmental and behavioural aspects of individuals in relationship to host plant characteristics and greenhouse climate. The model consists of several submodels each simulating a subprocess, for example the dispersal behaviour of adult whiteflies and parasitoids from leaf to leaf, the foraging behaviour of the parasitoids on leaves, and the development of the whitefly and parasitoid populations. The submodel of the parasitoids' foraging behaviour is explained in detail in Chapter 5. Demographic input data for the submodels of population development of both insects can be found in Chapters 8 and 9.

Mathematical models have been developed to study the greenhouse whitefly- *E. formosa* interaction (Burnett, 1958; Varley et al., 1974; Yamamura & Yano, 1988; Yano, 1989a,b; Baumgärtner & Yano, 1990; Xu Rumei, 1991a,b). The present model is, however, unique in that it is an individual-based model which simulates local searching and parasitization behaviour of a large number of individual parasitoids in

a whitefly-infested crop. The model includes stochasticity and spatial structure which is based on location coordinates of plants and leaves. In many other parasitoid-host models one parameter for searching efficiency has been used which is difficult to determine. Here, searching efficiency has been split up in several components, which can be independently measured in laboratory studies. Individual-based models are a necessity when local interactions and stochasticity are important (Huston et al., 1988; De Angelis & Gross, 1992; Judson, 1994).

This study describes the results obtained with the individual-based model of tomato- whitefly- *E. formosa*. With the model, we are able to (1) explain the ability of *E. formosa* to reduce whitefly populations in greenhouses on crops like tomato, (2) improve introduction schemes of parasitoids for crops where control is more difficult to attain and (3) predict effects of changes in cropping practices (e.g. greenhouse climate, choice of cultivars) on the reliability of biological control.

THE SIMULATION MODEL

Development from one insect stage to the next

In models for a population of identical, synchronized individuals, development can be treated as a single variable. Insect populations are characterized by several stages of development, which may occur simultaneously. Each stage then requires separate simulation. In addition, individuals of one development stage are not identical and variation in duration of development (dispersion) occurs. In our model, the so-called boxcar train technique was used for simulation of development, which is able to handle all possible development stages simultaneously. Before the simulation starts, the development axis of one stage is broken up into a number of classes or boxcars, each with identical development duration. Such a set of boxcars is called a boxcar train and represents one development stage. Several separate boxcar trains will be chained, for instance, one to allow for the egg stage, one for the first larval stage, and so on.

Development is mimicked by transferring individuals from one boxcar to the next. Mortality is mimicked by deleting individuals from the boxcars. Dispersion depends on the amount and timing of the transfer process. If every now and then the whole content of each boxcar is shifted to the next, dispersion does not occur (escalator boxcar train). If during every time step a constant fraction of each boxcar is shifted to the next, a fixed dispersion occurs, which depends on the number of boxcars (fixed boxcar train). Several experimental data sets of insect development show evidence that the development duration of a certain stage and the dispersion are not equally influenced by e.g. temperature, and so the relative dispersion also varies. The fractional boxcar train allows the dispersion between individuals to be altered during the simulation process. Every now and then a fraction of the contents of each boxcar is shifted to the next one. Mathematics for and computer programs of these methods can be found in Goudriaan & van Roermund (1993). Input for the simulation is the observed mean development duration, the relative dispersion (or coefficient of

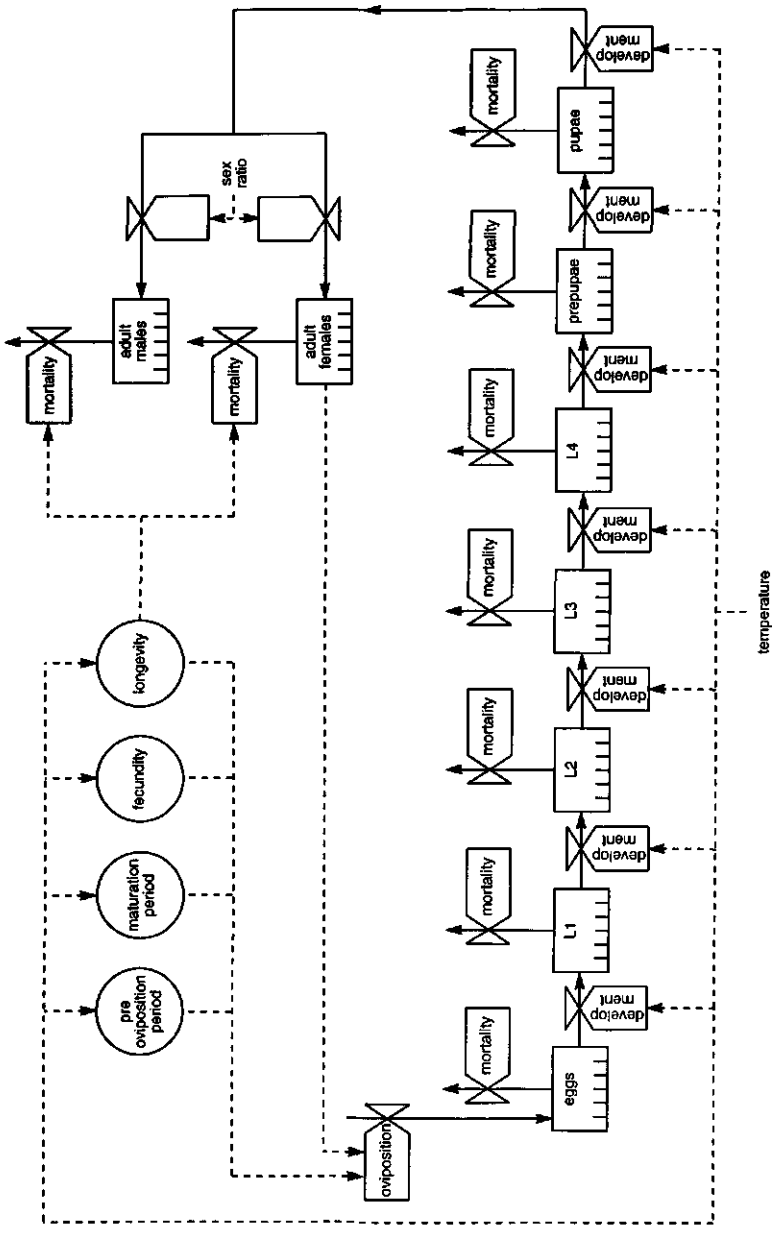


Figure 1. Relational diagram for the population growth of greenhouse whitefly. The state variables or integrals (insect numbers) are presented within rectangles, the rates of change within valve symbols, auxiliary variables within circles. The flow of material is presented by solid arrows and the flow of information by dotted arrows. Small bars in a rectangle indicate a series of integrals (boxcar train).

variation, *cv*: SD/mean) and the mortality of each development stage. All these variables may depend on for instance temperature.

Whitefly population model

Females of the greenhouse whitefly (*T. vaporariorum*) lay their eggs on the underside of the plant leaves. The first instar larva (L1) is initially mobile, and settles down after a few hours and inserts its mouth parts into the leaf. Subsequently, the larva moults into the second (L2), and third (L3) instar, which differ in size. The next moult results in the last instar, which is initially flat and translucent, like the previous instars (fourth instar larva, L4). As the last instar larva develops, it thickens and becomes white-coloured with waxy spines (prepupa). During the last phase of its development the red pigmented eyes of the adult can be seen (pupa). Many studies use different terms to describe these phases (for terminology, see Chapter 8).

The model of whitefly population growth is presented in the relational diagram of Figure 1. It is an explanatory state-variable model (Rabbinge et al., 1989), also referred to as an *i*-state distribution model (DeAngelis & Gross, 1992). State and rate variables are distinguished and mathematical expressions are given to calculate the value of each rate variable from the state of the system. The state variables are updated by rectilinear integration of the rate variable over short time intervals. The program structure of the model (and other submodels described in this paper) is conform the concepts of van Kraalingen (1993).

Each immature whitefly stage is described by a fractional boxcar train. The number of boxcars representing one stage varies between 3-10, depending on the dispersion to be mimicked. The development rate (reciprocal of development duration) of each stage is affected by temperature. Observed data on development rate, its relative dispersion and mortality of the immature stages of greenhouse whitefly on tomato were used as input and can be found in Chapter 8.

Pupae develop into adult females and males, with ratio 1:1 (Chapter 8). Adult females are divided into many age classes (50), because oviposition strongly depends on age. Aging of adults is mimicked by the escalator boxcar train. The observed mean longevity and the dispersion (*cv*) are used as input to calculate mortality of each age class in such a way that the survivalship curve fits to a decreasing cumulative normal distribution. This decreasing S-curve was observed for greenhouse whitefly, with mean longevity depending on temperature (Chapter 8). Ageing of adult males is described by a fractional boxcar train with 2 boxcars, with mean longevity and the dispersion as input. Longevity of greenhouse whitefly males is about half as long as for females (Chapter 8).

For greenhouse whitefly females, the oviposition frequency is zero during the pre-oviposition period. During ageing it increases linearly with maturation to a maximum. This level remains constant until mean longevity is attained and then decreases linearly to zero at maximum longevity (Chapter 8). This oviposition curve is simulated by using the observed pre-oviposition period, the maturation period, the mean and maximum longevity and the mean fecundity, which are all affected by

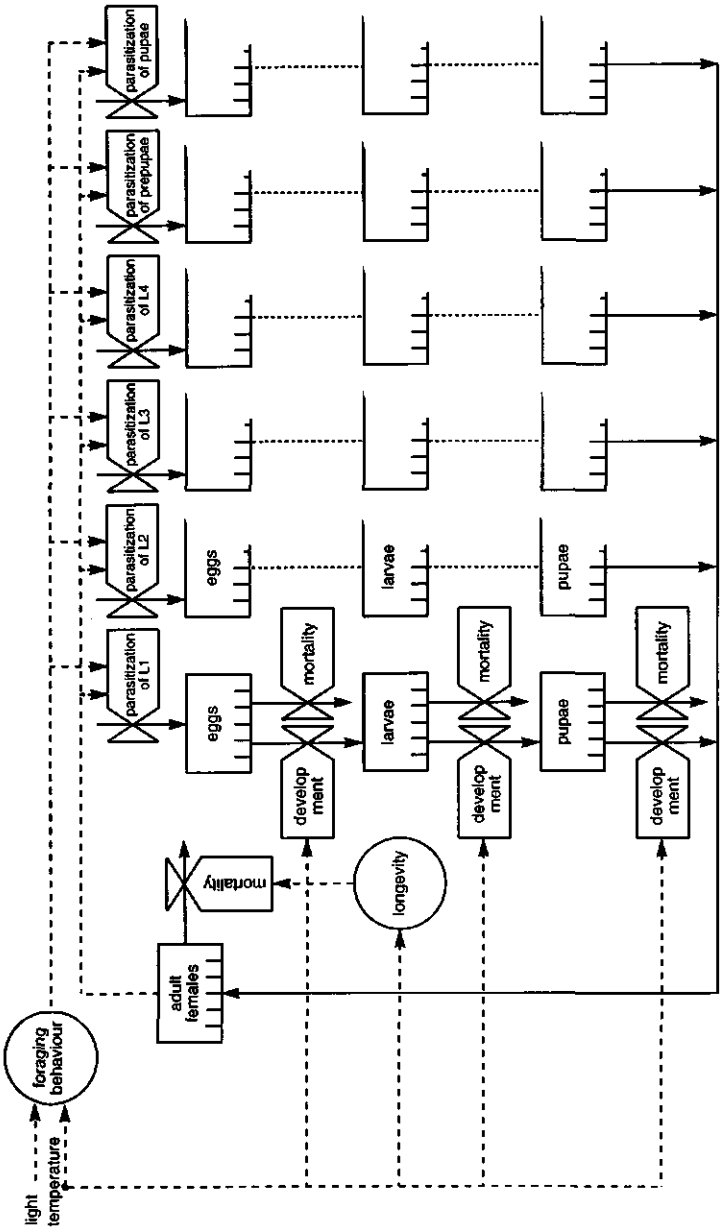


Figure 2. Relational diagram for the population growth of *E. formosa*. Symbols are explained in Figure 1.

temperature. With this curve, the oviposition rate of one female of a certain age class is derived and subsequently the total oviposition rate of all females is computed.

The model is initialized by introduction of adult females. Temperature is the driving variable. The time step of the model is chosen to be 0.05 day (1.2 h). This is about one-tenth of the smallest time-coefficient (residence time of individuals in one boxcar), which is needed for accurate numerical integration. Accuracy was tested by comparing the simulation results with those obtained at a time step double or half in size.

Parasitoid population model

E. formosa is a solitary, larval parasitoid of whitefly. Males are rarely observed. Females produce daughters parthenogenetically. They lay one egg per host, preferably in the third, fourth and prepupal stages of the greenhouse whitefly (Nell et al., 1976). The first, second and pupal stages are less preferred for oviposition. The egg stage of the parasitoid develops successively into three larval stages. During these stages, the parasitized whitefly immature is translucent and parasitization can only be observed after dissection ('white' stage). The *Encarsia* larva can pupate only when the immature whitefly reaches the fourth instar. After pupation of the parasitoid larva, the immature greenhouse whitefly turns black and parasitism can easily be seen from the outward appearance of the whitefly ('black' stage).

The model of parasitoid population growth is presented in the relational diagram of Figure 2. The model is of the same type as the whitefly population model. In the model, the three larval stages are taken together, because life-history data for each separate stage are lacking. Each immature parasitoid stage (egg, larva and pupa) is described by a fractional boxcar train. Observed data on development rate, its relative dispersion and mortality of the egg+larval ('white') stage and of the pupal ('black') stage of *E. formosa* were used as input and can be found in Chapter 9. The development duration of the egg stage is about the same as that of the larva (three larval stages together). Dispersion and mortality are assumed to be the same as well. A distinction is made between immature parasitoid individuals of the same stage based on the whitefly stage originally parasitized, because the observed development duration and mortality of *E. formosa* immatures depended on the whitefly stage which was originally parasitized (Chapter 9). Thus, 3x6 fractional boxcar trains were used for simulation of the immature parasitoid stages.

Ageing of adult females and mortality is simulated in the same way as for whitefly adult females. Input is the adult longevity in the presence of whitefly immatures, which is affected by temperature (Chapter 9). A different appoach is followed for oviposition frequency. For *E. formosa*, oviposition can be assumed to remain constant during ageing. In Chapter 9 it was found that the relationship between oviposition frequency (or fecundity) and temperature of *E. formosa* was very weak. For parasitoids, oviposition does not depend on temperature alone, and host density, host plant effects and parasitoid behaviour also play an important role.

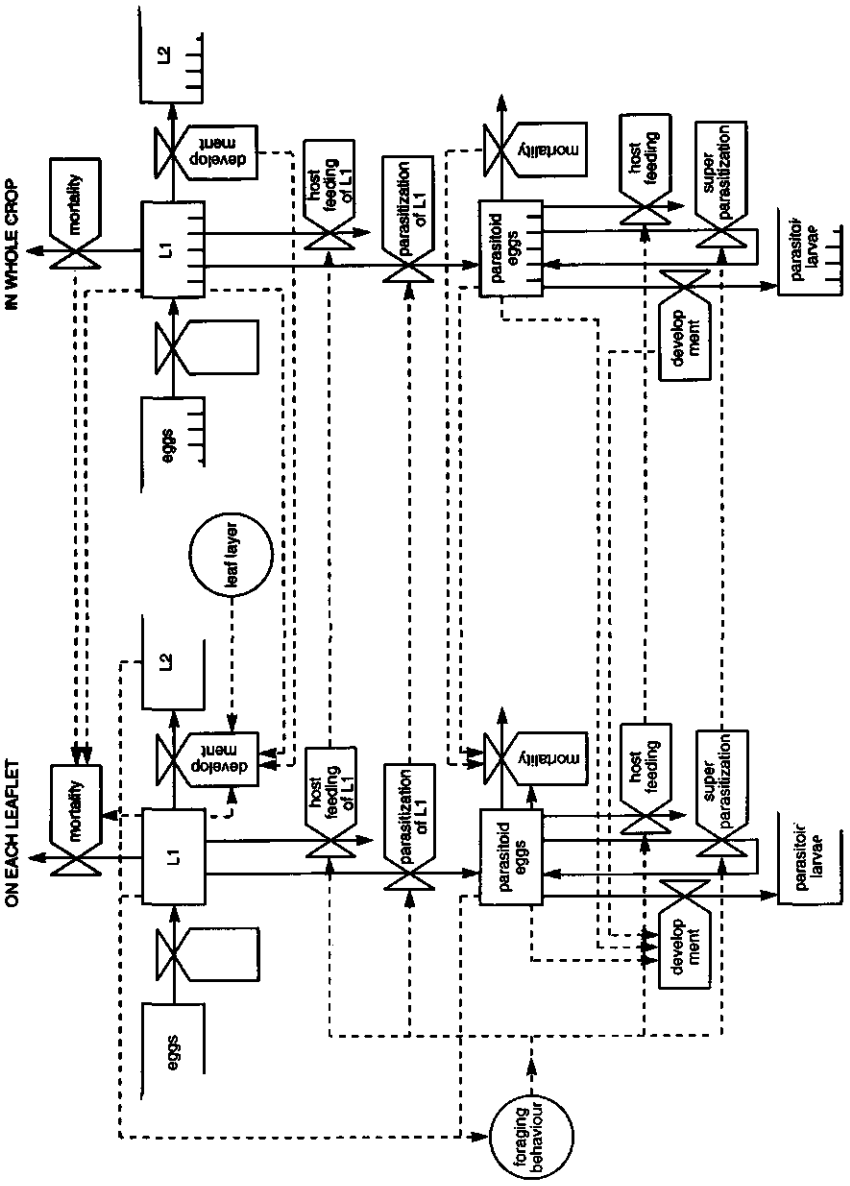


Figure 3. Relational diagram for the population growth of greenhouse whitefly and *E. formosa* with details on the interaction between host and parasitoid. Symbols are explained in Figure 1.

Therefore, oviposition is simulated by a separate model of the foraging behaviour of the parasitoid. Maximum daily oviposition of one female was simulated on a heavily infested tomato leaflet (480 hosts with stable age distribution) during a 16 h daylength. Details of this model can be found in Chapter 5. The parasitoid started with an egg load matured during the preceding night (4.9 eggs at 25°C). The simulations yielded maximum daily oviposition rates of 5.55, 10.26, 13.11 and 15.83 at 15, 20, 25 and 30°C respectively. The percentage of ovipositions in L1, L2, L3, L4, prepupae and pupae were 5.0, 4.7, 37.8, 38.7, 11.7 and 2.0 % respectively at 25°C.

These simulation results are used as input in the population model to simulate the *maximum* population growth of *E. formosa* at a constant temperature. The model is initialized by introduction of adult females. Temperature is the driving variable. The time step is chosen to be 0.05 day (1.2 h) for accurate numerical integration.

Combined host and parasitoid population growth

The final model combines both population models and simulates the population dynamics of whitefly and parasitoid during a growing season of a crop. The interaction between both populations in the greenhouse is realized by the local foraging behaviour of the parasitoid adults on leaves. New parasitoids are 'born' after parasitizations, while the whitefly immatures which were parasitized, die. Host feeding of parasitoids kills additional whitefly immatures. The foraging behaviour and the resulting parasitizations and host feedings on leaves depend to a large extend on local host density. After emergence, whitefly adults usually disperse over short distances before settling on a leaf, on which oviposition continues for days (Noldus et al., 1986a). As a result, whiteflies (and many other pest insects) show a strongly clustered distribution over plants and leaves (Ekbom, 1980; Eggenkamp-Rotteveel Mansveld et al., 1982a,b; Yano, 1983; Noldus et al., 1986a,b; Xu Rumei et al., 1989; Xu Rumei, 1991a; Martin et al., 1991).

Whitefly and *E. formosa* disperse in the canopy by flying from leaf(let) to leaf(let). Walking from one leaf(let) to the other is hardly observed. Therefore, the leaf(let) is chosen as the spatial unit. In the model, the canopy is divided into plants with a certain number of leaves. For tomato, each leaf is divided into seven leaflets. The coordinates of each plant, leaf and leaflet represent their location in the canopy. All immature stages of whitefly and parasitoid can be considered sessile. To simulate the local interaction between parasitoid and host properly, the model simulates the spatial distribution of all whitefly and parasitoid stages in the canopy, based on flight behaviour of individual adults, subsequent oviposition and immature development on leaflets, and on production of new leaves in the top of the plants. The model of combined whitefly and parasitoid population growth is presented in the relational diagram of Figure 3 and is explained in the following sections. Only details on the interaction of the two populations are given. The interaction between parasitoid and host on infested leaflets is simulated by an individual-based or *i*-state configuration submodel (DeAngelis & Gross, 1992). The whitefly and parasitoid populations in the

whole crop are simulated by variable-state submodels (see population models for whitefly and parasitoid).

On each infested leaflet (Figure 3, left) and for the whole canopy (Figure 3, right), the number of each development stage of whitefly and parasitoid are simulated simultaneously: adult females, adult males, eggs, all unparasitized whitefly stages (from L1 to pupa), parasitized hosts (originally parasitized as L1, L2,...,pupa) which contain a parasitoid egg, larva or pupa, and dead hosts or empty pupal cases. The location of the adult parasitoids in the canopy is kept track of as well. The numbers of individuals on each infested leaflet are integers (whole numbers), whereas those for the whole canopy are reals (broken numbers). At each time step, the numbers on each leaflet are added up and compared with those for the whole crop to check for simulation errors. In the submodel of error check, a difference of only 10 individuals per stage was allowed.

Foraging behaviour of the parasitoid

Parasitoid adults fly from leaflet to leaflet during the day in the model. The infested leaflets can be considered as local host patches. The 'giving up time' (GUT) of each parasitoid on an uninfested leaflet is drawn from an exponential distribution with median and mean of 18.6 and 26.8 min respectively (Chapter 3). In the model, the parasitoid leaves when this time is reached. On infested leaflets, the foraging behaviour and the resulting number of parasitizations and host feedings of each parasitoid are simulated simultaneously. Changes in egg load of each parasitoid and in host numbers on each of these leaflets are adapted immediately (Figure 3, left). A detailed description of this stochastic submodel can be found in Chapter 5. The time-step of this submodel is only 0.00005 day (4.32 s).

E. formosa forages on a leaf by walking randomly on both leaf sides. Therefore the walking pattern does not have to be described for the simulations, but the calculation of the encounter rate suffices (Skellam, 1958). Hosts are only present on the lower leaf side. After each encounter with an unparasitized or parasitized whitefly larva, prepupa or pupa, the parasitoid stays another GUT on the leaflet. Median GUT is again 18.6 min and is doubled when one or more parasitizations occurred on the leaflet (Chapter 3). When no hosts are encountered within the simulated GUT, parasitoids fly to other leaflets. The parasitoid does not show an arrestment effect after encountering whitefly eggs (Sebestyen, 1995). This was also assumed in the model when encountering whitefly adults. From Hussey et al. (1958) and Parr et al. (1976) it was estimated that 75 whitefly larvae, pupae or adults produce a film of honeydew on the leaflet and on the leaflet below. Median GUT on such leaflets is 99.6 min (Chapter 3).

The median time for changing from one leaf side to the other (TUC) was initially 11.6 min, and dropped to 5.7 min after both leaf sides had been visited (Chapter 3). The first oviposition in an unparasitized host lead to longer TUC's on the lower leaf side. In the model, TUC is also drawn from exponential distributions.

Mortality caused by the parasitoid

The parasitization and host feeding rates of all individual parasitoids, simulated using the small time step, are accumulated during each large time step of 0.05 day for population growth (development, mortality and change of abiotic factors). These rates are then used in the whitefly and parasitoid submodel to adapt the total whitefly and parasitoid population in the whole crop (Figure 3, right). In the whitefly submodel, the sum of both parasitization and host feeding rate is the mortality rate caused by parasitoids. In the parasitoid submodel, the parasitization rate is the birth rate of new eggs and the host feeding rate on parasitized hosts is the mortality rate caused by parasitoids. Superparasitization does not change the number of parasitoid immatures of *E. formosa*, because only one parasitoid can develop within a host.

E. formosa is very selective in accepting hosts for oviposition or host feeding. In about 50% of encounters with the most preferred stage, the host is rejected (Nell et al., 1976). Therefore, it is assumed in the model that the parasitoids only accept healthy hosts which are not dying (by a natural cause) in the same time-step of 0.05 day. Even if this assumption is not correct, the numerical consequences for the model output are negligible, because the natural mortality of immature whitefly stages is very low. Thus, in the whitefly and parasitoid submodels the relative mortality rate of each development stage in the whole canopy (by natural cause and caused by parasitoids) is the sum of both relative mortality rates.

Change in number of individuals on each leaflet

Mortality and development of all development stages in the whole canopy is simulated in the whitefly and parasitoid submodels by the boxcar train method (Figure 3, right). Subsequently, the number of individuals per stage on each leaflet is updated proportionally for natural mortality and development, in the submodel of spatial distribution (Figure 3, left). Only those individuals not accepted by parasitoids for oviposition or host feeding during the same time-step are updated here. Natural mortality of a certain stage is equal in all leaf layers where that stage is present, but the change from one stage to the next only occurs with the oldest individuals of that stage, which are on the lowest leaf layer. The same is done for dead hosts or empty pupal cases falling from the leaves. Their average residence time on the leaf is assumed to be one week.

The proportional correction yields reals (broken numbers) for, for instance, the individuals of a certain stage dying during the time step on a particular leaflet. These numbers are usually far below 1. Therefore, for each leaflet these numbers are rounded off to the nearest integer (whole number) by a method which compares the decimal with a random number between 0 and 1. If that number is higher than the decimal, rounding off occurs to the nearest integer below. Rounding off is sometimes forced to the nearest integer up or below when the rounding off error for dying individuals of that stage, cumulated for all leaflets, becomes larger than 1 individual. The same procedure is followed for individuals developing or falling from the leaf.

The total whitefly oviposition rate in the whole crop is simulated in the whitefly submodel as explained earlier. Then the average oviposition rate for one female is calculated. The oviposition rate on each leaflet is derived from the number of adult females on the leaflet and the average oviposition rate.

Production of new leaves

New leaves develop at the top of the plants. For tomato, the node initiation rate (NIR) depends on temperature only and available carbohydrates or sink-source ratio do not play a role (after three leaves, a truss develops; both are called nodes). In the submodel of plant growth, the equation of Jones et al. (1991) is used:

$$NIR = INIR * f$$

in which INIR is the maximum node initiation rate (0.55 nodes/day at 28°C) and f is the temperature (T) response. The increase to the optimum at temperatures below 28°C is much slower than the decrease above 28°C:

$$\text{if } 12 < T < 28°C, \quad f = 1 - 0.0281 * (28-T)$$
$$\text{if } 28 < T < 50°C, \quad f = 1 - 0.0455 * (T-28)$$

Adult whiteflies only settle in the upper three leaf layers of a tomato crop (Noldus et al., 1985). If during the simulation a new leaf has fully expanded, adult whiteflies on leaf 3 will then be on leaf 4 (counted from the top) and migration occurs to the upper leaf layer of the same plant. Due to development of immatures and leaf initiation at the top, older whitefly stages are situated in the lower leaf layers during the simulation. This was also observed on tomato and cucumber in the greenhouse (Noldus et al., 1985; Yano, 1983; Martin & Dale, 1989; Xu Rumei, 1991a). In the model, as in commercial greenhouses, the side shoots of the tomato plants are pruned and old leaves are removed and kept at the bottom of the plants, because they can bear black pupae. The maximum number of leaves per plant is about 20.

Dispersion of adults

Noldus et al. (1986a) found that young adult whiteflies disperse on average 125 cm from the plant on which they had emerged. About 10% of the whiteflies settled on the plant of emergence. In the submodel of whitefly dispersion, the probability of landing (and settling) on a new plant at a distance r from the source plant is given by the exponential distribution (in all directions):

$$P(r) = \alpha \exp(-\alpha r) / 2 \pi r$$

in which the parameter α describes the decrease of P(r) with r. This probability distribution can be represented by a plane, with its top in the middle (the source plant). Total volume under the plane is 1. It is a continuous distribution, whereas in a

greenhouse the distribution of whiteflies is discrete: they cannot land between two plants. The discrete distribution is derived by dividing the canopy into grids, each with one plant in the center. Thus, grid area is 1 plant-distance^2. The probability of landing in this grid (on the plant) can be represented by the relative volume between grid and plane. This is numerically solved by dividing each grid into 100 (or more) subunits. The probability of landing in the middle of each subunit is approximated by multiplication of P(r) with subunit-area. Summation of all these probabilities yield the probability of landing on the plant.

Based on these probabilities, a plant is selected for each emerging adult female whitefly. Edge effects are solved by mirroring to avoid accumulation of individuals in the outside boundary of the crop. Then, a leaflet is selected randomly in the upper three leaf layers of this plant on which the adult settles. Each emerging adult male joins a female. Thus, dispersion of adults is a stochastic process. For greenhouse whitefly, the parameter α was set to 0.30/plant-distance, which yielded an average dispersion distance of 2.87 plant-distances, which is 1.15 m in a tomato crop. The percentage of whiteflies staying on the plant of emergence was then 15.6%.

E. formosa moves from leaflet to leaflet by flying or hopping, without distinguishing between infested and clean plants or leaves before landing (Noldus & van Lenteren, 1990; Sütterlin & van Lenteren, in prep.). Each time when an adult parasitoid leaves a leaflet, the submodel of parasitoid dispersion follows the same procedure for the selection of a new plant as for whitefly. A new leaflet is selected randomly from all leaf layers on that plant. Landing on the upper or lower leaf side occurs at the same frequency. Thus, parasitoid flight behaviour is also a stochastic process in the model. For *E. formosa*, the parameter α was set to 0.95/plant-distance, which yielded an average flight distance of 1.0 plant-distance (0.4 m in a tomato crop). The percentage of parasitoids staying on the same plant was then 40.5%.

Input data

The model is initialized by introduction of adult whiteflies and their location in the crop. Number of plant rows, plants per row and initial number of leaf layers determine the initial crop size. Parasitoids are introduced as emerging black pupae on paper cards or leaves. Day(s) of release, number of parasitoids per card, number of cards per plant row and between rows are input data for parasitoid introduction. Temperature and light period for each day are the driving variables. For tomato, the light period is the time between sunrise and sunset, because artificial light is not used. All input on time, crop, whitefly, parasitoid, parasitoids' foraging behaviour, temperature and light period are stored in separate data files.

Validation

The simulation results of the whitefly population model were validated with six independent population counts on tomato (var. 'Allround') (de Ponti & Steenhuis, unpubl.; Elzinga, 1982; Joosten & Elings, 1985). In small greenhouse compartments, 100 or 300 one-day-old female whiteflies were released, together with males, on 10 or

15 plants respectively. After about 40, 60 and 80 days, the number of emerged pupae were counted. The temperature was measured 3 or 4 times during a day, and fluctuated between 15 and 35°C.

The final model of the combined whitefly and parasitoid population was validated with data from an experiment in a commercial greenhouse (Eggenkamp-Rotteveel Mansveld et al., 1982a,b). White and black pupae were counted from 1 January until 22 April 1974 (112 days) in a commercial greenhouse with 18000 tomato plants (var. 'Extase') in The Netherlands. During that period, plants increased from 30 cm and six leaves to about 300 cm and 44 leaves, of which only the upper 15-20 leaves were kept on the plant.

Simulations were done for 'patch 12', which was the heaviest infested plot in the greenhouse, consisting of 32 plant rows and 42 plants per row (Eggenkamp-Rotteveel Mansveld et al., 1982b). Five replicates were simulated, because of the stochastic processes. Counted adult whiteflies in the greenhouse fluctuated during the first three weeks, and the highest count of 36 adults was chosen to initialize the model. Observed densities were 1 adult per plant. In the model, one adult female and one male were initialized on a leaflet of 18 plants in the centre of the plot. Parasitoids were released on 23 January, 6 February, 20 February and 6 March (day 23, 37, 51 and 65) as emerging black pupae on cucumber leaves. From the publication, the location of the release sites was not clear. Leaves carried large numbers of black pupae (435-1209) and the number of release-leaves in the whole greenhouse was relatively small. Therefore, in the model all parasitoids were released in the centre of the plot. The release rates for the four introductions in 'patch 12' were 0.97, 2.70, 4.50 and 2.48 parasitoids per plant, respectively. Temperature data of 'Bay 47', measured every two hours, were used for the simulation, because these were measured close to 'patch 12'. Weekly minimum, mean and maximum temperatures are summarized in Eggenkamp-Rotteveel Mansveld et al. (1982a).

Simulations were also validated with counts of the total greenhouse (Eggenkamp-Rotteveel Mansveld et al., 1982a). For this purpose, one twentiest of the whole greenhouse was simulated (900 plants) and all counts were reduced with the same factor. The model was then initialized with 3 infested leaflets bearing one male and female whitefly each. At the four introductions 0.75, 2.09, 4.50 and 2.48 parasitoids were released per plant, respectively. During the first two releases, more parasitoids were released in 'patch 12' than in the rest of the greenhouse.

Many other population counts were made of greenhouse whitefly and *E. formosa* on tomato (Burnett, 1949; Burnett, 1960a,b; Curry & Pimentel, 1971; Parr et al., 1976; Stenseth, 1976; Hulspas-Jordaan et al., 1987; Yano, 1990). These studies could not be used to validate the present model. In most cases, validation was not useful because of the small spatial scale and high whitefly densities, which excluded the possibility to determine the importance of parasitoid searching. In addition, for many studies temperature data or initial whitefly numbers were lacking.

Sensitivity analysis

For the sensitivity analysis of the final model, initial whitefly densities of 'patch 12' were taken. The plot consisted of 25 plant rows and 25 plants per row and the model was initialized with 9 infested leaflets bearing one male and female whitefly each. The timing and number of released parasitoids per plant was the same as for the total greenhouse (see above). Parasitoids were released as emerging black pupae on 25 paper cards, which were evenly distributed in the crop. This method of introduction is comparable with that in Dutch tomato greenhouses today (Koppert Biological Systems, pers. comm.). Simulations were always done for 5 replicates.

RESULTS

Maximum population growth of whitefly and parasitoid

The validation results of the whitefly population model are shown in Figure 4. The simulated curves agree well with the observed population counts. During day 40-60 a slower increase of empty pupae (emerging adults) is simulated by the model. During that period, other whitefly stages were more numerous, caused by the discrete generations in the beginning. After about 60 days, the curves of Figure 4 become straight lines and the whitefly populations increased exponentially.

The percentage of each development stage in the total population then stabilizes: a stable age distribution is attained. For greenhouse whitefly, the model predicted a stable age distribution of 55.3% eggs, 16.7% L1, 8.1% L2, 6.0% L3, 3.6% L4, 3.2% prepupae, 2.3% pupae, 2.7% female adults and 2.2% male adults respectively at 20°C.

For *E. formosa*, the maximum population growth could not be validated, because experimental data were not available. The model predicted a stable age distribution of 67.1% eggs, 22.7% larvae, 10.5% pupae and 1.8% female adults respectively at 20°C.

The intrinsic rate of increase (r_m) is a measure of exponential population growth (Birch, 1948) under exceptional circumstances where food and/or hosts are abundantly available and restrictions due to other environmental circumstances are absent. With the whitefly and parasitoid models, the r_m values of both insects could be derived by using the simulated number of individuals (N) of the exponentially increasing population on two moments, t_1 and t_2:

$$r_m = (\ln N_{t2} - \ln N_{t1}) / (t_2 - t_1)$$

In this way, r_m is determined by all life-history parameters used as input in the models. Results are given in Figure 5. The temperature range for population growth is 8-35°C for greenhouse whitefly and 11.4-35°C for *E. formosa*. Below 8°C the immature whitefly stages do not develop; at 35°C whitefly eggs and pupae do not survive (Chapter 8). Van Lenteren & van der Schaal (1981) found a lower-temperature threshold for oviposition of *E. formosa* of 11.4°C. Figure 5 shows that the r_m value of *E. formosa* is much higher than that of the greenhouse whitefly above 14°C.

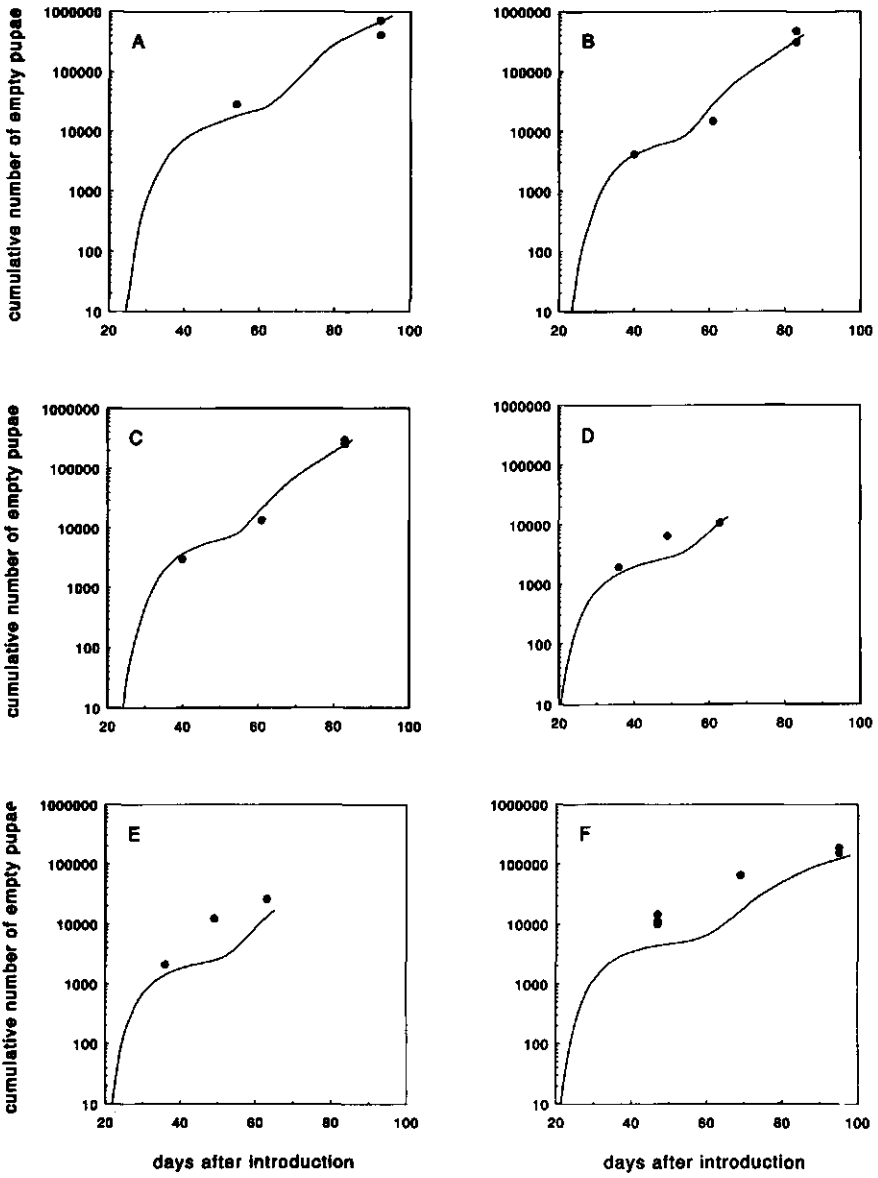


Figure 4. Simulated (lines) and observed (dots) number of empty pupae of greenhouse whitefly in population experiments on tomato (var. 'Allround'): (A) 300 females released on 19-3-1981 on 15 plants (De Ponti & Steenhuis, unpubl.); (B) and (C) 100 females released on 28-4-1983 on 10 plants (Joosten & Elings, 1985); (D) and (E) 50 females released on 19-8-1983 on 5 plants (Joosten & Elings, 1985); (F) 100 females released on 27-8-1981 on 10 plants (Elzinga, 1982).

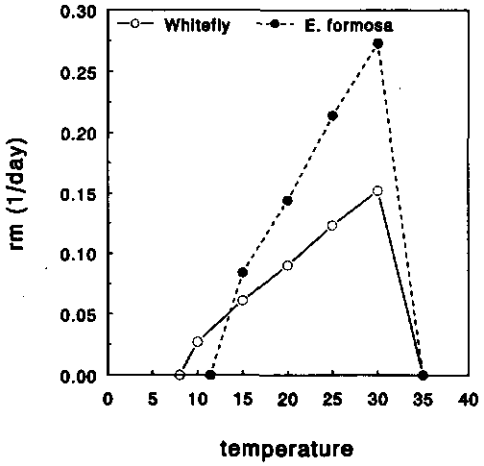


Figure 5. Simulated intrinsic rate of increase (r_m) of greenhouse whitefly on tomato and of *E. formosa*.

Table 1. Change (%) in r_m value after a decrease of 10% of input parameter

Parameter	Greenhouse whitefly	*E. formosa*
Development rate	-7.32	-8.01
Daily oviposition[1)]	-2.90	-2.43
Sex ratio	-2.90	-
Adult longevity[2)]	-0.73	-0.22
Immature mortality	0.66	0.26
Relative dispersion	-0.30	-0.50
Maturation period	0.31	-
Pre-oviposition period	0.07	-

[1)] or fecundity. [2)] Fecundity also decreased with 10%, and therefore daily oviposition was hardly affected.

A sensitivity analysis of the r_m value for each life-history parameter was done using the whitefly and the parasitoid model. The change in r_m value was simulated after the value of one particular input parameter was decreased with 10% (Table 1). Increasing instead of decreasing each input parameter yielded about the same absolute change in r_m value.

Combined host and parasitoid population growth

The number of unparasitized prepupae and pupae in 'patch 12' (1344 plants) was simulated from 1 January onwards with and without introduction of parasitoids (Figure 6). Whitefly densities were kept at extremely low densities by the parasitoids and never exceeded 0.3 unparasitized pupae per plant on average. After 112 days the whitefly population without control was 317 times larger than when parasitoids were introduced. The decrease in number of prepupae and pupae after 40 days when no parasitoids were introduced was caused by the discrete whitefly generations in the beginning. During that period, other whitefly stages were more numerous and the total number of

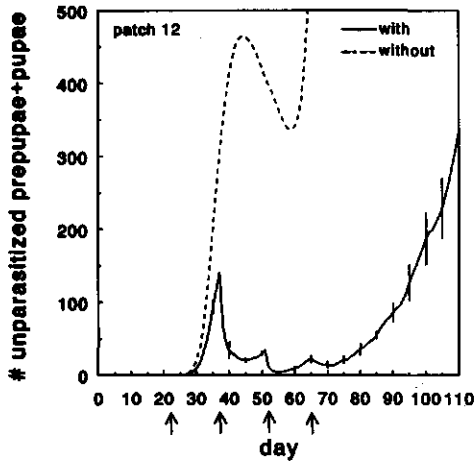


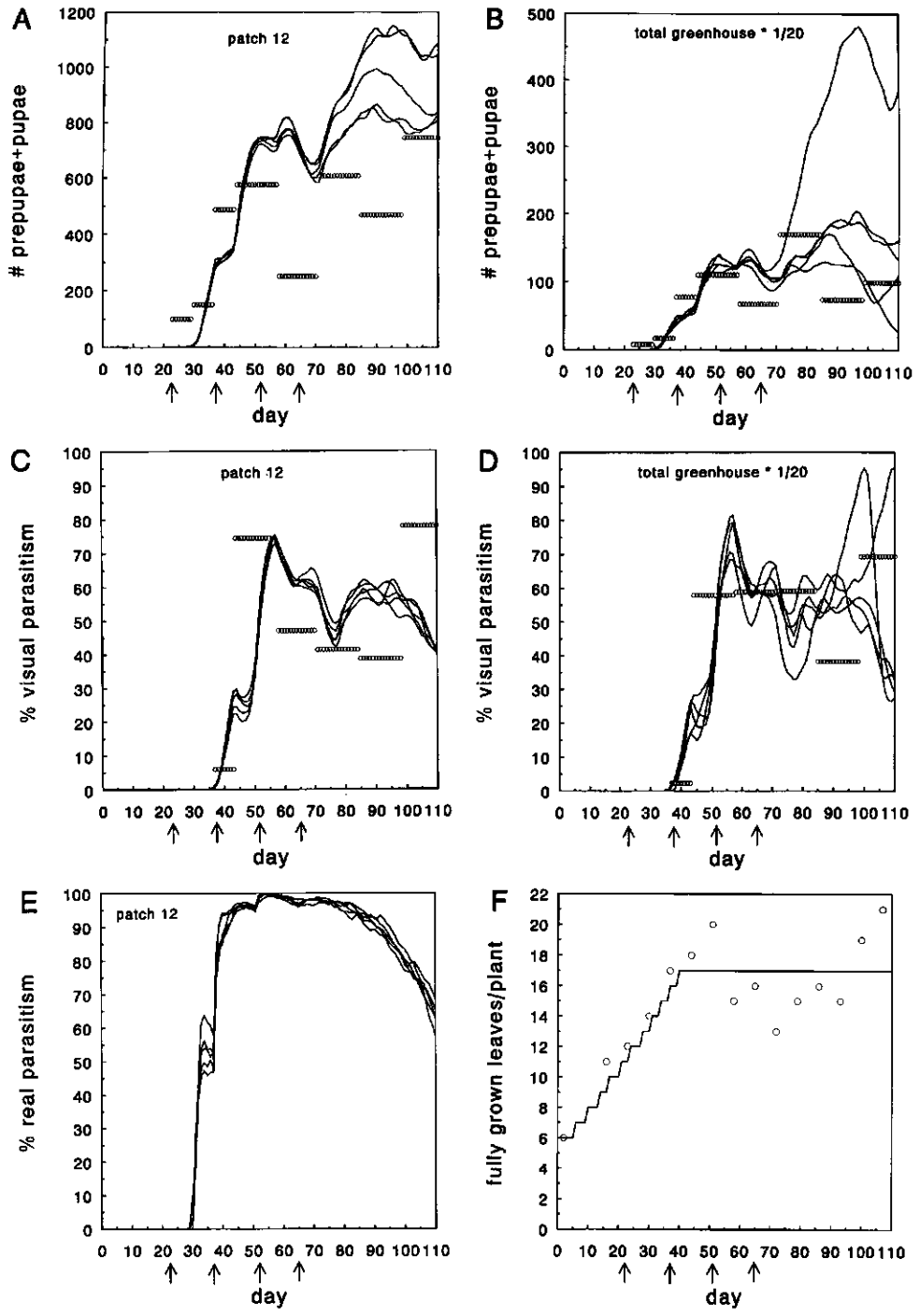
Figure 6. Simulated number of unparasitized whitefly prepupae+pupae with and without biological control with *E. formosa* in 'patch 12' (1344 plants; Eggenkamp-Rotteveel Mansveld et al., 1982b) during 1 January-20 April. Bars represent standard deviations (n=5). Arrows indicate release of parasitoids.

individuals did not decrease.

Figure 7A shows the total number of prepupae and pupae of five simulation runs. The simulation results can be compared with observations. The simulated increase in number of prepupae and pupae during the first 50 days was very close to the observations. From day 60, the simulations were somewhat higher. However, counts were based on only one experiment, and differences between replicates of a factor 2 over 100 days are common in population studies when initiated with only a few adults. The difference might also be caused by whitefly adults leaving 'patch 12' after about 50 days. Eggenkamp-Rotteveel Mansveld et al. (1982b) show that at that time adults reached the edge of the plot in which pupae were counted. Immigration of whiteflies can be excluded because other patches were far away. Some adults probably left the plot and their offspring is not included in the counts. This is supported by simulations for the whole greenhouse which are similar to the observations (Figure 7B). The variation between simulations is now larger however, due to a lower initial whitefly density.

Parasitism of pupae can easily be estimated from their outward appearance. The percentage of black pupae in 'patch 12' and in the whole greenhouse is shown in Figures 7C-D. The agreement between simulations and observations is clear, although the observed increase in parasitism at the end was not simulated for 'patch 12'. According to the model, the real (visible and unvisible) percentage parasitism was

Figure 7 (next page). Validation of the model. Simulation results of 5 replicates (lines) and observations (dots) during 1 January-20 April: (A) number of prepupae+pupae in 'patch 12' (1344 plants) and (B) in 1/20 of total greenhouse (900 plants); (C) percentage visual parasitism of prepupae+pupae (% black pupae) in 'patch 12' and (D) in 1/20 of total greenhouse; (E) percentage real parasitism of prepupae+pupae in 'patch 12'; (F) number of fully grown leaves per tomato plant. Arrows indicate release of parasitoids. Each population count took 7-14 days (Eggenkamp-Rotteveel Mansveld et al., 1982a,b).


A
patch 12
prepupae+pupae
day
B
total greenhouse * 1/20
prepupae+pupae
day
C
patch 12
% visual parasitism
day
D
total greenhouse * 1/20
% visual parasitism
day
E
patch 12
% real parasitism
day
F
fully grown leaves/plant
day

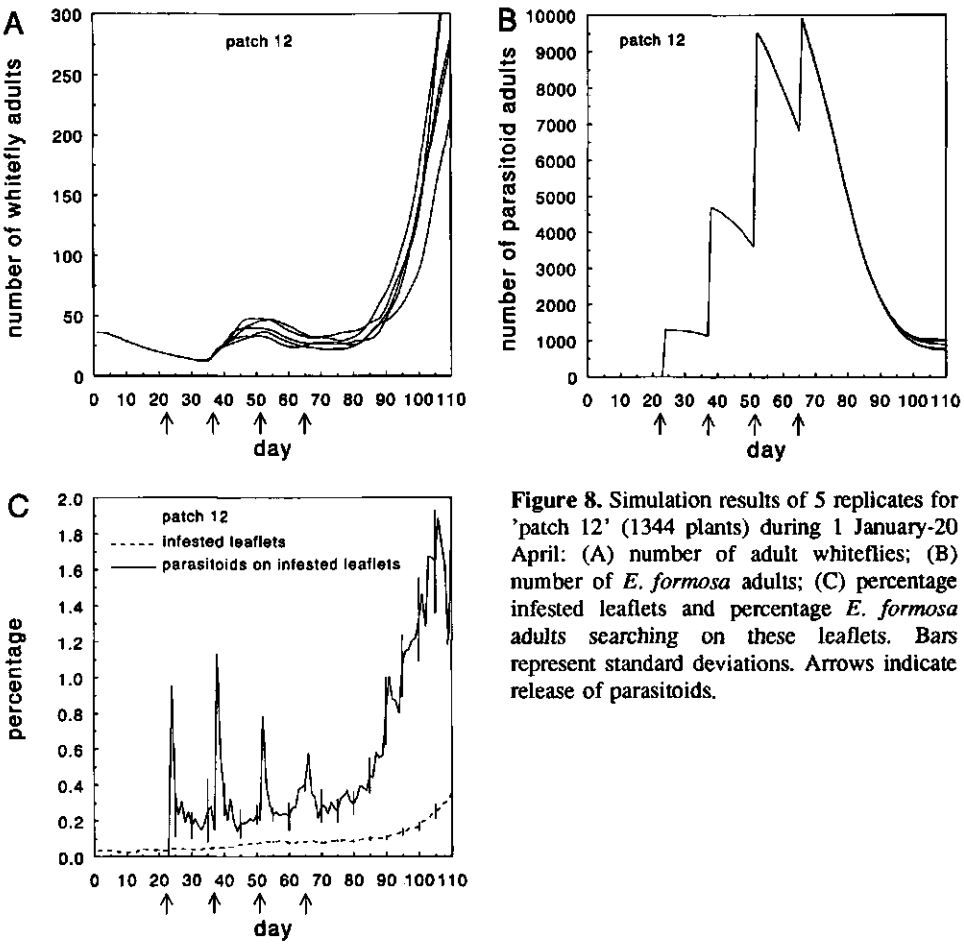


Figure 8. Simulation results of 5 replicates for 'patch 12' (1344 plants) during 1 January-20 April: (A) number of adult whiteflies; (B) number of *E. formosa* adults; (C) percentage infested leaflets and percentage *E. formosa* adults searching on these leaflets. Bars represent standard deviations. Arrows indicate release of parasitoids.

about twice as high and close to 100%, due to parasitized prepupae and pupae containing a parasitoid egg or larva which cannot be seen (Figure 7E). This percentage cannot be compared with that of the greenhouse experiment, because hosts were not dissected.

The number of fully grown leaves per plant in the greenhouse is given in Figure 7F. The simulated increase was very close to the observations. Maximum number of leaves per plant was set to 17 in the model, which was the average of that in the greenhouse when old leaves were removed.

The simulated number of adult whiteflies and parasitoids in 'patch 12' is shown in Figures 8A-B. During 90 days, whitefly adults were kept at a constant density, but then increased. Their number, however, was still very low and never exceeded 0.3 per

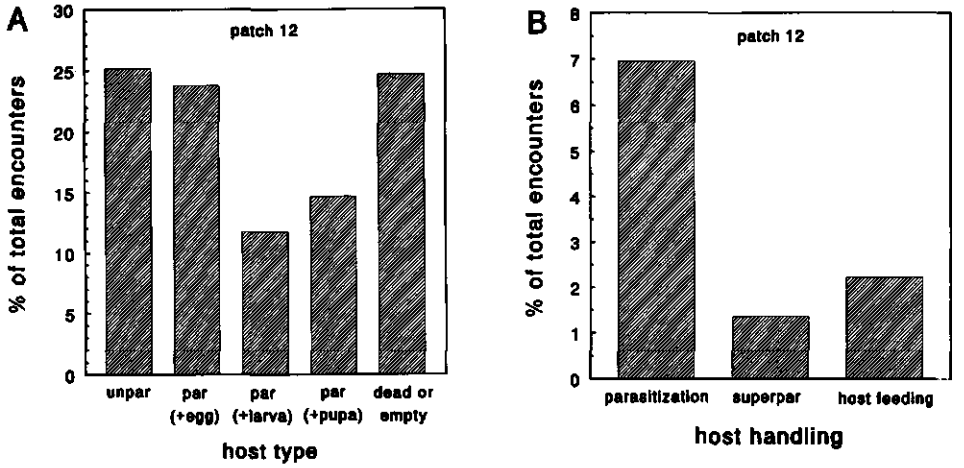


Figure 9. Simulation results for 'patch 12' during 1 January-20 April. Means of 5 replicates are given: (A) percentage encounters of parasitoids with unparasitized (unpar) hosts, with parasitized (par) hosts containing an egg, larva or pupa, and with dead hosts or empty pupal cases; (B) percentage of host encounters followed by parasitizations, superparasitizations and host feedings.

plant. The parasitoid adults reached very high densities of 7.4 per plant, of which the majority was searching on clean leaflets. Most of the time, percentage infested leaflets in the crop and percentage parasitoids searching on these leaflets was less than 1% (Figure 8C).

The parasitoids were searching for hosts in a greenhouse where host density was low and many hosts were parasitized. Only in 25% of the host encounters, hosts were unparasitized during the simulated period of 112 days (Figure 9A). Mostly, encounters were with parasitized hosts. Some of the encountered hosts were accepted for parasitization, super-parasitization or host feeding, but the majority was rejected (Figure 9B).

When considering unparasitized hosts only, the picture becomes clearer. The young and small whitefly immatures were the most encountered stages in the greenhouse, because of their relatively high densities in the population (Figure 10). As a result, most ovipositions took place in L1, L2 and L3 and, subsequently, most emerged adult parasitoids originated from these stages. In total, only 2127 parasitoids emerged as offspring of the 14318 released in 'patch 12' during the simulated period.

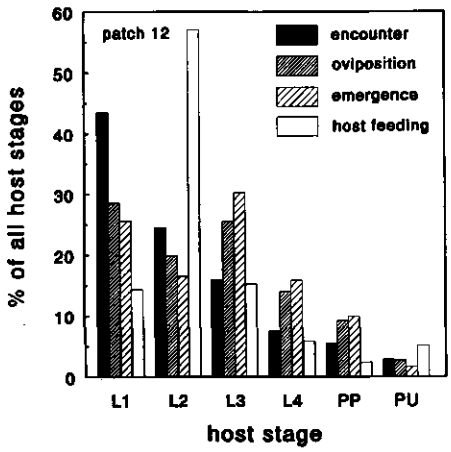


Figure 10. Simulated distribution of host encounters, ovipositions and host feedings over (unparasitized) host stages and distribution of parasitoid emergence over host stages which were originally parasitized. Means of 5 replicates for 'patch 12' during 1 January-20 April are given.

Sensitivity analysis

For the sensitivity analysis of the final model, attention was focused on the number of unparasitized prepupae and pupae during a 100 day period. The area under this curve is the cumulative number of unparasitized prepupae and pupae and can be considered as a measure of the whitefly population under biological control. The reduction of this whitefly population was simulated after the value of one particular input parameter was changed with 25% compared to the 'standard run'. This was done for 32 input parameters. Results are shown in Figure 11, in which input parameters used in the submodel of the parasitoids' foraging behaviour were separated from the other, mainly life-history parameters. SE/mean for the whitefly population of 5 replicates (standard run) was 4.0%.

The most important life-history parameters determining the whitefly population under biological control were the whitefly development rate (Dw) and the parasitoid longevity (Lp) (Figure 11A). The leaf initiation rate (LI) and the number of released parasitoids (Np) also had a strong effect on the whitefly population under biological control.

Important parameters used in the submodel of foraging behaviour were those determining the host encounter rate: the leaflet size (AR), the parasitoids' walking speed (WS) and walking activity (AC) and, to a lesser extent, width of the parasitoids' searching path (WI) and diameter of the immature hosts (DM) (Figure 11B). Also important were the probability of oviposition after encountering a host (Po, success ratio) and the parameters determining the parasitoids' searching time on lower and upper leaf side (LS and US).

The effects of the driving variables temperature and daylength were studied as well. When temperature was decreased in the model with 1°C during the total period, the whitefly population was reduced with 29.2% when no parasitoids were released.

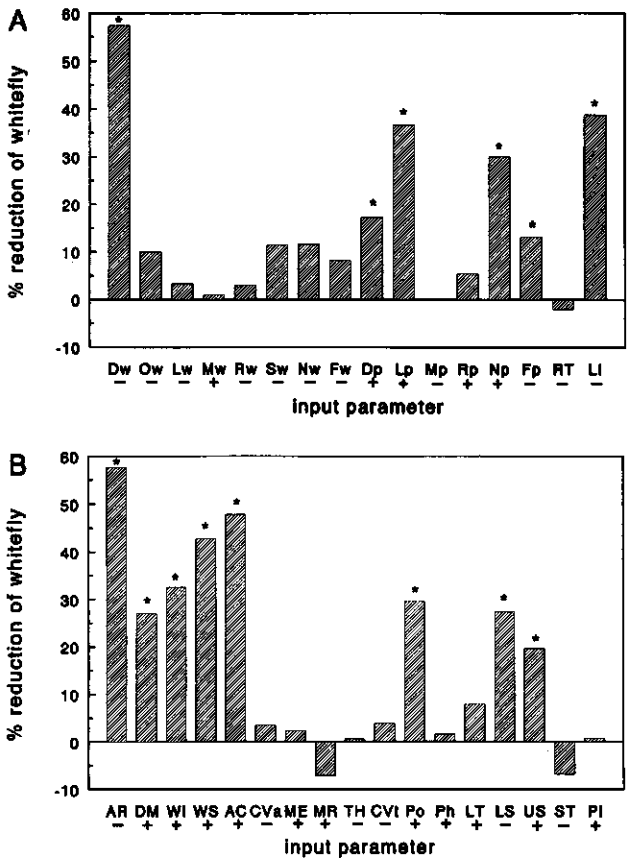


Figure 11. Reduction (%) of the whitefly population (cumulative number of unparasitized prepupae+ pupae during 100 days) after a 25% decrease (-) or increase (+) in input parameter. Means of 5 replicates are given. Bars marked by * are significantly different from 0 (Student t-test on population mean; α=0.05).

(A) Life history parameters, with subscript w (whitefly) or p (parasitoid) are: immature development rate (D), daily oviposition (or fecundity) (O), longevity (L), immature mortality (M), relative dispersion (coefficient of variation of stage duration) (R), and sex ratio (S). Other parameters are: number of released adults (for whiteflies equal to initial number) (N), average flight distance from one plant to the next (F), average residence time on leaf of dead hosts and empty pupal cases (RT), and leaf initiation rate (LI).

(B) All parameters are used in the submodel of the parasitoids' foraging behaviour: leaflet area (AR), diameter of host stages (DM), width of parasitoids' searching path (WI), parasitoids' walking speed (WS), walking activity (AC), coefficient of variation of walking activity (CVa), maximum egg load (ME), egg maturation rate (MR), host handling time (TH), coefficient of variation of handling time (CVt), probability of oviposition after encountering a host (success ratio, Po), probability of host feeding after encountering a host (Ph), parasitoids' leaving tendency (LT), tendency of changing from the lower leaf side to the upper (LS), tendency of changing from the upper leaf side to the lower (US), both tendencies of changing from one leaf side to the other (ST), the probability of landing on the lower leaf side compared to upper side (PI).

This temperature chance however, hardly affected the whitefly population (+5.0%) when parasitoids were released. Apparently, the lower whitefly population growth was compensated by a less efficient biological control, due to a lower walking speed of the parasitoids. A change in threshold temperature of *E. formosa* for searching from 18 to 12.1°C did not affect the whitefly population (+2.5%). Temperatures below 18°C mostly occurred during the night, when parasitoids were not active. A reduction in daylenght of 1 h, reducing it by 12.8 and 7.3% on day 1 and 100 respectively, had a much greater effect on parasitoid efficiency: the whitefly population increased with 19.0%.

For *E. formosa* the GUT after landing on the leaflet or, if it occurred, from the latest host encounter until leaving varied to a large extent (Chapter 3). The same was found for the time until changing (TUC) from one leaf side to the other. In the model each GUT and TUC of a parasitoid is drawn from an exponential distribution. The whitefly population was not sensitive to the *average* GUT or its reciprocal, the leaving tendency (LT, Figure 11B). The same was found for TUC on both leaf sides.

Figure 12A shows the reduction of the whitefly population for different GUT values, when *variation* in GUT and TUC was excluded in the model. The reduction was calculated by comparing the whitefly population with that when variation was included and minimal GUT was 100 s (see also model of Chapters 6 and 7). The figure shows that when variation was excluded, the whitefly population was extremely reduced and went nearly extinct at GUT values close to the observed mean (1610 s). Even a change of 50% in GUT (805 or 2416 s) did not have a large effect. However, at low GUT values the population was not reduced as severely and did not become extinct. Figure 12B shows the whitefly population during day 1 to 100 when variation in GUT and TUC was excluded in the model. The exclusion of low GUT values (< 800 s) on infested leaflets was mainly responsible for the effect.

Thus, the whitefly population is very sensitive to low GUT and TUC values of the parasitoid. Analysis of the observed giving up times on tomato leaflets of Chapter 3 showed that such a minimum GUT and TUC was not found on clean leaflets, but GUT's lower than 100 s were never found after host encounters. The parasitoids hardly changed leaf sides within 100 s and hardly left the leaflet within 500 s when one or more parasitizations had occurred on the leaflet earlier (Figure 12C) or when leaflets were covered with honeydew. These minimum values are part of the present model.

In the present model, honeydew is only present on leaflets when host number exceeds 75 per leaflet, which hardly ever occurred during the simulations. Honeydew did not play a role on leaflets with 1-4 immature whiteflies (Chapter 3). A recent study showed that *E. formosa* also continued searching for at least 500 s and on average 20 minutes after encountering a tiny droplet of honeydew on tomato leaflets (Doodeman, pers. comm.). This might significantly increase the parasitoid's arrestment effect at host densities of less than 75 per leaflet.

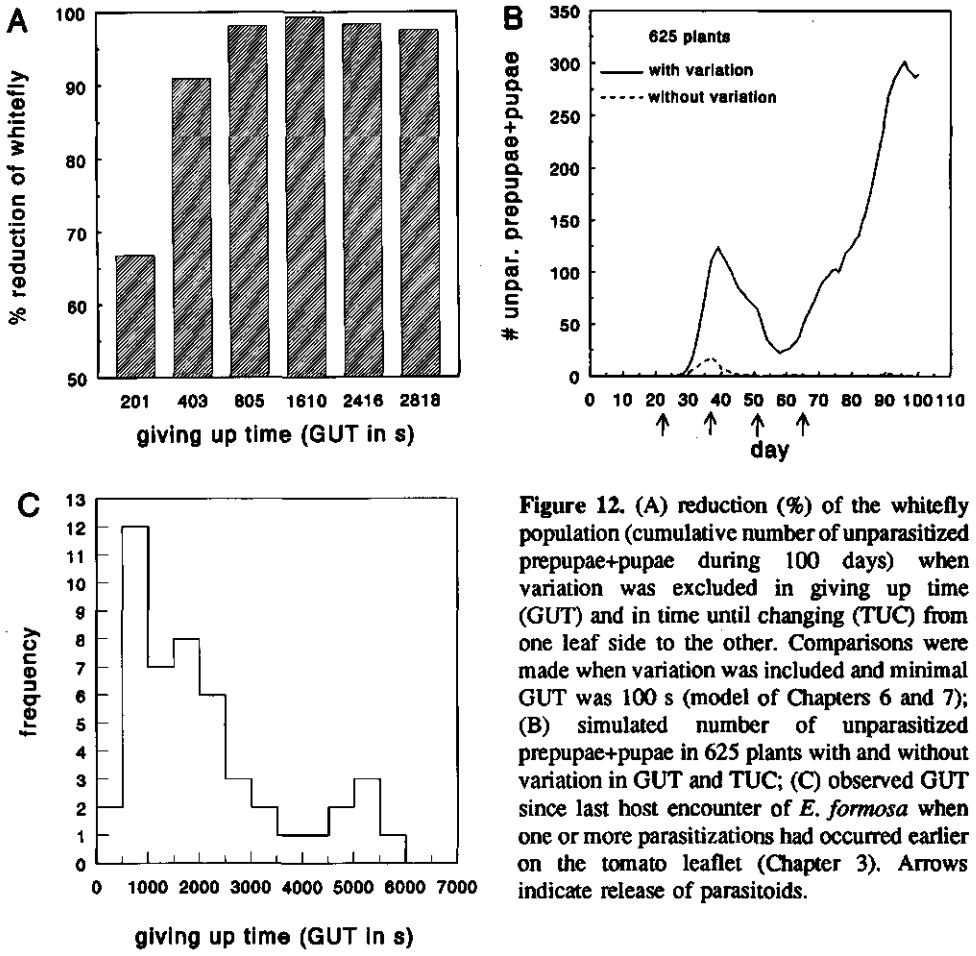


Figure 12. (A) reduction (%) of the whitefly population (cumulative number of unparasitized prepupae+pupae during 100 days) when variation was excluded in giving up time (GUT) and in time until changing (TUC) from one leaf side to the other. Comparisons were made when variation was included and minimal GUT was 100 s (model of Chapters 6 and 7); (B) simulated number of unparasitized prepupae+pupae in 625 plants with and without variation in GUT and TUC; (C) observed GUT since last host encounter of *E. formosa* when one or more parasitizations had occurred earlier on the tomato leaflet (Chapter 3). Arrows indicate release of parasitoids.

Release strategies

The influence of number, location and timing of parasitoid release was studied with the model. The location of release sites and the number of released parasitoids were both important factors for the reduction of the whitefly population. When all parasitoids were released in the centre of the plot where the first adult whiteflies were observed instead of released at regular spatial intervals, the whitefly population was reduced with 63.2% (Figure 13A). When the number of released parasitoids was increased with 25%, the whitefly population decreased with 30.0% (Figure 13A, see also Figure 11A).

Timing of release is not that important when parasitoids were released four times (Figure 13B). Early introductions, starting on day 9, resulted in low infestations which rapidly increased after 60 days. Later introductions, starting on day 23 or 30,

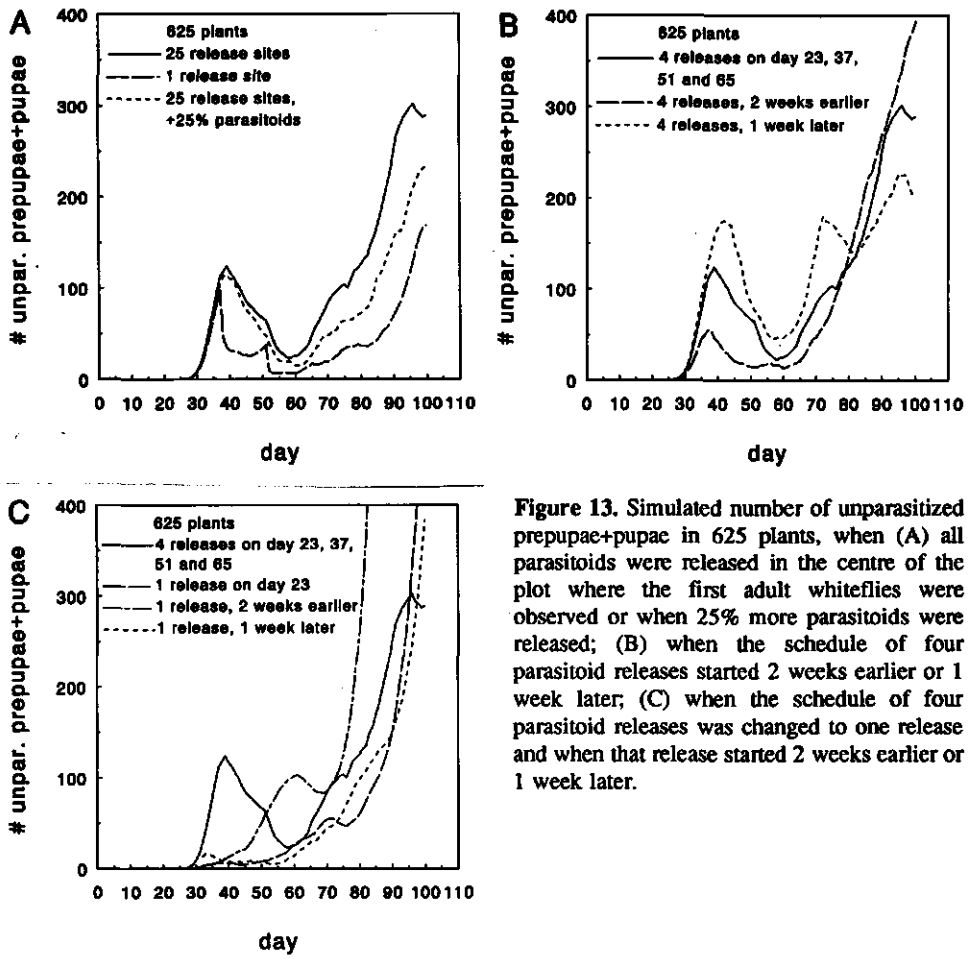


Figure 13. Simulated number of unparasitized prepupae+pupae in 625 plants, when (A) all parasitoids were released in the centre of the plot where the first adult whiteflies were observed or when 25% more parasitoids were released; (B) when the schedule of four parasitoid releases started 2 weeks earlier or 1 week later; (C) when the schedule of four parasitoid releases was changed to one release and when that release started 2 weeks earlier or 1 week later.

resulted in more stable populations. If all parasitoids were released at once, the cumulative whitefly population (area under the curve) was much more sensitive to timing (Figure 13C). Single introductions resulted always in low but unstable whitefly populations.

DISCUSSION

The simulated population increase of greenhouse whitefly in the *absence* of parasitoids agreed well with observations on tomato. This result can be explained by the accurate estimates of the life-history parameters, which were based on many experimental data at a wide temperature range (Chapter 8). The intrinsic rate of increase (r_m) was strongly influenced by temperature and by the development duration and, to a lesser extent, daily oviposition and sex ratio. Similar results were found by Xu Rumei (1982), Hulspas-Jordaan & van Lenteren (1989) and Yano et al. (1989). From the present model we can conclude that plant resistance breeding aimed at an increase in egg-to-adult duration is very efficient for successful control of whitefly, also when they are under biological control. De Ponti et al. (1990) also stress that pest resistant plant varieties can improve biological control. Development time of whitefly differs very little between tomato genotypes, and a much larger difference is found for whitefly longevity, oviposition rate and immature mortality (Romanow et al., 1991). These parameters have a smaller effect on whitefly population development.

The intrinsic rate of increase (r_m) of *E. formosa* is much higher than that of the greenhouse whitefly above 14°C. The r_m of a natural enemy however, plays a limited role when identifying good candidates in biological control (see also van Lenteren & Woets, 1988), because r_m is only valid under exceptional circumstances where food and/or hosts are abundantly available and restrictions due to other environmental circumstances are absent. Such conditions are very rare and parasitoids can only lay their daily egg load at extremely high host densities when they do not have to search for hosts. In greenhouses whitefly densities are ususally much lower and the realized whitefly density depends on the parasitoids' searching efficiency. Therefore, to evaluate and understand success or failure of biological control, r_m values are inappropiate and it is essential to built models which include searching and parasitization behaviour of the natural enemy at very low host densities, like the present model.

Also in the *presence* of parasitoids, the simulation results agreed well with greenhouse observations on tomato. Apparently, the hypothesized searching and parasitization behaviour of *E. formosa* in a tomato crop is reliable. In the model, the parasitoid does not distinguish between uninfested and infested leaflets before landing, the parasitoid searches randomly for hosts once on the leaflet, and shows a strong arrestment effect: it stays longer on the leaflet once a host is encountered.

The initial whitefly density was only 0.007 adults per plant in the greenhouse, whereas about 10 parasitoids per plant were released during the season (Eggenkamp-Rotteveel Mansveld et al., 1982a,b). Simulations showed that the adult parasitoid-whitefly ratio was very high and peaked at 250 on day 65. As a result, whiteflies were suppressed rather than regulated, at extremely low densities, less than 0.3 unparasitized pupae per plant, but never became extinct. These whitefly densities are much lower than the economic damage threshold for greenhouse whitefly. Hussey et al. (1958) measured significant yield reduction on tomato at an average pest density (between start of pest and final picking of fruits) of 22 scales/cm^2 leaf or more, and economic

damage at 6 scales/cm^2 or more. These threshold densities seem very high and would not be accepted in the present practice of growing tomatoes in greenhouses in the Netherlands (Koppert Biological Systems, pers. comm.).

The whitefly population in a greenhouse usually consists of a few local populations in loose patches (Eggenkamp-Rotteveel Mansveld et al., 1982a,b). The dynamics of such a metapopulation can be studied with the present model. However, the whitefly metapopulation dynamics in the whole greenhouse did not differ from that of local populations such as 'patch 12'. Local populations developed quite synchronized, because they started from infested seedlings and they received parasitoids at the same time. *E. formosa* does not stay in a patch, apparently because the parasitoid does not use chemical cues to locate its hosts from a distance (Noldus & van Lenteren, 1990; Romeis & Zebitz, in press; Sutterlin & van Lenteren, in prep.). Whitefly patches do not go extinct, but gradually increase in size with decreasing whitefly density (Eggenkamp-Rotteveel Mansveld et al., 1982a,b). This metapopulation dynamics is different for spider mite-predatory mite interactions, where predatory mites use chemical cues and stay in a patch for a few weeks until the local spider mite population goes extinct, while dispersing spider mites develop new patches at the same time (Sabelis & van der Meer, 1986; Sabelis et al., 1991).

The degree of whitefly control is very sensitive to those giving up times (GUT) lower than 800 s of the parasitoids. The whiteflies are suppressed at much lower densities when the parasitoids stay *at least* five minutes on each leaflet (infested or uninfested) and after each host encounter. This minimum time increases the arrestment effect and the resulting percentage of parasitoids on infested leaflets, thereby reducing the chance that clustered hosts escape from parasitism. When variation in GUT was excluded in the model, the whitefly population became less stable and nearly went extinct. Variation in GUT on leaflets induces host refuges from parasitoid attack. Also from more theoretical studies, host refuges are known to stabilize populations (Bailey et al., 1962; Murdoch & Oaten, 1975; Chesson & Murdoch, 1986).

The whitefly population under biological control was sensitive to the leaf initiation rate. In the model, a slower leaf production resulted in a longer stay and more ovipositions of whitefly adults on a particular leaflet. Thus, the same number of hosts were distributed over fewer leaflets, resulting in a more aggregated host distribution. Whiteflies were then suppressed by *E. formosa* to much lower numbers. Parasitism of one *E. formosa* female on a tomato leaflet is inversely density-dependent, which is caused by a decreasing walking activity and success ratio (Chapter 6). Host aggregation thus 'dilutes' the per capita parasitization pressure caused by one parasitoid on the leaflet. However, the effect on population level depends on the balance between this 'dilution' effect and the strength of the arrestment and aggregation of *E. formosa*. Therefore, the stronger whitefly reduction was caused by a stronger parasitoid arrestment and subsequent increase in the relative number of parasitoids on infested leaflets. More details on the spatial aspects of the whitefly-*E. formosa* interaction will be published elsewhere. Many parasitoid species stay longer in high-density patches and field studies suggest that many parasitoids do tend to aggregate (reviews in Walde

& Murdoch, 1988; Godfray, 1994). Summy et al. (1985) found that the parasitoid *Encarsia opulenta* aggregates in high-density patches of citrus blackfly and percentage parasitism in the field is density dependent. The aphelinid *Aphytis melinus* tend to aggregate on oranges with high densities of California red scale though the relationship between number of parasitoids per patch and host density is weak (Smith & Maelzer, 1986). Parasitism in the field is density independent of or inversily dependent on host density, whereas red scale populations are well-regulated (Murdoch, 1994). His group tested and failed to find evidence for eight hypotheses that might account for the system's stability.

Many theoretical studies showed that aggregation of natural enemies may increase population stability (see e.g. Hassell & May, 1974; Chesson & Murdoch, 1986; Reeve et al., 1989; Pacala et al., 1990). Kareiva & Odell (1987) avoided making general remarks about the effects of aggregation. They showed that differences in the detailed behaviour of the species involved could lead to opposite effects. Murdoch & Stewart-Oaten (1989) and Godfray & Pacala (1992) argue that the effect of aggregation on stability depends on the type of analytical model used and the biological assumptions one makes. In greenhouse biological control we are not interested in long-term stability per se, but in suppression of host numbers below the economic threshold during the growing season. Murdoch & Steward-Oaten (1989) show that there is a strong trade-off between stability and the degree of suppression of host density, which is undesirable in biological control. It is interesting to study this for whitefly, because the present model is based on observed behaviour of individuals and, therefore, biologically more realistic than analytical models.

In biological control programs, parasitoids are usually tested in small-scale experiments at high host densities before introduction in the field. As a result, maximum daily oviposition of parasitoids is measured, whereas this study showed that egg storage capacity and egg maturation rate of *E. formosa* was not important for the level of whitefly control. In commercial greenhouses, whitefly densities have to be very low for biological control to be successful, therefore effective host searching is the most essential process. When selecting parasitoids for biological control, attention should be focused on the parasitoids' arrestment effect (minimum GUT), walking speed, walking activity, success ratio, the ratio of search times on both leaf sides and on longevity, when comparing different synovigenic and solitary parasitoid species with random search. These characteristic attributes of parasitoids are easily measured in laboratory studies. They cannot be compared independently however, because the attributes of natural enemies are often found in particular combinations (Waage, 1990). The combined effect of these important attributes of a parasitoid can be tested with this model. When comparing the success of *E. formosa* on different crops, attention should be focused on the same parameters, plus the whitefly development duration and the number, size and production of leaves in the canopy.

Thus, the present study resulted in increased understanding of the relative importance of basic processes known to affect the population interaction of prey and natural enemy. Systems analysis and simulation are very helpful for integration of the

relevant processes. The tremendous effect of variation in patch times of individual parasitoids on the whitefly population in the greenhouse shows that individual-based models which include stochasticity and local searching behaviour are a necessity when developing models of host-parasitoid interaction at extremely low host densities and aggregated host distributions. The model will now be used to evaluate a number of release strategies on several crops and under various greenhouse climate conditions.

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Chapter 11

Summarizing discussion

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae), is a very common, highly polyphagous pest insect all over the world. Biological control of whiteflies with the parasitoid *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) was already applied in the 1920s in England, Australia, New Zealand and Canada. 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 in Western Europe, interest in using the parasitoid increased again. A reliable introduction scheme of the parasitoid was found by a 'trial and error' approach: natural enemies were released at different times and in different numbers, and their level of control was examined. In 20 of the 35 countries with a greenhouse industry, the parasitoid is used on about 5000 ha. Biological control with *E. formosa* is now used commercially in 90% of the tomato growing areas in the Netherlands. On several other important greenhouse crops such as cucumber and gerbera, biological control of whitefly is not so successful.

This study aims at integrating existing knowledge on the major processes known to affect the whitefly-parasitoid interaction in a crop by means of an explanatory simulation model. The goal is to obtain quantitative understanding of the tritrophic system crop- greenhouse whitefly- *E. formosa* to explain failure or success of biological control. With the model we are able to (1) explain the ability of *E. formosa* to reduce whitefly populations in greenhouses on crops like tomato, (2) improve introduction schemes of parasitoids for crops where control is more difficult to obtain and (3) predict effects of changes in cropping practices (e.g. greenhouse climate, choice of cultivars) on the reliability of biological control.

Direct observation experiments on foraging of *E. formosa*

When the present research project started, the behaviour of *E. formosa* had been observed in various experiments. These experiments resulted in the following picture. *E. formosa* is a solitary larval parasitoid: females lay one egg per host during an oviposition. Like in other synovigenic parasitoids new eggs mature when the egg load of the parasitoid drops below the storage capacity, which is 8-10 mature eggs for *E. formosa*. About ten days after oviposition the immature parasitoid pupates in the host pupa, which (in case of greenhouse whitefly) then turns black and parasitism can easily be seen from the outward appearance of the whitefly. Female parasitoids produce daughters parthenogenetically. Males are rarely observed.

The parasitoid searches for the sessile whitefly immatures by flying or hopping from leaf(let) to leaf(let), without distinguishing between infested and clean plants or leaves before landing. Once on the leaf she starts walking and drumming the leaf with her antennae. Hosts are encountered randomly and the walking pattern is not changed

after an encounter with a host. After an encounter, four behaviours on that host can be distinguished: the parasitoid may reject the host after an inspection with the antennae (antennal rejection) or after insertion of the ovipositor (ovipositorial rejection), she may parasitize (oviposition) or she may use the host as a food source (host feeding).

However, these earlier experiments did not lead to a complete picture of foraging behaviour. Quantitative data on some aspects were lacking, such as the parasitoids' searching or walking activity between host encounters, and the effect of temperature on the foraging processes. In many of the earlier experiments parasitoids were confined to an experimental arena, and therefore little was known about the time allocation of the parasitoid on leaves, such as the time until leaving, the time spent on upper and lower leaf side, and how these are affected by encounters with or ovipositions in hosts.

In this thesis, these gaps in our knowledge are first identified and studied experimentally. **Chapters 2, 3 and 4** describe experiments where individual parasitoids were observed continuously until they flew away, either on clean tomato leaflets, on leaflets with honeydew, or on leaflets with unparasitized and parasitized whitefly larvae. In Chapter 2 the residence times of the parasitoids on leaflets are discussed. In Chapter 3 the leaving tendency of the parasitoid from the leaflet and effects of several intra-patch experiences with hosts are quantified. In Chapter 4 other basic aspects of foraging are quantified, such as the parasitoids' walking speed and walking activity, the probability of each handling behaviour to occur after an encounter with a host and the host handling times. These data enable quantification of the foraging process of the parasitoid from landing on a leaf until departure. For an overview of the subsequent processes, see Figure 1 of Chapter 4. The work described in Chapters 2, 3 and 4 resulted in the following conclusions:

- The parasitoid *E. formosa* searches at random without a preference for the edge or the middle of a leaf, or for the upper or lower leaf side, whereas whitefly immatures (the hosts) are present only on the lower side of a tomato leaflet.
- The median residence time of the parasitoid on uninfested tomato leaflets (or giving up time, GUT) is 18.6 min at 20, 25 and 30°C and equal to that on infested leaflets on which no hosts are encountered.
- Parasitoids are arrested on the leaf by encounters with, and especially by ovipositions in, unparasitized hosts, by encounters with parasitized (unsuitable) hosts and by contact with honeydew. GUT since latest host encounter is again 18.6 min, also when the hosts were parasitized, but increases to 40 min after the first oviposition in an unparasitized host.
- Parasitoids are arrested on the lower leaf side by encounters with hosts, and especially by ovipositions in unparasitized hosts. The median time since the arrival on a particular leaf side or, if it occurred, since the latest host encounter on that leaf side until changing to the other side (TUC) is initially 11.6 min and drops to 5.7 min after both leaf sides have been visited. After the first oviposition in an unparasitized host, TUC since latest host encounter on the lower leaf side (where hosts are present) becomes twice as long.

- Parasitoids usually leave from the upper leaf side, where no hosts are present.
- The patch-leaving behaviour of the parasitoid can be described by a stochastic threshold mechanism, which is characterized by a certain tendency (probability per time) to leave. The parasitoid leaves after the host encounter rate falls below a certain threshold (encounters per time, which is the reciprocal of GUT). This threshold is not fixed, however, but shows a great variation and is expressed as a probability.
- The parasitoids' walking speed increases linearly between 15 and 25-30°C.
- The parasitoids' walking activity is very low at temperatures below 18°C and increases to about 75% of the total time on the leaf at 20, 25 and 30°C. The walking activity is not affected by host encounters, but decreases with decreasing egg load after 4 ovipositions.
- The percentage of encounters resulting in an oviposition is about 75% for the most preferred stage (unparasitized L4 larva), but decreases with decreasing egg load.
- Host handling behaviour and handling time is not influenced by the host plant.
- The total handling time (including drumming etc.) for antennal rejection of an unparasitized hosts is about 20 s, for oviposition and for ovipositional rejection about 6 min, and for host feeding about 15 min. These handling times slightly differ when hosts are parasitized.
- Self-superparasitism is not observed. Conspecific-superparasitism occurs in 14% of the contacted hosts containing a parasitoid egg, but is not observed anymore when the parasitoid egg had hatched.
- No difference is observed in host handling behaviour between naive and experienced parasitoids.
- Many inactive parasitoids are observed when the barometric pressure had decreased over a time span of at least 12 h.

Simulation models of foraging behaviour of *E. formosa*

The information described above is used as input in the simulation models of *E. formosa*'s foraging behaviour, which is described in **Chapters 5, 6 and 7**. Here, foraging behaviour is analyzed using Monte Carlo simulation at three spatial scales: in a small experimental arena, on a tomato leaflet and on a tomato plant. For an overview of the models, see the flow diagrams (Figure 1) of these chapters. Foraging behaviour is first studied at these small spatial scales, to better understand the quantitative effects of parasitoids on whitefly populations as observed in a crop.

The above simulation models are *mechanistic*, that is, they explain *how* parasitoids, in terms of searching efficiency, host handling and available eggs, realize the observed level of parasitism. Mechanistic explanations can help to understand failure or success of biological control in practice. The models do not explain *why* the parasitoids choose to behave in this way, in terms of the selection pressure acting on them. Thus, they do not provide a *functional* explanation of the observed behaviour. This is subject of study in optimal foraging models.

The simulated number of hosts encountered, parasitized and killed by host feeding, and the residence times on leaflets are validated with experimental data and the simulation results agree well with these observations. According to the model, *E. formosa* can parasitize 16 hosts per day on average at 25°C on a tomato leaflet if they start searching with a full batch of mature eggs and if host density is not limiting. Thus about 7 new eggs mature during the day (16 h) at that temperature. From the second day onwards, the parasitoid can parasitize 11 hosts per day, due to egg limitation: if the parasitoid laid all eggs the preceding day, only 4 eggs mature during the night (of 8 h) at 25°C, so the parasitoids do not have a full batch of mature eggs the next morning. The model shows that at a density of 1 L3 larva per tomato leaflet, 15.7% of the parasitoids discover the larva before they leave. Also at higher host densities, not all hosts are encountered and patches (leaflets) are not depleted after one visit. Variation in number of encounters and ovipositions between parasitoids is considerable, mainly caused by the random encounter of hosts, the variation in handling behaviour of an encountered host and by the variation in GUT and TUC.

In greenhouses, whiteflies show a clustered distribution over plants and leaves and average numbers are usually very low. The models show that at such conditions the number of parasitizations on tomato leaflets or plants is strongly affected by the leaf area, the parasitoids' walking speed and walking activity, the probability of oviposition after encountering a host, the initial egg load (egg load at the beginning of the experiment) and the ratio of search times on both leaf sides. At extremely high host densities, the egg storage capacity and the initial egg load of the parasitoid are most important, and on plants with a clustered host distribution also the parasitoids' GUT.

At all spatial scales tested, the number of encounters, ovipositions and host feedings increase with host density with a decelerating rate until a maximum level is reached. This shape of the curves resemble a Holling Type II functional response, which is caused by the parasitoids' decreasing walking activity and probability of oviposition after encountering a host when egg load decreases. This is predominant at all levels, and even a change in GUT from 18.6 to 40 min after the first oviposition on the leaf does not result in an accelerating increase of the curve. The shape of the curves, describing the effect of host density on parasitism as a result of the basic processes, helps to understand the dynamics of the host-parasitoid interaction at the population level. In case of a Type II functional response, percentage parasitism declines with increasing host density and parasitism is inversily density dependent. A high host density thus reduces the per capita parasitization pressure caused by one parasitoid. According to theory, inversely density dependence tends to have a destabilizing effect on the dynamics of host and parasitoid. However, the functional response or the parasitization pressure caused by one parasitoid is only one factor in determining the dynamics at the population level. Another factor is the number of parasitoids on the leaf. For *E. formosa*, the effect on the population level depends on the balance between the parasitization pressure caused by one parasitoid and the arrestment and subsequent aggregation of parasitoids on leaves with high host density (see Chapter 10).

Life-history parameters of greenhouse whitefly and *E. formosa*

In **Chapters 8 and 9**, life-history parameters of the greenhouse whitefly and *E. formosa* are reviewed. Data from literature were selected on development rate of each immature stage, percentage mortality of each immature stage, sex ratio, longevity, pre-oviposition period, period of increase of daily oviposition, fecundity and oviposition frequency. Most of these experiments have focused on the effect of temperature with little attention to other environmental factors such as humidity or light. With these data, the relationship between the life-history parameters and temperature are assessed by non-linear regression. Five mathematical equations were fitted, the best being selected on the basis of the coefficient of determination (r^2) and on visual comparison of the curves, which was necessary to check whether a curve was biologically realistic, particularly the tails. Coefficients to describe the mean of each life-history parameter as a function of temperature are summarized in these chapters. Coefficients of variation (*cv*: sd/mean) among individuals are also given. These coefficients are used as input in the submodels of population development of whitefly and parasitoid (see Chapter 10).

For greenhouse whitefly, the life-history parameters depend very much on the type of host plant. For *E. formosa*, data for several host plants were combined. The high r^2 values indicate that host plant effects can be disregarded for the parasitoids' life-history parameters, except for oviposition at low host densities, which is caused by differences in the parasitoids' walking speed and walking activity on leaves with a different morphology. The host stage originally parasitized strongly affects the immature development rate and immature mortality of the parasitoid.

The development rate is calculated as the reciprocal of the stage duration. For all immature stages of whitefly and parasitoid the relationship between development rate and temperature is described by the Logan curve: just above the lower threshold temperature, the development rate increases exponentially to an optimum, whereafter it declines sharply until the upper lethal temperature has been reached. The relationships of longevity, fecundity, and oviposition frequency with temperature are described by the Weibull curve: they increase exponentially from the lower lethal temperature to an optimum, whereafter they decrease exponentially. Only for *E. formosa*, the longevity decreases exponentially with temperature and an optimum was not found at greenhouse conditions. No relationship with temperature is found for the immature mortality, the sex ratio and the *cv* values of the life-history parameters of whitefly and parasitoid.

Simulation model of whitefly-parasitoid interaction in a crop

The final model simulates the population dynamics of the pest insect-parasitoid interaction in a tomato crop and is described in **Chapter 10**. The model is based on the parasitoids' searching and parasitization behaviour and on developmental biology of the two insect species. This model comprises several submodels, such as the submodel for whitefly population development, for parasitoid population development, for the parasitoids' foraging behaviour on tomato leaflets (model of Chapter 6), for

spatial distribution of whitefly and parasitoid in the canopy, for dispersion of adult whiteflies and parasitoids from leaf to leaf, for leaf production and a submodel for checking simulation errors. Life-history parameters of Chapters 8 and 9 are used as input in the submodels for population development of whitefly and parasitoid on tomato. For an overview of the model, see the relational diagrams (Figures 1, 2 and 3) of Chapter 10. The model is unique in that it is an individual-based model which simulates local searching and parasitization behaviour of a large number of individual parasitoids in a whitefly-infested crop. The model includes stochasticity and spatial structure which is based on location coordinates of plants and leaves.

The model is validated with population counts from experiments on tomato with and without introduction of *E. formosa* in small greenhouse compartments and in a large commercial greenhouse. The simulated population increase of greenhouse whitefly in the *absence* of parasitoids agree well with the observations. This result can for an important part be explained by the accurate estimates of the life-history parameters, which are based on many experiments at a wide temperature range (see Chapters 8 and 9).

With these life-history parameters as input in the model, the intrinsic rate of increase (r_m) of both insect species is simulated. The r_m of *E. formosa* is much higher than that of the greenhouse whitefly above 14°C. The r_m of a parasitoid however, plays a limited role in biological control, because it is only valid when all parasitoids can lay their daily egg load. This can only happen at extremely high host densities when the parasitoids do not have to spent much time searching for hosts. In greenhouses whitefly densities are usually much lower and the realized whitefly density depends on the parasitoids' searching efficiency. Therefore, to evaluate and understand success or failure of biological control, r_m values are inappropiate and it is essential to built models which include searching and parasitization behaviour of the natural enemy at very low host densities.

Also in the *presence* of parasitoids, the simulation results agree well with greenhouse observations on tomato. Apparently, the hypothesized random host encounter of *E. formosa* in a tomato crop is reliable. In the model, the parasitoid does not distinguish between uninfested and infested leaflets before landing, the parasitoid searches randomly for hosts once on the leaflet, and shows a strong arrestment effect: it stays longer on the leaflet once a host is encountered. Simulations show that the adult parasitoid-whitefly ratio is very high and can even reach 250:1. As a result, whiteflies are suppressed rather than regulated by the parasitoids at extremely low host densities (<0.3 unparasitized pupae per plant), but never become extinct. These whitefly densities are much lower than the economic damage threshold for greenhouse whitefly. Percentage black pupae fluctuates between 40 and 70%. According to the model, the parasitoid adults reach high densities of 7.4 per plant, but due to the low whitefly density not more than 1% of the parasitoids is searching on infested leaflets.

The giving up times (GUT) of *E. formosa* vary to a large extend. The degree of whitefly control is very sensitive to those GUT's lower than 800 s of the parasitoids. The whiteflies are suppressed at much lower densities when the parasitoids stay *at least*

five minutes on each leaflet (infested or uninfested) and after each host encounter. This minimum time increases the arrestment effect and the resulting percentage of parasitoids on infested leaflets, thereby reducing the chance that clustered hosts escape from parasitism. When variation in GUT is excluded in the model, the whitefly population becomes less stable and nearly goes extinct. Variation in GUT on leaflets induces host refuges from parasitoid attack. Also from more theoretical studies, host refuges are known to stabilize populations.

Whitefly adults migrate to young leaves in the top of the plant. A slower leaf production results in a longer stay and more ovipositions of whitefly adults on a particular leaflet. Thus, the same number of hosts are distributed over fewer leaflets, resulting in a more aggregated host distribution. Whiteflies are then suppressed by *E. formosa* to much lower numbers, according to the model. Parasitism of one *E. formosa* female on a tomato leaflet is inversely density-dependent, which is caused by a decreasing walking activity and probability of oviposition after encountering a host (Chapters 5, 6 and 7). Host aggregation thus 'dilutes' the per capita parasitization pressure caused by one parasitoid on the leaflet. The effect on the population level however, depends on the balance between this 'dilution' effect and the strength of the arrestment and aggregation of *E. formosa*. Therefore, the stronger whitefly reduction when whiteflies are more aggregated is caused by a stronger parasitoid arrestment and subsequent increase in the relative number of parasitoids searching on infested leaflets.

This shows that differences in whitefly distribution among crops are one factor in causing differences in success of biological control. Other factors are the size, number and surface (hairiness) of leaves in the canopy. Leaf size and total leaf area have a strong effect on whitefly control according to the model, caused by their direct effect on host density. Furthermore, leaf size and leaf surface strongly affect the efficiency of *E. formosa* by changing the parasitoids' arrestment effect (GUT) and the walking speed and activity, respectively.

Another important factor is the whitefly development duration on the crop. The model shows that plant resistance breeding aimed at an increase in egg-to-adult duration of the whiteflies is very efficient in causing a severe reduction of whitefly numbers, when biological control is applied. Observed development times of whitefly differ very little between tomato genotypes, and a much larger difference is found for whitefly longevity, oviposition rate and immature mortality. These parameters have a smaller effect on whitefly population development.

The important factors or crop properties affecting the success of biological control cannot be compared independently. For instance crops with large leaves usually have lower number of leaves which are produced at a lower rate than crops with small leaves or leaflets. It is particularly the combined effect of these important factors that can be tested with this model for different crops or plant varieties.

In biological control programs, parasitoids are usually tested in small-scale experiments at high host densities before introduction in the field. As a result, maximum daily oviposition of parasitoids is measured, whereas this study shows that egg storage capacity and egg maturation rate of *E. formosa* is not important for the

level of whitefly control. In commercial greenhouses, whitefly densities have to be very low for biological control to be judged successful, therefore effective host searching is the most essential process. When selecting parasitoids for biological control, attention should be focused on the parasitoids' arrestment effect (minimum GUT), walking speed, walking activity, the probability of oviposition after encountering a host, the ratio of search times on both leaf sides and on longevity, when comparing different synovigenic and solitary parasitoid species with random search. These characteristic attributes of parasitoids are easily measured in laboratory studies. Again, they cannot be compared independently, however, because the attributes of natural enemies are often found in particular combinations. The combined effect of these important attributes of a parasitoid can be tested with this model.

Epilogue

The present study aimed at integrating existing knowledge on the major processes known to affect the whitefly-parasitoid interaction in a crop. Because of the multitude of relationships between the three trophic levels (crop-pest-parasitoid), it was decided to follow a combined experimental-simulation approach. The goal was to obtain quantitative understanding of the tritrophic system to explain failure or success of biological control. With the model we now unravelled the ability of *E. formosa* to reduce whitefly populations on greenhouse tomato. The study resulted in increased understanding of the relative importance of basic processes that affect the population interaction of whitefly and natural enemy. The life-history of parasitoids, often summarized in a r_m value, are less important than the parasitoids' searching capacity. This shows that in addition to the traditional selection criteria, a criterion based on searching efficiency is essential. The study has further generated knowledge on foraging behaviour of *E. formosa*. The tremendous effect of variation in patch times of individual parasitoids on the whitefly population in the greenhouse shows that individual-based models which include stochasticity and local searching behaviour are a necessity when developing models of host-parasitoid interaction at extremely low host densities and aggregated host distributions.

One of the main questions was to identify the main causal factors for differences among crops in success of biological control of whitefly. The parasitoid is more successful on tomato than on cucumber or gerbera. The present study showed that attention should be focused on differences in the parasitoids' arrestment effect (GUT), the parasitoids' walking speed and activity, the whitefly development duration and the number, size and production of leaves in the canopy. These parameters have also been quantified for cucumber and gerbera and some are very different from those of tomato (see Chapters 2, 3 and 8). The next step in the research is to use the simulation model presented in Chapter 10 for the other two crops and evaluate the main causal factors for success or failure of biological control.

When adapting the parameters in the model for gerbera and cucumber we are able to (1) explain the lower ability of the parasitoid to reduce whitefly populations on these crops, (2) improve introduction schemes of parasitoids for these crops, and (3)

predict effects of changes in cropping practices (e.g. greenhouse climate, choice of cultivars) on the reliability of biological control. Furthermore, with the model we can identify the characteristics which compose an efficient natural enemy. These characteristics can later be used as evaluation criteria in natural enemy selection programs. In fact ideotypes of natural enemies may be designed, tailored to crop, whitefly and environmental conditions. In that way, a new field of ecological engineering may be explored. The present study already pointed at important selection criteria when comparing different synovigenic, solitary parasitoids showing random search. The model can be adapted for other parasitoids with different foraging strategies or for other natural enemies of whitefly.

Samenvatting

Inzicht in de biologische bestrijding van kaswittevlieg met de sluipwesp *Encarsia formosa*
Van individueel gedrag naar populatiedynamica

Witte vlieg: plaag, schade en bestrijding

Er zijn ongeveer 1200 wittevliegsoorten beschreven, maar slechts enkele staan bekend als veroorzakers van plagen. Slechts twee wittevliegsoorten zijn schadelijk in kassen: de kaswittevlieg, *Trialeurodes vaporariorum*, en de tabakswittevlieg, *Bemisia tabaci*. Beide soorten komen op heel veel plantesoorten over de hele wereld voor en leiden tot aanzienlijke economische schade. In tegenstelling tot de naam misschien doet vermoeden, zijn witte vliegen geen vliegen maar behoren zij tot de plantesap-zuigende insekten (Homoptera), waartoe ook bladluizen behoren. Volwassen witte vliegen zijn slechts 1-1.5 mm groot.

Schade aan gewassen veroorzaakt door witte vlieg is drieledig. Ten eerste voeden volwassen witte vliegen en hun larven zich met het floeemsap uit de plant en dragen daarmee direkt bij aan opbrengstderving door het consumeren van koolhydraten, stikstof en nutrienten. Ten tweede produceren ze daarbij grote hoeveelheden honingdauw op de bladeren, die schimmelgroei op het blad stimuleert, waardoor de bladfotosynthese gereduceerd wordt. Veel belangrijker is echter de economische schade door de verontreiniging van vruchten en bloemen met de plakkerige honingdauw. Op tomaat is opbrengstderving gemeten bij een gemiddelde wittevliegdichtheid (tussen het begin van de plaag en het oogsten van de vruchten) boven 22 larven/cm^2 op het blad, en economische schade boven 6 larven/cm^2. Ten derde kunnen witte vliegen verschillende plantevirussen overbrengen.

In natuurlijke ecosystemen en landbouwsystemen waar geen pesticiden worden gebruikt, wordt het aantal witte vliegen op een laag niveau gehouden door diverse natuurlijke vijanden: predatoren, parasitoiden en pathogenen. Predatoren zijn rovers die hun prooi doden door ze op te eten of leeg te zuigen. Parasitoiden (sluipwespen en sluipvliegen) leggen één of meer eitjes in of op een ander insekt (de gastheer), en de daaruit ontwikkelde parasitoidlarve consumeert de gastheer totdat die sterft. Pathogenen zijn ziekteverwekkers, zoals bacterien, schimmels of virussen, die vaak de gastheer doden. Ervaring met twee gewassystemen - tomaat in de zestiger jaren in Californie en katoen in de jaren 1925-1992 in Sudan - hebben aangetoond dat witte vlieg van nature op een laag aantalsniveau blijft door natuurlijke vijanden. Door het gebruik van pesticiden worden natuurlijke vijanden echter uitgeroeid en kan witte vlieg een plaag worden. Daarnaast hebben veranderingen in gewasrotatie, verkorting van braakperiodes en opeenvolgende teelt van wittevlieg-gevoelige gewassen er toe geleid dat de

natuurlijke vijanden niet langer in staat waren witte vlieg voldoende onder controle te houden.

Sinds de Tweede Wereld Oorlog zijn chemische pesticiden het belangrijkste middel voor de bestrijding van insektenplagen. De voordelen van chemische bestrijding waren de goede bescherming van de gewassen, de betrouwbaarheid en de eenvoudige toepassing. Pas later werden nadelen van het volledig afhankelijk zijn van pesticiden duidelijk: het risico voor mens en milieu en de ontwikkeling van resistentie van de insekten tegen de middelen. Dit gaf aanleiding tot onderzoek naar andere bestrijdingsmethoden. Deze problemen zijn recentelijk erkend door de politiek en dit heeft in Nederland in 1991 geleid tot het Meerjarenplan Gewasbescherming (MJP-G). Dit plan heeft als doel een 50% reduktie in het gebruik van pesticiden te realiseren in het jaar 2000. Eén van de belangrijke alternatieven voor chemische bestrijding is biologische bestrijding, waar predatoren, parasitoiden of pathogenen worden uitgezet of toegediend om plaaginsekten te bestrijden. Omdat wittevliegplagen tegenwoordig over de hele wereld voorkomen, is een intensieve zoektocht naar geschikte natuurlijke vijanden gaande.

Geschiedenis van biologische bestrijding van witte vlieg

De kaswittevlieg, *T. vaporariorum* (Westwood) (Homoptera, Aleyrodidae) werd voor het eerst in Europa aangetroffen in kassen in Engeland in 1856. Westwood beschreef de soort in dat jaar en nam aan dat het insekt was geimporteerd met bloemen of planten van orchideeësoorten uit Mexico. Tegenwoordig heeft de soort zich verspreid over de hele wereld en belaagt veel plantefamilies en genera. In 1926 vroeg een tomateteler de engelse entomoloog Speyer wat de zwarte poppen die tussen de normaal witte larven en poppen van de kaswittevlieg voorkwamen, zouden kunnen zijn. Uit deze zwarte poppen kwamen sluipwespen die werden geïdentificeerd als *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae). Deze sluipwesp van slechts 0.6 mm lengte parasiteert witte vlieg, dat wil zeggen het vrouwtje legt haar ei in de wittevlieglarve, waardoor uiteindelijk geen volwassen witte vlieg maar een nieuwe sluipwesp ontstaat. Na enkele jaren produceerde een onderzoeksinstituut in Engeland jaarlijks ca. 1.5 miljoen exemplaren van deze sluipwesp voor zo'n 800 kwekerijen. Gedurende de dertiger jaren werd de sluipwesp uitgevoerd naar andere Europese landen, Canada, Australie en Nieuw Zeeland. Na de Tweede Wereld Oorlog werd de sluipwesp steeds minder gebruikt omdat insekticiden de plaag op de meeste kasgewassen goed bestreed.

De interesse in het gebruik van natuurlijke vijanden kwam weer terug nadat de spintmijt *Tetranychus urticae* resistent werd tegen pesticiden, waardoor chemische bestrijding niet meer het gewenste resultaat opleverde. Een belangrijke roofmijt, *Phytoseiulus persimilis*, bleek de spintmijtpopulaties goed onder controle te houden. Dit betekende dat breedwerkende pesticiden niet meer gebruikt konden worden tegen andere insektenplagen, omdat deze de roofmijt negatief beinvloeden. Daardoor werd de aandacht gericht op natuurlijke vijanden van de plaaginsekten in de kas. In de zeventiger jaren ontstonden enorme wittevliegplagen in kassen in West Europa, voornamelijk door de toegenomen resistentie tegen pesticiden, en de interesse voor *E.*

formosa nam weer toe. De kennis opgedaan tijdens eerdere introdukties van de sluipwesp in de dertiger jaren versnelde de ontwikkeling van introduktiemethoden voor de praktijk.

Deze efficiënte sluipwesp baande het pad voor de ontwikkeling van biologische en geintegreerde bestrijdingsprogramma's in kassen. Gedurende de laatste 25 jaar zijn 25 soorten natuurlijke vijanden geidentificeerd en geintroduceerd tegen zo'n 20 plaaginsekten in kassen. Tegenwoordig wordt kaswittevlieg biologisch bestreden met *E. formosa* in meer dan 20 van de 35 landen met glastuinbouw. De sluipwesp wordt voornamelijk uitgezet op tomaat. In West Europa vindt biologische bestrijding van kaswittevlieg plaats op 4000 ha en tuinders vinden het inmiddels betrouwbaarder dan chemische bestrijding. Het positieve resultaat is een verminderde belasting van het milieu, een gezondere werkomgeving voor tuinders en tuinbouwprodukten met minder of geen chemische residuen.

Probleemomschrijving en doel van het onderzoek

Biologische bestrijding van kaswittevlieg met *E. formosa* is erg betrouwbaar in gewassen zoals tomaat, paprika en augurk, maar veel minder in aubergine en komkommer. In de sierteelt, zoals in gerbera, zijn de resultaten wisselvallig. De introduktiemethode van de sluipwesp is gevonden door een 'trial and error' benadering: natuurlijke vijanden werden losgelaten op verschillende tijden en in verschillende aantallen, en vervolgens werd het succes van de bestrijding bekeken. Kennis op het gebied van regulatiemechanismen op populatieniveau is nog steeds gering. Tot nog toe is er geen goede verklaring waarom het introduktieschema van de sluipwesp in tomaat geen betrouwbare resultaten geeft in andere belangrijke kasgewassen. Voor dit verschil zijn wel diverse kwalitatieve verklaringen gegeven, die gebaseerd zijn op gedragsstudies van individuele insekten in het laboratorium en op populatiestudies in de kas. De hoofdoorzaken konden echter nog niet geidentificeerd worden.

De verschillen in bestrijdingsresultaat tussen de gewassen kunnen worden veroorzaakt door verschillen in (1) de kastemperatuur, (2) de demografische parameters en dus de populatieontwikkeling van plaag en natuurlijke vijand, (3) de gewasstructuur en de bladgrootte, (4) de bladstructuur (beharing), en (5) de wittevliegverdeling in het gewas. Factor (1) heeft invloed op de demografische parameters en (1), (3), (4) en (5) beinvloeden het zoekgedrag van de sluipwesp, en als gevolg daarvan de parasiteringsefficiëntie. Door de veelheid aan relaties tussen de drie trofische niveau's (gewas-plaaginsekt-sluipwesp) kunnen de belangrijkste factoren alleen geëvalueerd worden na integratie van alle relevante processen.

Systeemanalyse en simulatie zijn goede instrumenten voor dit doel. Deze benaderingswijze overbrugt het hiaat tussen kennis op individu-niveau en het verkrijgen van inzicht op populatie-niveau. In het hier beschreven onderzoek wordt de kennis over belangrijke processen die een rol spelen bij de interactie tussen witte vlieg en sluipwesp in een gewas geïntegreerd met behulp van een verklarend simulatiemodel. Het doel is om kwantitatief inzicht te verkrijgen in het tritrofische systeem gewas-kaswittevlieg-*E. formosa* om daarmee het succes of het falen van biologische

bestrijding te kunnen verklaren. Het model is *mechanistisch*, dat wil zeggen het verklaart *hoe* witte vliegen en sluipwespen in termen van demografische parameters, en *hoe* sluipwespen, in termen van zoekefficiëntie, het behandelen van wittevlieglarven en de beschikbare ei-voorraad, het geobserveerde parasiteringsniveau realiseren. Mechanistische verklaringen helpen om het succes of het falen van biologische bestrijding in de praktijk te kunnen begrijpen. Het model verklaart niet *waarom* de witte vliegen en sluipwespen zich gedragen zoals dat geobserveerd wordt, in termen van de selectiedruk die op hen van toepassing is. Dus, het model verschaft geen *functionele* verklaring van het geobserveerde gedrag. Dat kan worden bestudeerd met behulp van optimaal fourageermodellen.

Het model simuleert de populatiedynamica van witte vlieg (gastheer) en sluipwesp in een gewas, dat wil zeggen het model berekent het verloop van de aantallen witte vliegen en sluipwespen in de kas gedurende een groeiseizoen. Het is gebaseerd op de ontwikkelingsbiologie van de twee insektesoorten en op het zoek- en parasiteringsgedrag van de sluipwesp, in relatie tot waardplant en kasklimaat. Witte vlieg is sterk geclusterd verdeeld over planten en bladeren en lokale gastheerdichtheden beinvloeden in sterke mate het gedrag van de sluipwesp. Daarom zijn de lokale interacties tussen witte vlieg en sluipwesp erg belangrijk. Het model is uniek wat betreft de benadering van populaties opgebouwd uit individuen en het simuleert het lokale zoek- en parasiteringsgedrag van een groot aantal individuele sluipwespen in een met witte vlieg besmet gewas. Het model is stochastisch, dat wil zeggen dat er rekening gehouden wordt met variatie in gedrag tussen individuen. Ruimtelijke structuur wordt onderscheiden door middel van lokatiecoördinaten van planten en bladeren in het gewas. Op individu-gebaseerde modellen zijn noodzakelijk wanneer lokale interacties en stochasticiteit een belangrijke rol spelen. Met het model zijn we in staat om (1) de capaciteit van *E. formosa* te verklaren om wittevliegpopulaties onder controle te houden op gewassen zoals tomaat, (2) introduktieschema's te verbeteren van de sluipwesp op gewassen waar de bestrijding moeilijker is, en (3) effekten te voorspellen van veranderingen in teeltmaatregelen (e.g. kasklimaat, plantcultivars) op het succes van biologische bestrijding.

In de meeste modellen op het gebied van de populatiedynamica worden waargenomen functionele responscurves gebruikt als invoer. De functionele responscurve is de relatie tussen het aantal geparasiteerde gastheren per sluipwesp per dag en de gastheerdichtheid. Meestal zijn deze curves experimenteel vastgesteld op bladeren en worden zij vervolgens doorgetrokken naar het gewasniveau door de parasiteringssnelheid af te leiden met behulp van de gemiddelde gastheerdichtheid in het gewas. Dit houdt impliciet in dat men aanneemt dat de waargenomen relatie op bladeren ook opgaat op grotere ruimtelijke schaal. Dat is echter onrealistisch in het geval gastheren een sterk geclusterde verdeling vertonen in het gewas en wanneer functionele responscurves niet-lineair zijn.

Opzet van het proefschrift

Toen het onderzoeksprojekt van start ging, was reeds veel onderzoek gedaan aan de demografische parameters van kaswittevlieg en *E. formosa*: de larvale ontwikkelingsduur, de larvale sterfte, de levensduur van de volwassen individuen, de geslachtsverhouding, de eilegcapaciteit gedurende het leven (fecunditeit) en de dagelijkse eileg (ovipositie-frequentie). Verder was uitvoerig onderzoek verricht aan de voorkeur van kaswittevlieg voor diverse waardplanten en voor diverse plaatsen op de plant om zich te voeden en eieren te leggen, aan de geschiktheid van de waardplanten voor kaswittevlieg en aan ruimtelijke verdelingspatronen van kaswittevlieg in een gewas. Van de sluipwesp was het foerageergedrag in bladkooitjes of petrischaaltjes gedetailleerd bestudeerd.

Er was echter niet veel bekend over de tijdsbesteding van de sluipwesp op het blad, wanneer de sluipwesp zelf kon besluiten om te vertrekken. In **Hoofdstuk 2, 3 en 4** worden de hiaten in kennis geïdentificeerd en wordt experimenteel onderzoek hieraan beschreven, om zodoende het foerageerproces van de sluipwesp van het moment van landen op het blad tot wegvliegen te kunnen kwantificeren. Deze hoofdstukken beschrijven experimenten waarin foeragerende sluipwespen voortdurend worden geobserveerd op tomateblaadjes tot ze wegvliegen.

De gegevens van Hoofdstuk 3 en 4 worden gebruikt als invoer in de simulatiemodellen die beschreven worden in **Hoofdstuk 5, 6 en 7**. In deze hoofdstukken wordt het foerageergedrag van *E. formosa* bestudeerd met behulp van een stochastisch simulatiemodel op drie ruimtelijke niveau's: in een klein bladkooitje, op een tomateblaadje en op een tomateplant.

In **Hoofdstuk 8 en 9** wordt een overzicht gegeven van de demografische parameters van de kaswittevlieg en *E. formosa*. Met behulp van literatuurgegevens zijn deze parameters bepaald als functie van temperatuur door middel van niet-lineaire regressie.

Hoofdstuk 10 beschrijft het uiteindelijke model dat de populatiedynamica simuleert van de interactie tussen witte vlieg en de sluipwesp in een tomategewas. Dit model is opgebouwd uit verschillende submodellen, o.a. uit het model van het foerageergedrag van de sluipwesp op tomateblaadjes uit Hoofdstuk 6. Gegevens uit Hoofdstuk 8 en 9 voor tomaat zijn gebruikt als invoergegevens om de populatieontwikkeling van de twee soorten te simuleren.

Hieronder volgt de samenvattende discussie van **hoofdstuk 11** waarin de wetenschappelijke en praktische conclusies van het onderzoek en de toekomstplannen voor verder onderzoek uiteengezet worden.

Directe waarneming van het fourageergedrag van *E. formosa*

Eerder onderzoek leidde tot het volgende beeld van het gedrag van de sluipwesp. *E. formosa* is een solitaire, larvale sluipwesp van witte vlieg: vrouwtjes leggen één ei per gastheer gedurende een parasitering. De sluipwesp is synovigeen, dat wil zeggen dat elke dag nieuwe eieren afrijpen wanneer de ei-voorraad van de sluipwesp lager wordt dan de opslagcapaciteit, die voor *E. formosa* 8-10 eieren is. Ongeveer tien dagen na parasitering verpopt de sluipwesplarve in de pop van de gastheer, die in het geval van kaswittevlieg dan zwart kleurt, waardoor geparasiteerde poppen duidelijk zichtbaar worden. Een *E. formosa* populatie bestaat vrijwel geheel uit vrouwtjes; mannetjes komen nauwlijks voor. Vrouwelijke sluipwespen produceren dochters zonder te paren (parthenogenese).

De sluipwesp zoekt naar de immobiele wittevlieglarven en poppen door van blad naar blad te vliegen, zonder daarbij vóór het landen onderscheid te maken tussen wel- of niet-besmette planten of bladeren. Eenmaal op het blad begint de sluipwesp te lopen en met haar antennes op het blad te trommelen op zoek naar gastheren. Deze worden lukraak ontmoet en het looppatroon van de sluipwesp verandert niet na een ontmoeting met een gastheer. Na het ontdekken van een gastheer kunnen vier gedragingen worden onderscheiden: de sluipwesp kan de gastheer afwijzen na een inspectie met haar antennes of nadat de legboor in de gastheer is gestoken, ze kan de gastheer parasiteren door er een ei in te leggen (ovipositie), of ze kan de gastheer als voedselbron gebruiken en leegzuigen (voeden met gastheren = gastheervoeding).

Deze eerdere experimenten hadden echter nog niet geleid tot een volledig beeld van het fourageergedrag. Kwantitatieve gegevens over somminge aspecten ontbraken, zoals de zoek- of loopactiviteit van de sluipwesp op het blad en het effect van temperatuur op de fourageerprocessen. In veel van de eerdere experimenten werden de sluipwespen opgesloten in een bladkooitje of petrischaaltje. Daarom was er weinig bekend over de tijdsbesteding van de sluipwesp op het blad, zoals de tijd tot vertrek van het blad, de tijd doorgebracht op de boven- en onderkant van het blad, en beinvloeding van deze tijdsbestedingen door ontmoetingen met, of oviposities in gastheren.

Hoofdstuk 2, 3 en 4 beschrijven experimenten waarin individuele sluipwespen voortdurend werden geobserveerd totdat ze van het blad wegvlogen. Deze proeven zijn gedaan met schone tomateblaadjes, met blaadjes met honingdauw, en met blaadjes met alleen ongeparasiteerde en met alleen geparasiteerde wittevlieglarven. In Hoofdstuk 2 worden de verblijfstijden van de sluipwespen op de blaadjes beschreven. In Hoofdstuk 3 wordt de neiging van de sluipwesp gekwantificeerd om van het blad te vertrekken en de effecten hierop van temperatuur en verschillende ervaringen met gastheren op het blad. In Hoofdstuk 4 worden andere onderliggende processen van het fourageren gekwantificeerd, zoals de loopsnelheid en loopactiviteit van de sluipwesp, de kans op één van de vier gedragingen na een ontmoeting met een gastheer en de duur van zo'n gastheerbehandeling. Met deze gegevens is het fourageerproces van *E. formosa* vanaf landen op het blad tot vertrek gekwantificeerd. Voor een overzicht van de

achtereenvolgende fourageerprocessen wordt verwezen naar figuur 1 van Hoofdstuk 4. Het werk beschreven in Hoofdstuk 2, 3 en 4 heeft tot de volgende resultaten geleid:

- De sluipwesp *E. formosa* zoekt lukraak naar gastheren op het blad, zonder een voorkeur te hebben voor de rand of het middengedeelte van het blad, of voor de boven- of onderkant van het blad, terwijl wittevlieglarven (de gastheren) alleen op de onderkant van een tomateblaadje voorkomen.
- De mediane verblijfstijd van de sluipwesp (ofwel de opgeeftijd = giving up time, GUT) op schone tomateblaadjes is 18.6 min bij 20, 25 en 30°C en hetzelfde op een besmet blaadje wanneer geen gastheren ontmoet worden.
- De sluipwespen blijven langer op het blad na ontmoetingen met gastheren, en met name na oviposities in ongeparasiteerde gastheren. Ze blijven ook langer na ontmoetingen met geparasiteerde (ongeschikte) gastheren en na contact met honingdauw. De opgeeftijd na de laatste ontmoeting met een gastheer is steeds 18.6 min, ook als de gastheer geparasiteerd is, maar wordt verlengd tot 40 min na de eerste ovipositie in een ongeparasiteerde gastheer op het blad.
- De sluipwespen blijven langer op de onderkant van het blad na ontmoetingen met gastheren, en met name na oviposities in ongeparasiteerde gastheren. De mediane tijd vanaf het begin op een bepaalde bladkant, of als dat plaats vond, vanaf de laatste gastheerontmoeting op die bladkant tot het verplaatsen naar de andere bladkant (tijd tot wisselen = time until changing, TUC) is 11.6 min, maar wordt 5.7 min wanneer beide bladkanten bezocht zijn door de sluipwesp. Na de eerste ovipositie in een ongeparasiteerde gastheer wordt deze tijd (TUC na laatste gastheerontmoeting) op de bladonderkant twee keer zo lang.
- De sluipwespen vertrekken meestal vanaf de bladbovenkant, waar geen gastheren aanwezig zijn.
- Het vertrekgedrag van de sluipwesp van een blad kan worden beschreven met een zogenaamd 'stochastisch-drempelwaarde mechanisme', dat gekarakteriseerd wordt door een bepaalde neiging (kans per tijdseenheid) om te vertrekken. De sluipwesp vertrekt nadat de ontmoetingssnelheid met gastheren beneden een bepaalde drempelwaarde komt. Deze drempelwaarde (ontmoetingen per tijd, ofwel 1/GUT) is echter geen constante, maar vertoont grote variatie en wordt uitgedrukt als een kans.
- De loopsnelheid van de sluipwesp neemt lineair toe met de temperatuur tussen 15 en 25-30°C.
- De loopactiviteit van de sluipwesp is erg laag bij temperaturen beneden 18°C, en bedraagt ongeveer 75% van de totale tijd op het blad bij 20, 25 en 30°C. De loopactiviteit wordt niet beinvloed door ontmoetingen met gastheren, maar neemt wel af met afnemende ei-voorraad van de sluipwesp na ca. 4 oviposities.
- Het percentage ontmoetingen dat resulteert in een ovipositie is ca. 75% voor het meest geprefereerde gastheerstadium (ongeparasiteerde L4 larve). Dit percentage neemt af met afnemende ei-voorraad van de sluipwesp.
- Het behandelingsgedrag van de gastheer door de sluipwesp en de behandelingsduur worden niet beinvloed door de waardplant.

- De totale behandelingsduur (inclusief het trommelen met de antennes etc.) voor afwijzing van een ongeparasiteerde gastheer na inspectie met de antennes is ca. 20 s, voor afwijzing na inbrenging van de legboor en voor ovipositie ca. 6 min, en voor het zich voeden met de gastheer ca. 15 min. Deze tijden veranderen iets als de gastheren geparasiteerd zijn.
- Zelf-superparasitisme, waarbij door een sluipwesp een ei gelegd wordt in een gastheer die al eerder door dezelfde sluipwesp geparasiteerd was, is niet waargenomen voor *E. formosa*. Opvolgend-superparasitisme ('conspecific'), waarbij het ei gelegd wordt door een andere sluipwesp, komt voor in 14% van de ontmoette gastheren die reeds een sluipwesp-ei bevatten. Superparasitisme is niet meer waargenomen wanneer het sluipwesp-ei zich ontwikkeld had tot een larve.
- Er is geen verschil gevonden in het behandelingsgedrag van gastheren door naieve of door ervaren sluipwesp-vrouwtjes.
- Veel inactieve sluipwespen worden waargenomen nadat de luchtdruk gedaald was gedurende een periode van tenminste 12 uur.

Simulatiemodellen van het foerageergedrag van *E. formosa*

De zojuist beschreven informatie is gebruikt als invoer in de simulatiemodellen van het foerageergedrag van *E. formosa* in **Hoofdstuk 5, 6 en 7**. Hier is het foerageergedrag geanalyseerd met behulp van Monte Carlo simulatie op drie ruimtelijke niveau's: in een kleine experimentele arena, op een tomateblaadje en op een tomateplant. Voor een overzicht van de modellen wordt verwezen naar de stroomdiagrammen (de figuren 1) in deze hoofdstukken. Het foerageergedrag is eerst bestudeerd op deze kleine ruimtelijke schaal om het kwantitatieve effect van de sluipwesp op wittevliegpopulaties in een gewas beter te kunnen begrijpen.

Het gesimuleerde aantal ontmoette, geparasiteerde en geconsumeerde gastheren, en de gesimuleerde verblijfstijd van sluipwespen op het blad zijn gevalideerd met experimentele gegevens. De simulatieresultaten komen goed overeen met deze gegevens. Volgens het model kan *E. formosa* op een tomateblaadje bij 25°C gemiddeld 16 gastheren per dag parasiteren, als de sluipwespen beginnen met een maximale ei-voorraad en als de gastheerdichtheid niet beperkend is. Dit houdt in dat er ongeveer 7 nieuwe eieren worden aangemaakt gedurende een dag van 16 uur bij 25°C. Vanaf de tweede dag kan de sluipwesp dagelijks nog maar gemiddeld 11 gastheren parasiteren. Dit wordt veroorzaakt door ei-beperking: als de sluipwesp de dag ervoor al haar eieren gelegd heeft, dan rijpen er bij 25°C ca. 4 eieren gedurende de daaropvolgende nacht van 8 uur, zodat de sluipwespen de volgende morgen geen maximale ei-voorraad hebben.

Het model laat zien dat bij een dichtheid van 1 L3 larve per tomateblaadje 15.7% van de sluipwespen die larve ontdekken voordat ze wegvliegen. Ook bij hogere gastheerdichtheden worden niet alle gastheren ontmoet en plekken (blaadjes) met gastheren worden niet na één bezoek volledig geparasiteerd. De variatie in het aantal ontmoetingen en oviposities tussen sluipwespen is aanzienlijk, voornamelijk door het

lukraak ontmoeten van gastheren, door de variatie in behandeling van een ontmoette gastheer en door variatie in opgeeftijd (GUT) en tijd tot wisselen van bladhelft (TUC).

In de kas vertoont witte vlieg een geclusterde verdeling over planten en bladeren en het gemiddeld aantal witte vlieg per plant is meestal erg laag. De modellen laten zien dat onder zulke omstandigheden het aantal parasiteringen op tomateblaadjes of planten sterk afhankelijk is van de volgende parameters: de bladgrootte, de loopsnelheid en de loopactiviteit van de sluipwesp, de kans op ovipositie na ontmoeting met een gastheer, de initiële ei-voorraad van de sluipwesp (de ei-voorraad aan het begin van het experiment), en de verhouding tussen zoektijden op boven- en onderkant van het blad. Bij extreem hoge gastheerdichtheden zijn de ei-opslagcapaciteit en de initiële ei-voorraad van de sluipwesp het meest belangrijk. Op planten met een geclusterde gastheerverdeling speelt dan ook de GUT van de sluipwesp een belangrijke rol.

Op alle ruimtelijke niveau's die getest zijn, neemt het aantal gastheer-ontmoetingen, oviposities en gastheervoedingen in afnemende mate toe met de gastheerdichtheid, totdat een maximum niveau bereikt wordt. Deze vorm van de curve komt overeen met die van een 'Holling-type-II-functionele-respons', en wordt veroorzaakt door de afnemende loopactiviteit van de sluipwesp en de afnemende kans op ovipositie na een gastheerontmoeting wanneer de ei-voorraad afneemt. Dit effect is dominant op alle ruimtelijke niveau's, en zelfs een toename in GUT van 18.6 naar 40 min na de eerste ovipositie op het blad veroorzaakt geen S-vormige curve. De vorm van de curve beschrijft enkel het effect van gastheerdichtheid op parasitisme als resultaat van de onderliggende processen. Het helpt de dynamica van de gastheer-parasitoid interactie op populatieniveau beter te begrijpen. In het geval van een Type II functionele respons neemt het percentage parasitisme af met toenemende gastheer-dichtheid en parasitisme is dus omgekeerd-dichtheidsafhankelijk. Bij een toenemende gastheerdichtheid wordt dan de per capita parasiteringsdruk veroorzaakt door één sluipwesp lager. Volgens de theorie heeft omgekeerde dichtheidsafhankelijkheid een destabiliserend effect op de dynamica op populatieniveau. De functionele respons van of de parasiteringsdruk veroorzaakt door één sluipwesp is echter slechts één van de factoren die een rol spelen op populatieniveau. Een andere factor is het *aantal* sluipwespen op het blad. Voor *E. formosa* hangt het effect op populatieniveau af van de balans tussen de parasiteringsdruk veroorzaakt door één sluipwesp en het langer blijven op een blad na een ervaring met een gastheer en de daarmee gepaard gaande aggregatie van sluipwespen op bladeren met hoge gastheerdichtheid (zie Hoofstuk 10).

Demografische parameters van de kaswittevlieg en *E. formosa*

In **Hoofdstuk 8 en 9** wordt een overzicht gegeven van de demografische parameters van de kaswittevlieg en *E. formosa*. Literatuurgegevens werden verzameld over de ontwikkelingssnelheid van ieder onvolwassen insektestadium, de sterfte gedurende ieder stadium, de levensduur van het volwassen stadium, de geslachtsverhouding, de pre-oviposite periode van de volwassen vrouwtjes, de periode waarin de dagelijkse oviposite toeneemt tot een maximum niveau, de eilegcapaciteit gedurende het leven

(fecunditeit) en de dagelijkse eileg (ovipositie-frequentie). In de meeste experimenten werd het effect van temperatuur op deze parameters bestudeerd, zonder naar andere factoren te kijken, zoals luchtvochtigheid of licht. Met deze literatuurgegevens werden met behulp van niet-lineaire regressie de relaties bepaald tussen de demografische parameters en de temperatuur. Vijf wiskundige vergelijkingen werden getest, waarbij de beste werd geselecteerd op basis van de coëfficiënt van determinatie (r^2) en visuele beschouwing van de curves. Dat laatste was nodig om na te gaan of de curves wel biologisch realistisch waren, met name de staarten van de curves. De coëfficiënten die de demografische parameters beschrijven als functie van temperatuur worden in deze hoofdstukken vermeld. De coëfficiënten van variatie (*cv*: sd/gemiddelde) tussen individuen zijn ook gegeven. Al deze coëfficiënten worden gebruikt als invoergegevens in de submodellen van populatieontwikkeling van witte vlieg en sluipwesp (zie Hoofdstuk 10).

De demografische parameters van kaswittevlieg zijn erg afhankelijk van de waardplant. Voor *E. formosa* zijn de gegevens van diverse waardplanten gecombineerd. De hoge r^2-waardes laten zien dat waardplanteffecten kunnen worden verwaarloosd voor de demografische parameters van de sluipwesp, behalve voor ovipositie bij lage gastheerdichtheden. Dit wordt veroorzaakt door verschillen in de loopsnelheid en loopactiviteit van de sluipwesp op bladeren met een verschillende morfologie. Het stadium van de oorspronkelijk geparasiteerde gastheer heeft een belangrijk effect op de ontwikkelingssnelheid en sterfte van de onvolwassen sluipwesp in de gastheer.

De ontwikkelingssnelheid is berekend als omgekeerde van de duur van een stadium (1/duur). Voor alle onvolwassen stadia van witte vlieg en sluipwesp kan de relatie tussen ontwikkelingssnelheid en temperatuur het beste beschreven worden door de Logan-curve: net boven de drempeltemperatuur neemt de ontwikkelingssnelheid exponentieel toe tot een optimum bereikt wordt, waarna hij snel afneemt tot de lethale maximum temperatuur bereikt wordt. De levensduur, fecunditeit en ovipositie-frequentie van de volwassen vrouwtjes als functie van de temperatuur kunnen het best beschreven worden met behulp van de Weibull-curve: deze parameters nemen exponentieel toe vanaf de minimumtemperatuur tot een optimum, waarna ze exponentieel afnemen. Alleen voor *E. formosa* nam de levensduur van volwassen sluipwespen exponentieel af met de temperatuur en een optimum werd niet gevonden bij normale kastemperaturen. Voor sommige parameters werd geen significant verband met temperatuur gevonden, zoals de sterfte tijdens de onvolwassen stadia, de geslachtsverhouding en de *cv*-waardes van de demografische parameters van witte vlieg en sluipwesp.

Simulatiemodel van de witte vlieg-sluipwesp interactie in een gewas

Het uiteindelijke model simuleert de populatiedynamica van de plaag-sluipwesp interactie in een tomategewas en wordt beschreven in **Hoofdstuk 10**. Het model is gebaseerd op het zoek- en parasiteringsgedrag van de sluipwesp en op de ontwikkelingsbiologie van de twee insektesoorten. Het model is opgebouwd uit diverse submodellen, zoals het submodel voor de populatieontwikkeling van witte vlieg, voor

de populatieontwikkeling van de sluipwesp, voor het foerageergedrag van de sluipwesp op tomateblaadjes (model van hoofdstuk 6), voor de ruimtelijke verdeling van witte vlieg en sluipwesp in het gewas, voor de verplaatsing van volwassen witte vliegen en sluipwespen van blad naar blad, voor de produktie van nieuwe bladeren en een submodel voor het nagaan van fouten tijdens de simulatie. Demografische parameters van Hoofdstuk 8 en 9 worden gebruikt als invoergegevens in de submodellen voor de populatie-ontwikkeling van witte vlieg en sluipwesp op tomaat. Voor een overzicht van het model wordt verwezen naar de relatiediagrammen (figuren 1, 2 en 3) van Hoofdstuk 10. Het model is uniek in het feit dat individuen centraal staan. Het lokale zoek- en parasiteringsgedrag van een groot aantal individuele sluipwespen wordt gesimuleerd in een met witte vlieg besmet gewas. Het model is stochastisch, dat wil zeggen dat er rekening gehouden wordt met variatie in gedrag tussen individuen. Er wordt ook rekening gehouden met de ruimtelijke structuur: de positie van de witte vliegen en sluipwespen in het gewas wordt bijgehouden met behulp van lokatiecoördinaten van planten en bladeren.

Het model is gevalideerd met populatietellingen van experimenten op tomaat waarbij sluipwespen wel of niet werden geintroduceerd. Deze experimenten zijn gedaan in kleine kascompartimenten en in een grote, commerciele kas. Wanneer geen sluipwespen zijn geintroduceerd, komt de gesimuleerde populatietoename van kaswittevlieg goed overeen met de observaties. Dit resultaat kan voor een groot deel worden toegeschreven aan de nauwkeurige schattingen van de demografische parameters, die gebaseerd zijn op vele experimenten bij sterk uiteenlopende temperaturen (zie Hoofdstuk 8 en 9).

Met deze demografische parameters als invoergegevens in het model is de intrinsieke populatiegroeisnelheid (r_m) van beide insektesoorten gesimuleerd. De r_m van *E. formosa* is veel hoger dan die van kaswittevlieg boven 14°C. De r_m van een sluipwesp speelt echter een beperkte rol voor de biologische bestrijding, omdat zij alleen geldt wanneer alle sluipwespen hun dagelijkse ei-voorraad kunnen leggen. Dit gebeurt alleen bij extreem hoge gastheerdichtheden als de sluipwespen niet veel tijd kwijt zijn met zoeken. In kassen zijn wittevliegdichtheden veel lager en de gerealiseerde wittevliegdichtheid hangt af van de zoekefficiëntie van de sluipwesp. Daarom zijn r_m-waardes onvoldoende voor het evalueren van het succes of falen van biologische bestrijding. Het gebruik van modellen die het zoek- en parasiteringsgedrag van de natuurlijke vijand simuleren bij lage gastheerdichtheid zijn daarvoor essentieel.

Ook wanneer sluipwespen geintroduceerd worden, komen de simulatieresultaten goed overeen met de populatietellingen in een tomatekas. Blijkbaar is de hypothese juist dat *E. formosa* gastheren lukraak ontmoet in een tomategewas. In het model maakt de sluipwesp geen onderscheid tussen onbesmette en besmette blaadjes vóór het landen, en éénmaal op het blad zoekt de sluipwesp lukraak naar gastheren, en blijft langer op het blad na een ontmoeting met een gastheer. Simulaties laten zien dat de verhouding in het aantal volwassen sluipwespen en witte vliegen erg hoog is en kan oplopen tot ca. 250:1. Als gevolg daarvan worden witte vliegen meer onderdrukt dan gereguleerd door de sluipwespen tot extreem lage dichtheden (<0.3 ongeparasiteerde

poppen per plant), maar ze worden niet uitgeroeid. Deze dichtheden zijn veel lager dan de economische schadedrempel voor kaswittevlieg. Het percentage zwarte poppen fluctueert tussen de 40 en 70%. Volgens het model bereiken de volwassen sluipwespen hoge dichtheden tot 7.4 per plant, maar door de lage gastheerdichtheid zoekt niet meer dan 1% van deze sluipwespen op besmet blad.

De opgeeftijden (GUT) van *E. formosa* varieren aanzienlijk. De mate waarin witte vlieg onder controle gehouden wordt, is erg gevoelig voor die GUT-waardes lager dan 800 s van de sluipwespen. Witte vlieg wordt tot veel lagere dichtheden onderdrukt als de sluipwespen *ten minste* vijf minuten door blijven zoeken op ieder blaadje (besmet of onbesmet) en na iedere gastheerontmoeting. Door deze minimale tijd blijven de sluipwespen langer op besmet blad en wordt het uiteindelijke percentage sluipwespen op besmet blad groter, waardoor de kans kleiner wordt dat de geclusterde gastheren ontsnappen aan parasitisme. Wanneer in het model de variatie in GUT wordt uitgesloten, wordt de wittevliegpopulatie instabiel en sterft vrijwel uit. Variatie in GUT op blaadjes heeft tot gevolg dat refugia ontstaan voor de gastheer waar geen of minder parasitisme voorkomt. Ook uit puur theoretische studies is bekend dat gastheer-refugia populaties stabiliseren.

Volwassen witte vliegen migreren steeds naar de jonge bladeren in de top van het gewas. Een langzame produktie van nieuwe bladeren heeft tot gevolg dat de adulten langer op een blad blijven en er meer eieren leggen. Zodoende wordt hetzelfde aantal gastheren verdeeld over minder bladeren, zodat de wittevliegverdeling sterker geclusterd is. Witte vliegen worden dan volgens de simulaties sterker onderdrukt door *E. formosa*. Parasitisme door één *E. formosa* vrouwtje op een tomateblaadje is omgekeerd-dichtheidsafhankelijk, hetgeen veroorzaakt wordt door een afnemende loopactiviteit en een kleinere kans op ovipositie na ontmoeting met een gastheer (Hoofdstuk 5, 6 en 7). Een hogere gastheerdichtheid 'verdund' dus de per capita parasiteringsdruk veroorzaakt door één sluipwesp op het blad. Het effect op het populatieniveau hangt echter af van de balans tussen dit 'verdunningseffect' en de mate waarin *E. formosa* sluipwespen langer blijven en aggregeren op een blad. De sterkere reduktie van de wittevliegpopulatie wanneer ze meer geclustered zijn, wordt dus veroorzaakt door het langer blijven na een ontmoeting met een gastheer en de daaruit voortvloeiende toename in het relatieve aantal sluipwespen op besmette bladeren.

Dit betekent dat het verschil in wittevliegverdeling één van de factoren is die verschillen veroorzaakt in het succes van biologische bestrijding tussen gewassen. Andere factoren voor deze verschillen zijn de grootte, het aantal en het oppervlak (beharing) van bladeren in het gewas. Volgens het model hebben bladgrootte en totaal bladoppervlak een sterk effect op de reduktie van witte vlieg, door het direkte effect op gastheerdichtheid. Verder beinvloeden bladgrootte en bladoppervlak de efficiëntie van *E. formosa* door hun effect op de opgeeftijd (GUT), de loopsnelheid en de loopactiviteit van de sluipwesp.

Een andere belangrijke factor voor het verschil in biologische bestrijding tussen gewassen is de ontwikkelingsduur van de witte vlieg. Het model toont aan dat plantenveredeling gericht op een langere ontwikkelingsduur van wittevlieg-ei tot adult

erg efficiënt is om het aantal plaaginsekten in combinatie met biologische bestrijding flink te reduceren. Ontwikkelingstijden van kaswittevlieg op diverse tomategenotypen verschillen echter weinig van elkaar, en een veel groter verschil is gevonden voor de levensduur van de adulte witte vlieg, de dagelijkse ovipositie en de sterfte tijdens de onvolwassen stadia. Deze parameters hebben een geringer effect op de populatieontwikkeling van witte vlieg.

Deze belangrijke factoren of gewaseigenschappen die het succes van de biologische bestrijding beinvloeden, kunnen niet onafhankelijk van elkaar vergeleken worden. Zo hebben gewassen met grote bladeren meestal een lager aantal bladeren die langzamer geproduceerd worden dan gewassen met kleine bladeren of deelblaadjes. Het gecombineerde effect van de belangrijke factoren kan echter getest worden met het model voor verschillende gewassen of plantevarieteiten.

In biologische bestrijdingsprogramma's worden sluipwespen vaak eerst getest in experimenten op kleine schaal bij hoge gastheerdichtheden, voordat de sluipwesp wordt uitgetest in het veld. Dan wordt echter de dagelijkse maximale eileg van sluipwespen gemeten, terwijl deze studie aantoont dat de maximale ei-voorraad en de ei-afrijpingssnelheid van *E. formosa* geen rol speelt voor de mate van plaagbestrijding bij de zo gewenste lage plaagdichtheden. In commerciele kassen moet de wittevliegdichtheid erg laag zijn wil men over geslaagde biologische bestrijding spreken. Daarom is effektief zoeken naar gastheren door de sluipwesp het meest essentiële proces. Als sluipwespen worden geselecteerd voor biologische bestrijding moet de aandacht vooral uitgaan naar het langer doorzoeken van de sluipwesp op besmette bladeren (minimale GUT), haar loopsnelheid en loopactiviteit, de kans op ovipositie na een gastheerontmoeting, de verhouding in zoektijden op boven- en onderzijde van het blad, en op de levensduur van de volwassen sluipwespen, wanneer verschillende synovigene en solitaire sluipwespen die een lukraak zoekgedrag vertonen worden vergeleken. Deze karakteristieke eigenschappen van sluipwespen zijn relatief eenvoudig te meten in laboratoriumproeven. Nogmaals, ook deze eigenschappen kunnen niet onafhankelijk van elkaar worden vergeleken, omdat de eigenschappen vaak in bepaalde combinaties aangetroffen worden in de natuurlijke vijanden. Het gecombineerde effect van deze eigenschappen kan wel met het model getest worden.

Epiloog

Het in dit proefschrift beschreven onderzoek richtte zich op het integreren van kennis over de belangrijke processen die een rol spelen bij de interactie tussen witte vlieg en *E. formosa* in een gewas. Door de veelheid aan relaties tussen de drie trofische niveau's (gewas-plaaginsekt-sluipwesp) werd gekozen voor een combinatie van experimenteel onderzoek en simulatiestudies. Het doel was om kwantitatief inzicht te verkrijgen in het tritrofische systeem zodat het falen of slagen van biologische bestrijding kan worden verklaard. Met het model hebben we nu het inzicht verkregen hoe *E. formosa* witte vlieg in tomaat onder controle kan houden. Het onderzoek heeft geleid tot een duidelijk beeld van de belangrijke onderliggende processen die een rol spelen bij de interactie tussen witte vlieg en natuurlijke vijand. Bij de lage plaag-

dichtheden die in kassen gerealiseerd moeten worden, zijn de demografische parameters van de sluipwesp, vaak samengevat in een r_m-waarde, minder belangrijk dan de zoekcapaciteit van de sluipwesp. Dit toont aan dat als aanvulling op de traditionele selectiecriteria, een criterium gebaseerd op zoekefficiëntie essentieel is. Het onderzoek heeft verder geleid tot uitgebreide kennis van het foerageergedrag van *E. formosa*. Het enorme effect van variatie in zoektijden van individuele sluipwespen op bladeren toont aan dat op-individu-gebaseerde, stochastische modellen van lokaal zoekgedrag nodig zijn wanneer de gastheer-parasitoid interactie bij extreem lage gastheerdichtheden en geclusterde gastheerverdelingen gesimuleerd wordt.

Eén van de belangrijke vragen van het onderzoek was om de hoofdoorzaken te identificeren voor het verschil in het succes van biologische bestrijding van kaswittevlieg tussen gewassen. De sluipwesp is succesvoller op tomaat dan op komkommer of gerbera. Het onderzoek toont aan dat de aandacht gevestigd dient te worden op het langer doorzoeken van de sluipwesp op besmet blad (GUT), de loopsnelheid en loopactiviteit van de sluipwesp, de ontwikkelingsduur van witte vlieg en het aantal, de grootte en de produktie van bladeren in het gewas. Deze parameters zijn ook gekwantificeerd voor komkommer en gerbera en sommige verschillen aanzienlijk van die op tomaat (zie Hoofdstuk 2, 3 en 8). De volgende stap in het onderzoek is om het simulatiemodel van Hoofdstuk 10 te gebruiken voor de andere twee gewassen en om de hoofdoorzaken voor succes of falen van biologische bestrijding te evalueren.

Als de parameters van het model zijn aangepast voor komkommer en gerbera, zijn we in staat om (1) te verklaren waarom *E. formosa* op die gewassen witte vlieg moeilijker onder controle kan houden, (2) de introduktieschema's voor sluipwespen te verbeteren voor deze gewassen, en (3) de effecten te voorspellen van veranderingen in teeltmaatregelingen (e.g. kasklimaat, plantcultivars) op het succes van biologische bestrijding. Verder kunnen we met het model de eigenschappen identificeren die een efficiënte natuurlijke vijand zou moeten hebben. Deze eigenschappen kunnen dan worden gebruikt als evaluatiecriteria tijdens de selectie van een natuurlijke vijand. In feite kunnen ideotypes van natuurlijke vijanden ontworpen worden, afhankelijk van gewas, witte vlieg en kasklimaat. Op deze manier kan een nieuw terrein van 'oecologisch ontwerpen' verkend worden. Het onderzoek heeft al geleid tot de belangrijke selectiecriteria wanneer verschillende synovigene, solitaire sluipwespen die lukraak zoekgedrag vertonen worden vergeleken. Het model kan worden aangepast voor andere sluipwespen met verschillende foerageerstrategieen of voor andere natuurlijke vijanden van witte vlieg.

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Curriculum vitae

Hermanus Johannes Wilhelmus van Roermund werd geboren op 19 juli 1958 te Hengelo(o). Vanaf 1971 bezocht hij het R.K. Lyceum de Grundel, alwaar in 1977 het diploma Atheneum-B behaald werd. In datzelfde jaar begon hij een studie Planteziektenkunde aan de Landbouwuniversiteit in Wageningen. In 1978 en 1981 werden respectievelijk de propaedeuse en het kandidaatsexamen behaald (cum laude), waarna hij gedurende 8 maanden onderzoek verrichtte aan het Forest Pest Management Institute in Sault Ste Marie, Ontario, Canada. Na deze stagetijd werd de studie in Wageningen vervolgd met een viertal doctoraalvakken aan de vakgroepen Fytopathologie (2x), Entomologie en Theoretische Produktie-ecologie, waarna in het begin van 1985 het doctoraaldiploma behaald werd. In dat jaar begon hij als wetenschappelijk medewerker in tijdelijke dienst bij de vakgroep Theoretische Produktie-ecologie. Onderwijs in de populatiedynamica in Wageningen werd afgewisseld met onderwijs in simulatie van primaire produktie in Indonesie, Zambia, Ethiopie en Syrie. Onderzoek werd uitgevoerd waarin systeem-analyse en simulatie gebruikt werden om schade door ziekten en plagen in gewassen te bestuderen. In 1987 en 1988 vond dit onderzoek plaats in samenwerking met de Stichting voor Plantenveredeling (nu onderdeel van het CPRO-DLO) in Wageningen. In 1989 begon hij als wetenschappelijk medewerker in tijdelijke dienst bij de vakgroep Entomologie aan het in dit proefschrift beschreven onderzoek. Vanaf 1995 werd dit onderzoek gecontinueerd als post-doc projekt in samenwerking met de vakgroepen Tuinbouwplantenteelt en Theoretische Produktie-ecologie.