In the name of Allah The Compassionate The Merciful

To my late dear mother and father

BIOLOGICAL CONTROL OF GLASSHOUSE *Myzus persicae* (Sulzer) USING *Aphidius matricariae* Haliday.

BY

SAIF ELDIN MOHAMED KHEIR HAG AHMED

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Department of Biological Sciences
Wye College
University of London

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ABSTRACT

A review is presented on principles, status and future prospects in biological control with special reference to hymenopterous parasitoids as well as biology and status of both the green peach aphid Myzus persicae and Aphidius matricariae. A combination of laboratory and glasshouse experiments were carried out to examine the aphid-parasitoid system, to evaluate the potential of A. matricariae as a biological control agent against M. persicae.

The effect of temperature on development, longevity and fecundity was studied. Development rate of both species increased with a rise in temperature up to 24°C. Temperature constants were calculated for both species. The lower threshold for the parasitoid was a little higher than that of its host. An inverse relationship between temperature and longevity was found. Survivorship data was analysed using different methods, but it was best described using the Weibull function. There was an optimum range of temperature for each species outside of which fecundity declined. The effect of cycling temperature in the laboratory and fluctuating temperatures in the glasshouse on development of both species was investigated. Thermal summation and polynomial models based on laboratory temperature data was used to predict development of both species under the varying conditions of the glasshouse. The polynomial model was found to be more accurate. The intrinsic rate of increase for A. matricariae exceeded that of M. persicae within the range (12-24°C). A polynomial model was developed that more accurately predicted the effect of temperature on the intrinsic rate of increase of both species than previous models.

The effect of different aphid host densities on longevity, fecundity, functional response, superparasitism and demographic statistics of A. matricariae was studied. Survivorship was found to be independent of host density. Fecundity, hence intrinsic rate of increase, decreased with falling host density. The parasitoid showed a typical type 2 functional

response. The models used, especially the random parasitoid equation, provided a good fit to the data. The frequency distribution of parasitoid larvae were generally at random at low host density but differed significantly from random at high host densities indicating the parasitoids ability to distinguish between parasitized and unparasitized hosts.

Searching efficiency was influenced by the morphology of leaves, the structure of the plant and the presence of honey-dew or aphids.

Female parasitoids showed a positive response to odours emanating from the host aphids, aphid exuviae and honey-dew, but not from host plants. Female parasitoids were mainly attracted to green colour.

A. matricariae exhibited a tendency to aggregate at high host densities of their host. Parasitism by A. matricariae reduced fecundity and survival rates, and consequently the intrinsic rate of increase of their host aphid. The degree of severity depended on aphid age at the time of parasitization.

The parasitoid appeared to have some attributes essential for a successful biological control agent such as high searching efficiency, ability to aggregate in patches of high host density and high fecundity rates. The ability of the parasitoid to regulate or suppress its host and to maintain its own populations is due largely to the turnover rate of successive parasitoid generations which is mainly influenced by temperature. A. matricariae could be a potentially useful biological control agent for controlling M. persicae on secondary host plants in glasshouses over 12-24°C temperature range.

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GENERAL INTRODUCTION

Pests are species whose existence conflicts with people's profits, convenience or welfare (Clark, Geir, Hughes and Harris, 1967). The injuriousness of pests varies according to the nature of their damage, to the degree of man's sensitiveness to this destruction and to the numbers in which they occur. The control objective is mainly to reduce the numbers of a pest to levels at which the species ceases to be injurious.

Myzus persicae perhaps is the most important aphid pest in glasshouses in Britain. Attempts to control the aphid using chemicals so far have been unsuccessful or only partially successful. There is a special need for biological control or an integrated control approach.

The potential of biological methods in pest control is immense. The biological control is applied in practice by introducing or encouraging the density dependent regulating agents, such as predators, parasitoids and diseases. All major pests are attacked by a variety of natural enemies and these may be used as a primary means of control or as part of an integrated control programme (Varley, Gradwell & Hassell, 1980). Natural enemies complex of M. persicae is diverse. Few pathogens are capable of causing high mortality in aphid populations. Among these the fungi Entomophthora contains the most species that inflict epizootics in aphid population. The fungi Verticillium lecanii was used for control of aphids in glasshouses. A variety of predator species attack aphids, including Coccinellidae, Syrphidae, Anthocoridae, Chrysopidae and Cecidomyidae. The aphid parasitoids are mainly the hymenopterous Aphelinidae and Aphidiidae. Hymenopterous parasitoids of aphids have provided some of the more spectacular successes in the biological control of agricultural pests (Caltagirone, 1981). Their generally high fecundity, narrow host range and ability to find hosts over a broad range of densities have been noted as the possible reasons of their effectiveness (Hagen & van den Bosch, 1968).

However, few species have been studied in detail to allow an objective assessment of their use in biological control. This study was initiated to assess the effectivenesss of the parasitoid Aphidius matricariae in controlling the green peach aphid Myzus persicae. A. matricariae is an internal parasite of M. persicae; it can readily be found in the field and in glasshouses where it can parasitize M. circumflexus Buckt. and Aulacorthum solani Kalt. (Vevai, 1942). For a rational biological control we must know the insect pest and its parasitoid. Much of the previous research has focused on the morphology and biology of A. matricariae (Vevai, 1942; Rabasse & Shalaby, 1980; Giri, Pass, Yeargan & Parr, 1982). Little is known about ecology, population dynamics, searching behaviour and quantitative assessment of A. matricariae. The study of numerical changes occuring in a population is variously known as population dynamics, demology or larithmics and is really nothing more than quantitative population ecology, concerned not only with describing how population size of species varies in time and space, but also with separating out and understanding the processes which cause the variation (Coppel & Mertins, 1977).

A number of approaches have been adopted to gain knowledge of the parasitoid and its host including observational, descriptive, experimental ecological and biological studies. For population dynamics, the development of life tables is an important approach to data acquisition about an insect. Life tables allow us to identify biometrically the stage and factors in that stage that are most likely causative of variability in population density.

In order to take full advantage of the environmental pressures that are constantly being exerted against an aphid and its parasitoid we must learn more about their responses to such factors as temperature.

The information of practical importance to the ecologist is usually the speed of increase of population not the individual factors producing it, such as longevity, development and fecundity. Conclusions based only on

these individual factors without calculating intrinsic rate of increase are likely to be misleading because the maximum response to various factors may occur at different temperatures, or different densities, etc and because of interactions between these factors. Therefore the calculation of intrinsic rate of increase would serve as an important tool to understand the effect of various factors on population increase.

Host selection is an essential and complex behavioural component of any host-parasite relationship. The organisms involved must be seasonally, geographically, and ecologically coincident and physical, behavioural or physiological barriers must not be present (Doutt, 1964b). Mechanisms involved in host selection including vision and olfaction ecology, the influence of plant structure, leaf morphology should be known.

Since the selection of suitable hosts by parasitoids is crucial for survival of its progeny, host discrimination and the question of superparasitization is investigated.

The study of parasitoid-host population interactions such as functional and aggregative responses offers the numerical data for estimating the number of parasitoids required to regulate the estimated pest populations.

As a part of study of the population dynamics of green peach aphid the assessment of consequences of parasitism by A. matricariae is important.

The objective of this study is to exploit the knowledge about factors limiting the efficiency of A. matricariae and improve their performance by proper management. Such management will be easier to devise if the complex interactions which are involved in host-parasitoid system are appropriately described by a mathematical models.

SECTION 1 LITERATURE REVIEW

1.1 BIOLOGICAL CONTROL

1.1.1 HISTORY & CONCEPT

A century after the well-publicized successful introduction for the biological control of a pest, biological control has been proved to be an effective component of control programmes against pests (Waage & Greathead, 1988). DeBach (1964) defined natural control as the maintenance of a more or less fluctuating population density of an organism within certain definite upper and lower limits over a period of time by the action of abiotic and/or biotic environmental factors. Natural control is commonly referred to as the balance of nature or natural balance which is defined as the tendency of population densities of all species in the same general area to maintain a more or less consistent numerical relation to each other due to interaction between each other and between the physical environment (Huffaker, 1958). Fiske (1910) suggested that parasites and predators regulated populations of the pest by a simple negative feedback system and later the term density dependent factor was proposed by Smith (1935) to describe this effect. The term biocontrol was first used by Smith (1919) to describe the introduction of exotic insect natural enemies for permanent suppression of insect pests. It has since been applied to include virtually all pest control measures except the application of chemical pesticides. Biological control in its narrow classical sense is usually restricted to the introduction by man of parasites, predators and pathogenic micro-organisms to suppress populations of plants or animal pests (Coppel & Mertins, 1977). The first most famous classic example of biological control was the control of a citrus pest, the cottony cushion scale Icerya purchasi Mask. by a predatory coccinellid beetle Rodolia = (Vedalia) cardinalis (Muls.) (Doutt, 1964a). The cottony cushion scale is native to Australia and was introduced to California with imported citrus plants

without its natural enemies. The scale soon became a threat to the citrus industry in California. An entomologist was sent to Australia where he discovered that the scale is attacked by a number of natural enemies, two of these were a parasite fly Cryptochaetum icerya and the Vedalia beetle. Both species were liberated in 1888, and soon became established but the beetle was the more successful one. Within a year a startling high degree of control had been obtained throughout the citrus growing area in California at a total cost of less than $3000. To this day the Vedalia continues to give a satisfactory control of the cottony cushion scale in California and the savings it has brought to citrus growers there have been incalculable. Most cases of successful biological control have followed a similar pattern.

1. The search for natural enemies in the country of the origin of the pest.

2. The importation of one or more of these natural enemies and screening for possible injurious effects.

3. The establishment of one or more of released parasites after large scale breeding.

4. Their increase in numbers folowed by a decline in pest population.

5. The stable co-existence of host-parasite at low densities in relatively stable interactions at very much reduced population densities.

With the discovery of modern synthetic insecticides, e.g. D.D.T, during World War 2, it was expected that the problems of pest control would be solved within a few years. Thus the development of such powerful synthetic insecticides has led to negligence of biocontrol. However, the limitations of these chemicals, mainly organochlorine compounds, soon became obvious with the development of resistance in the insect pests against which the chemical control was aimed. The indiscriminate nature of most pesticides led to the death of many beneficial insect pollinators, predators and parasites. The resurgence of major pests and outbreaks of previously minor

pests which emerged to pest status. The increasing costs of chemicals. Pollution of the environment as most of these chemicals are persistent with long residual effects. Plant phytotoxicity, e.g. cucurbits, proved to be sensitive to organochlorine compounds. Toxicity to mammals. D.D.T and Lindane are found to be concentrated in animals at the ends of food chains in places far from the sites where insecticides have been used. A recent report from U.S Natural Resources Defence Council has concluded that American children are being harmed by the fruit and vegetable part of their diets. These foods routinely and lawfully contain dangerous amounts of pesticides which pose an increased risk of cancer, neurobehavioural damage and other health problems (Snell, 1989). Concern about pesticide residues in food has once again become front page news in Britain. Breast fed babies could exceed W.H.O acceptable daily intake level for the banned pesticide DDT through contamination present in their mothers milk and 43% of fruit and vegetable samples contained detectable residues (Snell,1989).

1.1.2 PRINCIPLES

Since the middle of this century entomologists worldwide have strongly advocated a more fundamental approach to pest control problems. It is gradually becoming a fact that the processes involved in the regulation of population density of insects are really quite complex and control measures could not be significantly improved without ecological knowledge of the species to be controlled. As a consequence much needed emphasis has been placed on ecological studies basic to an understanding of the causes of pest outbreaks and of the requirements for long term control of pests. These factors resulted in a return to a more rational approach to pest control exemplified by an integrated pest management concept and to a resurgence of interest in biological control (Waage and Greathead, 1988). Integrated control, synonymous with a pest management system that utilizes all suitable techniques either to reduce pest populations and maintain them at levels

below those causing economic injury or to manipulate the populations so that they are prevented from causing such injury (van den Bosch, 1971). To be most effective it requires comprehensive information about the agroecosystem under consideration and the co-operation of experts from different disciplines. When achieved properly it results in maximum profit with minimum costs and minimum injury to the ecosystem. Ecosystems are self sufficient habitats where living organisms and the non living environment interact to exchange energy and matter in a continuing cycle. Agroecosystems are special situations; variations here are caused mainly by the nature of the crop environment, the host plant and the arthropod species that are present, space and time boundaries and the distribution of species in a crop area during the rise and fall of local epidemics (National Academy of Sciences, 1969).

1.1.3 STATUS

Biocontrol, the use of living organisms as pest control agents, is well established today as an important component of integrated pest management (Waage & Greathead, 1988). The biocontrol of insects, mites and weeds has received great and enthusiastic acclaim during the past 70 years with highly successful practical results achieved in over 60 countries around the world (DeBach, 1964). Although the majority of natural enemies have failed to produce significant control, many early successes of biocontrol were in the Pacific islands. It was formerly widely presumed that biological control is best suited to island conditions. However, the experience with cottony cushion scale and successes in North America suggest that biocontrol can be just as effective on continents as on islands (Varley, Gradwell and Hassell, 1980). Still, biocontrol has been much less successful against pests of field and garden crops than against pests of forests, fruit or ornamental trees. Only 5% of field garden crops had been completely controlled by natural enemies in U.S.A. up to 1950, while 36% of orchard pests and 25% of

forest and ornamental trees were biologically controlled within the same period (DeBach, 1974). The main hindrance to the biological control of pests of annual field crops arises from cultural practices which cause a succession of ecological upheavals in an artificially simplified environment (Varley et al., 1980). The reasons for failures in biocontrol projects in general are unsuitable climatic conditions, differences in host biology as compared with the native country, and misidentification of hosts or natural enemy in addition to cultural practices.

1.1.4 ADVANTAGES AND DISADVANTAGES

Biological control has a number of advantages over chemical control:

1. The control agent does not have to be developed or synthesized, it is already there and we just need to look for it.
2. Cheap to breed and apply.
3. Once established it is permanent.
4. Insects do not develop resistance against it.
5. It does not pose an environmental hazard, nor endanger humans or wildlife through pollution.

The main disadvantage is the slow effect in comparison with pesticides. The risk of the control agent becoming a pest is minimized in biocontrol by the selection and screening of host specific agents against the target pests.

1.1.5 DESIRABLE ATTRIBUTES OF BIOLOGICAL CONTROL AGENTS (PARASITOIDS)

1. High searching capacity, the ability to find the host when the host is scarce at low densities.
2. High host specificity, which means a high degree of biological

adaptation to the host and greater degree of rapid and direct responsiveness to population density.

3. High potential rate of increase, including development period and relatively high fecundity.

4. Ecological compatibility, the ability to occupy all the host inhabited niches.

5. Dispersal capacity, the ability to easily and rapidly expand its sphere of influence in space to coincide with that of the host is closely tied to its searching capacity and ecological adaptability.

6. Temporal synchronization of life cycles, ovipositing females coincide with the required developmental stage of the host.

7. Species should be amenable to culture in an insectary which facilitates the breeding for distribution.

8. The ability to distinguish between parasitized and non-parasitized hosts and to avoid ovipositing in the latter (DeBach, 1964, 1974; Coppel & Mertins, 1977; Waage & Greathead, 1988).

1.1.6 RECENT ADVANCES

Recent trends in biocontrol seek to exploit the knowledge about factors limiting the efficiency of natural enemies and improve their performance by proper management. Varley et al., (1980) state that host parasite models have now reached the stage where they can indicate which searching characteristics are likely to result in stable and greatly reduced populations. Modified cultural practices may be an important way of preventing large scale mortality or emigration of beneficial insects such as planning spacing and cutting. Recent work in biocontrol suggests indigenous populations of parasites could often be a more important cause of pest

mortality if not inhibited by insecticides used in an attempt to achieve chemical control. So selective insecticides are always recommended. The establishment of high levels of parasitism at the start of the growing season can result in effective control; this is done by deliberate introduction. The provision of extra food for adult parasites can help their populations to increase more rapidly and increase the chances of successful biocontrol. Today biological control comprises several techniques (Waage & Greathead, 1988):

1. The classic biocontrol, the introduction of exotic agents for long term suppression and regulation of pest populations.

2. Inoculation is a similar strategy involving the periods of establishment of agents in conditions where they can not persist all the year around, hence each inoculation provides control over a number of pest generations.

3. Augumentation involves the supplemented release of indigenous natural enemies to increase control of the pest, strategically timed for the vulnerable stage of pest population growth.

4. Inundation involves the release of large numbers of agents to control a single generation with no anticipation of effects on subsequent generations.

The manipulation of indigenous natural enemies indicates that such a type of biocontrol is likely to become a crucial component in integrated pest management. It is the aim of biocontrol to manipulate natural enemies and use them to regulate pest numbers and keep them below economic injury levels.

1.2 PARASITOIDS AS BIOLOGICAL CONTROL AGENTS

1.2.1 PARASITOIDS

Insects that are parasites only during their immature stage are termed protelean parasites (Askew, 1971). The term parasitoid was used by Reuter to describe and distinguish from the more typical parasites those species of organisms which are parasites only during immature stages (Waage & Hassell, 1982; Vinson, 1984). Parasitoids differ from predators in that one parasitoid requires only one host (prey) for completing its development. Doutt (1959) described the parasitoids as having the following characters :

1. The developing individual destroys its host.

2. Only the immatures are parasitic whereas the adults are free living.

3. They do not live as parasites first on one host and then another i.e. they are not heteroecious.

4. They are relatively large in size in comparison with their host.

5. The host is usually of the same taxonomic class.

6. Their actions resemble predators more than true parasites.

Parasitoids include a vast number of species of the so called parasitic Hymenoptera and a few Diptera. The parasitoid life cycle has evolved in at least 87 families of insects belonging to 5 orders (Sweetman, 1936). Askew (1971) estimates that there are over 100,000 species of parasitic Hymenoptera worldwide. Hymenoptera is the dominant order among all entomophagous insects, both numerically and as regards their successful use in biological control. Over two thirds of the cases of successful biological control of pest species have been achieved by hymenopterous parasitoids. The superfamily Chalcidoidea comprises 20 families, and thousands of species. The superfamily Ichneumonoidea contains two major

families, the Braconidae and Ichneumonidae. The Diptera parasitoids are contained mainly in the family Tachinidae. Parasitoid species exhibit remarkable biological and taxonomical diversity, and this diversity poses considerable problems for taxonomists. Parasitoids usually appear as typical parasites during their early developmental stages and later destroy the host to live as free adults. Adult female parasitoids usually forage actively for hosts, depositing their eggs either in or on their hosts through an ovipositor. Upon hatching the larvae begin feeding on host tissues and pass through several developmental stages either within the host as endoparasitoids or on the hosts as ectoparasitoids. Solitary parasitoids develop singly in hosts while gregarious ones may develop in groups from eggs laid during one or more ovipositions.

1.2.2 USE IN BIOCONTROL

Serious consideration of the use of parasitoids as biological control agents was first made in the mid-nineteenth century (DeBach, 1974). During the first half of the twentieth century the use of parasitoids for pest control spread rapidly. Most cases were classical biological control dealing with pests which had invaded a new geographic region without their natural enemy. An alternative inundative release developed more slowly. Waage and Greathead (1988) pointed out that by the 1940s research on parasitoids had not only led to much successful pest control but had also served as a catalyst for the development of the field of population ecology (Nicholson and Bailey, 1935; Thompson, 1939). The advent of synthetic insecticides in the mid-twentieth century greatly retarded research and development of parasitoid-based biological control. But with the failure of insecticides, research on parasitoids has regained its former momentum (Coppel and Mertins, 1977). An impressive level of success has been achieved when parasitoids have been released for biological control. According to Laing and Hamai (1976), about 182 species of Hymenoptera and Diptera have been

established against insect pests and of these 19% have contributed to complete control. In the development process of insecticides less than 3% of new chemicals tested are selected for advanced screening and less than 3% of these ever reach the market (Lewis, 1977). This is much less than the establishment rate of Hymenopteran and Dipteran parasitoids which has been estimated at 34% (Hall & Ehler, 1979). A record of past biological control successes has been given by a number of authors (Huffaker, 1971; Van den Bosch & Messenger, 1973; DeBach, 1974; Huffaker & Messenger, 1976; Coppel & Mertins, 1977).

1.2.3 APHID CONTROL BY PARASITOIDS

Parasitism by species of hymenopterous families Aphidiidae and Aphelinidae is perhaps the most commonly observed cause of aphid mortality in the field (Mackauer & Way, 1976). A list of well over 300 species of Aphidiidae is given by Mackauer & Stary (1967). Several aphidiid and aphelinid parasites have been used with striking success in the biological control of introduced aphid pests. The general effectiveness of Aphelinus mali against the wooly apple aphid Eriosoma lanigerum in the United States where it is endemic has led to its introduction into most apple growing areas of the World (Hagen & van den Bosch, 1968). The successful introduction of 3 species from the Middle East into California Trioxys complanatus Quilis, Aphelinus asychis Walker and Praon exsoletum Nees to control the spotted alfalfa aphid Therioaphis trifolli Monell (Mackauer & Way, 1976). From California, the introduction of Aphidius smithi in Hawaii in 1960 which was outstandingly effective against Aphis craccivora (Stary, 1970). The introduction of Aphidius smithi from India to North America (Campbell & Mackauer, 1973). Adult aphelinids destroy a considerable proportion of their aphid hosts by feeding on the haemolymph which exudes from oviposition wounds. Parasitoids of aphids other than Hymenoptera are poorly studied. Many hymenopteran parasitoids exhibit a relatively narrow host range, often attacking only one

or a few related aphid species or genera (Mackauer & Stary, 1967). Besides the more obvious disadvantages of slow increase rates, hymenopterous parasitoids suffer from several less obvious shortcomings. For instance some species may not mummify the aphid until it has produced several young (Campbell & Mackauer, 1975b). However, Hymenoptera parasitois meet the attributes needed for effective biological control agents (Section 1.1.5). So, there is reason to be optimistic about the future of aphid parasitoids in biological control.

1.3 THE PARASITOID *Aphidius matricaricae* Haliday

1.3.1 IDENTIFICATION

Despite the recent keys to *Aphidius* species (Stary, 1981), many workers have reported difficulties in identification (Dransfield, 1979; Powell, 1982; Pungerl, 1983). The parasitoid species under the present study was identified as *Aphidius matricariae* Haliday by T. Huddleston of the British Museum, Natural History.

1.3.2 TAXONOMY, DISTRIBUTION AND STATUS

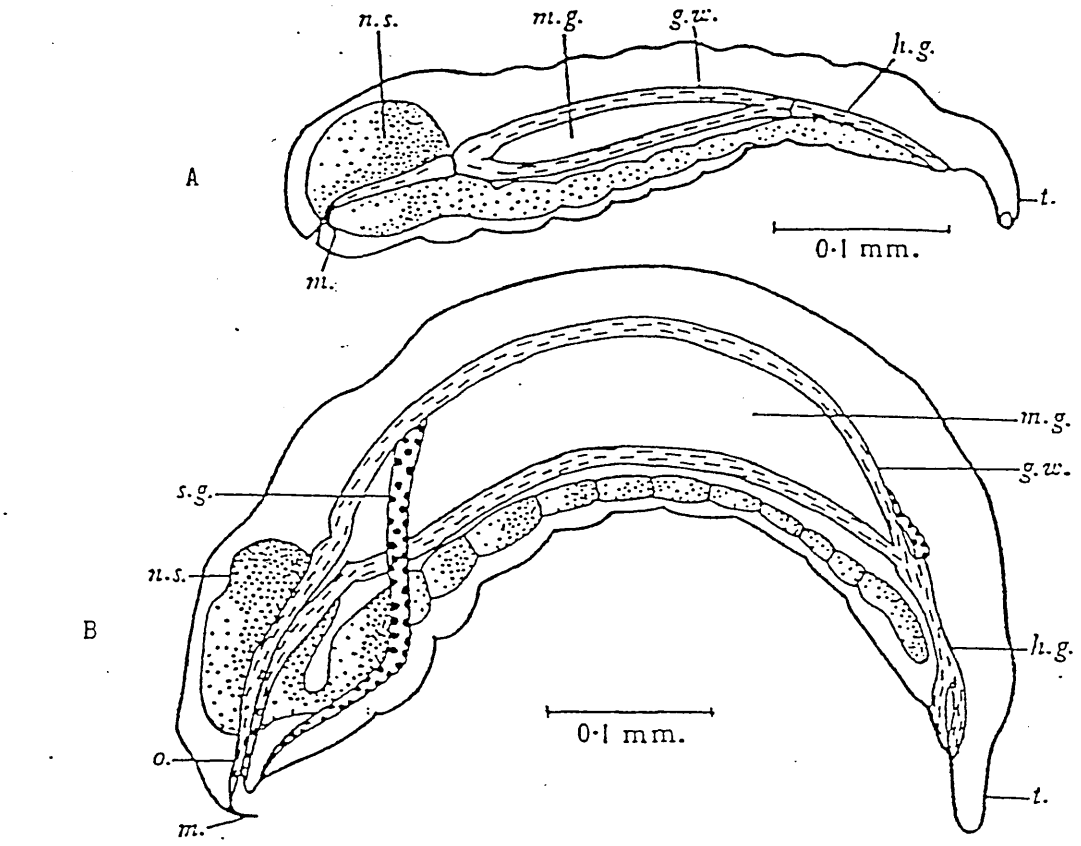
Aphidius matricariae belongs to the subfamily Aphidinae, family Aphidiidae (Braconidae), superfamily Ichneumonoidea of the order Hymenoptera. The Hymenoptera is a very diverse group. Minute to medium sized insects with membranous wings. The hind pair are smaller and connected with the fore pair by hooklets. The distinctive feature of Hymenoptera is the fusion of the first abdominal segment or propodeum with the thorax. In the suborder Apocrita which includes the majority of Hymenoptera (ants, bees and wasps) the abdomen is constricted between the propodeum and the true second abdominal segment (Imms, 1961). The ovipositor is a specialized egg laying organ composed of long interlocking chitinous plates through which the egg passes, and acts as a drill to pierce the host. It lacks muscles except at the base but it is supplied with nerves extending along its length to the

tip which bears sense organs that judge by chemical stimuli whether the host is suitable.

Interest in the control potential of hymenopterous aphid parasitoids particularly in the commonest and largest family Aphidiidae is increasing. Aphidius matricariae is an important parasite of green peach aphid Myzus persicae (Sulzer) and is known to parasitize 40 different species of aphids within 20 genera (Giri, Pass, Yeargan & Parr, 1982).

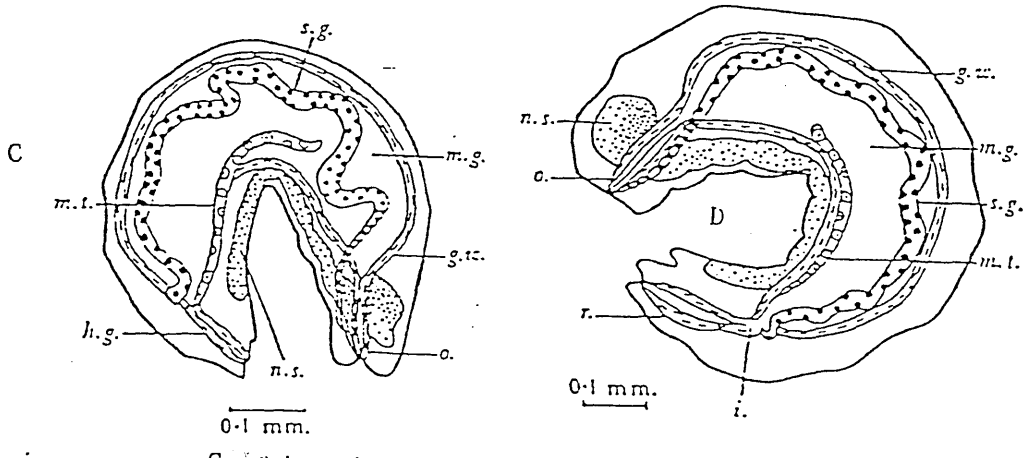
1.3.3 MORPHOLOGY AND LIFE CYCLE

The eggs of Aphidiids are of the mono-embryonic type as only a single larvae is produced from an individual egg (Stary, 1970). The egg is elliptical, white and is ornamented with spiral ridges and longitudinal furrows. It has a length of 0.05-0.07 mm and breadth of 0.013-0.23 mm. The embryonic development depends largely on temperature. At 21°C the eggs take 3-4 days (Vevai, 1942). The larva hatches by using its mandibles to cause a rupture of the embryonic envelope (Stary, 1970). The larva has 5 stages. The first is almost straight with its head as the largest of 13 segments. The body tapers posteriorly and terminates in a tail-like appendage which disappears in the 3rd stage (Figure 1.1). In the second stage the larvae is curved and tapers at both ends; the head is still the largest of the segments. In the 3rd, 4th and 5th stages the body curvature increases. The ends are more rounded and the body segments are smoother (Vevai, 1942). The 4th instar larva is mandibulate and uses its mandibles to cause injury to the vital organs of the host and completely consumes the inside of the aphid which is killed in consequence (Schlinger and Hall, 1960; Stary, 1970). After the larva has eatens all the contents of the aphid and has killed it, it starts to spin the cocoon. First, before the cocoon is spun, a small hole is cut on the ventral side of the aphid skin and the aphid is fixed to the surface by the secretion of a silk gland. The coloration of a mummified aphid is specific (Stary, 1970). Aphids mummified by A. matricariae are



A , 1st stage larva of *Aphidius matricariae* Hal. *m.* mandible; *n.s.* nervous system; *m.g.* mid-gut; *g.w.* gut wall; *h.g.* hind-gut; *t.* tail.

B , 2nd stage larva of *Aphidius matricariae* Hal. *o.* œsophagus; *s.g.* salivary gland. Other lettering as for A.



C , 3rd stage larva of *Aphidius matricariae* Hal. *m.t.* Malpighian tube. Other lettering as for A & B

D , 4th stage larva of *Aphidius matricariae* Hal. *r.* rectum; *i.* ilium. Other lettering as for C

Figure 1.1 SOME LARVAL STAGES OF Aphidius matricariae (AFTER VEVAI, 1942)

yellowish to brown. The pupa is of an exarate type. The fresh pupa is creamy white with bright red eyes. Forty eight hours later the thorax and abdominal dorsum begin to darken and these become almost black after a further elapse of 24 h. From the ecological point of view the pupal period may be considered as an intermediate state between the parasitic period of life and the period of free life of the adult (Stary, 1970). The emergence of the adult is generally effected by cutting out a circular lid in the abdominal dorsum of the sessile host, generally between the cornicles (Vevai, 1942). The cut portion remains feebly attached to the margin of the emergence hole in Aphidiids (Schlinger & Hall, 1960). The size of both adult males and females varies greatly and may be dependent upon host size (2.5-4.5 mm). Such variations have been reported for A. matricariae by Giri et al., (1982) and for other Aphidiid parasitoids (Fox, Pass and Thurston, 1967). The adult female has a narrow pointed abdomen ending with the ovipositor (Plate 1.1), while the male has a thick rounded abdomen. The antennae of the male has 17-19 segments being longer than those of the female which has 14-16 segments (Giri et al., 1982). The colour of the female is light brown and that of the male dark brown to black. The adult stage is the only free stage of the parasite during development. Consequently a great number of activities must be undertaken by the adult, including mating, reproduction and host finding.

1.3.4 BIOLOGY

1.3.4.1 MATING

The Aphidiids comprise mainly biparental species and for this reason mating is normal and a necessary part of the life cycle. The interval between the emergence and mating is different. Mating may take place immediately after emergence for many species (Schlinger and Hall, 1960; Hafez, 1961; Wiackowski, 1962). For A. matricariae the earliest mating observed took place 2 hours after emergence (Vevai, 1942).





Plate 1.1 THE PARASITOID Aphidius matricariae ATTACKING ITS HOST Myzus persicae

1.3.4.2 REPRODUCTION

Aphidiids are members of Hymenoptera which are characterized by a parthenogenetic type of reproduction (Stary, 1970). Doutt (1959) distinguished 3 groups of parthenogenetic reproduction in parasitic Hymenoptera - thelyotoky, deuterotoky and arrhenotoky.

1. Thelyotoky or obligatory parthenogenesis is characterized by the presence of only females in each generation, found in a few species e.g. Ephedrus persicae in California (Stary, 1970).

2. Deuterotoky is identified by the occurence of exceptional males, as with thelyotoky the individuals are all uniparental. It is relatively rare among Aphidiids.

3. Arrhenotoky - the eggs can develop either parthenogenetically or zygogenetically depending on the occurence of fertilization. In these cases the fertilized eggs are diploid and give rise to females whereas the zygotes from unfertilized eggs are haploid and are males. The females are biparental and the males are uniparental. Arrhenotoky results from non-mating, unsuccessful mating, before mating, extreme temperature, crowding of hosts, etc. (Vevai, 1942; Wiackowski, 1962; Force & Messenger, 1964). Arrhenotoky is widespread in Aphidiids: (Praon exoletum, Schlinger & Hall, 1960; Diaeretiella rapae, Hafez, 1961; Aphidius ervi, Stary, 1962 ; A. smithi, Wiackowski, 1962).

1.3.4.3 SEX RATIO

Sex ratio is a dynamic phenomenon; it is derived through the peculiar mechanisms of the parasite female which respond to the stimuli of extrinsic factors. Doutt, (1959) and Stary (1970) pointed out that the spermatheca becomes a sex determining mechanism when it contains spermatozoa. The sex of the egg is determined during oviposition and the stimulation of

spermatheca to discharge spermatozoa into the oviduct is usually brought about by external stimuli. Thus sex ratio is variable as a result of inconsistent environmental factors. Sperm is stored in the spermatheca and is considered to be quiescent and it needs activation to migrate down the sperm duct to fertilize the egg. The source of the activating agent appears to be the spermathecal gland which responds to external stimuli. Factors affecting sex ratio are many, e.g. successive matings of the male (Vevai, 1942; Sekhar, 1957), age of female (Sekhar, 1959), seasons (Hafez, 1961), times of mating by female (Wiackowski, 1962), temperature extremes (Force & Messenger, 1964).

1.3.5 SUPERPARASITIZATION

Superparasitization has frequently been observed in nature, therefore it has been assumed the parasites are unable to distinguish between healthy and parasitized hosts. However, hymenopterous parasitoids can generally discriminate between nonparasitized and parasitized hosts (Salt, 1934; Van Lenteren, Bakker and van Alphen, 1978; Vinson, 1984). The avoidance of superparasitization involves two distinct faculties, the ability to discriminate between healthy and parasitized hosts and the ability to refrain from oviposition when suitable hosts are not available (Salt, 1934). Superparasitization may occur not because of lack of discrimination on the part of a parasite but to its inability to refrain from ovipositing in hosts it knew to be parasitized, especially when the number of hosts is limited (Salt, 1934; van Lenteren, 1976). Aphidiids are solitary internal parasites, therefore only one completes its development to emergence. Supernumerary larvae are eliminated by physical attack (Vevai, 1942) or physiological suppression (Salt, 1934).

1.4 THE APHID *Myzus persicae* (Sulzer)

1.4.1 TAXONOMY, DISTRIBUTION AND HOST PLANTS

Aphids belong to the insect superfamily Aphidoidea, family Aphididae, within the suborder Homoptera, order Hemiptera. Homoptera possess piercing, sucking mouth parts with mandibles and maxillae stylet-like and lying in the projecting grooved labium. The labium arises far back on the head or even between the fore coxae (Imms, 1961). Aphidoidea bear a pair of cornicles, short dorsal tubes on the abdomen. Associated with Homoptera is a continuous discharge of a sugary waste product or honey-dew from the anus. The Aphidoidea are an immense group of about 4000 described species including many crop pests (Dixon, 1985). They are generally referred to as greenfly or plant lice. The green peach aphid *Myzus persicae* is an aphid of wide distribution, host plant range and economic importance (van Emden, Eastop, Hughes and Way, 1969; Mackauer & Way, 1976; Dixon, 1985). Although predominant in temperate regions, aphids have a worldwide distribution. *M. persicae* is virtually cosmopolitan and exists throuhout the world on a wide variety of host plants and presumably is adapted to a great diversity of environments (van Emden *et al.*, 1969; Mackauer & Way, 1976). The green peach aphid perhaps is the most important aphid pest on a world-wide basis. It is extremely polyphagous and is reported as a vector of well over 100 virus diseases of plants in over 50 different families, including important crops such as beans, sugar beet, sugar cane, brassicas, citrus, potatoes and tobacco (Kennedy, Day and Eastop, 1962).

1.4.2 DAMAGE

Damage is done both by direct feeding and transmission of diseases. Additional indirect damage may result from development of sooty moulds on honey-dew which may affect quality of some crops e.g. cotton. Most of the damage done by *M. persicae* is indirect through the transmission of plant

viruses (Hodgson, 1977). Direct effects in the field are unusual, possibly due to low infestation levels, although damage by spring populations to the primary host can induce severe leaf curl (Flanders & Fisher, 1959). The most severe direct damage has been noted in glasshouses where infestation can increase unchecked. Here the damage can take the form of stunting of terminal growth, distortion of flowers and mottling of the leaves of some crops, e.g. chrysanthemums (Hussey, Read and Hesling, 1969). M. persicae in particular creates serious problems because it can be a pest at very low densities and as a restless dispersive species it may be relatively unattractive to natural enemies and too scarce to be a reliable food for rapid increase of their population (Mackauer & Way, 1976).

1.4.3 DESCRIPTION

The adult is small to medium sized, 1.2-2.5 mm long, usually green with a darker thorax, antennae two third as long as the body. Siphunculi clavate, fairly long (Figure 1.2).

1.4.4 HOST SELECTION

The green peach aphid is remarkable because it is polyphagous but is severely restricted by the physiological condition of available food plants. Thus its host substrate selection mechanisms act for stability both in competition with other aphids (its polyphagy) and in their absence its restriction by host condition (van Emden & Williams, 1974). The density of M. persicae on year round chrysanthemums can depend on intraspecific interactions which create stable equilibrium populations, the size of which depends on the host plant resistance of the particular chrysanthemum variety (Wyatt, 1965). Aphids appear to respond predominantly to visual cues showing a marked orientation to yellow (Kennedy, Booth & Kershaw, 1959; Hodgson & Elbakhiet, 1985). Colour is a good indicator of the nutritive status of a plant as both highly nutritious young and senescent foliage

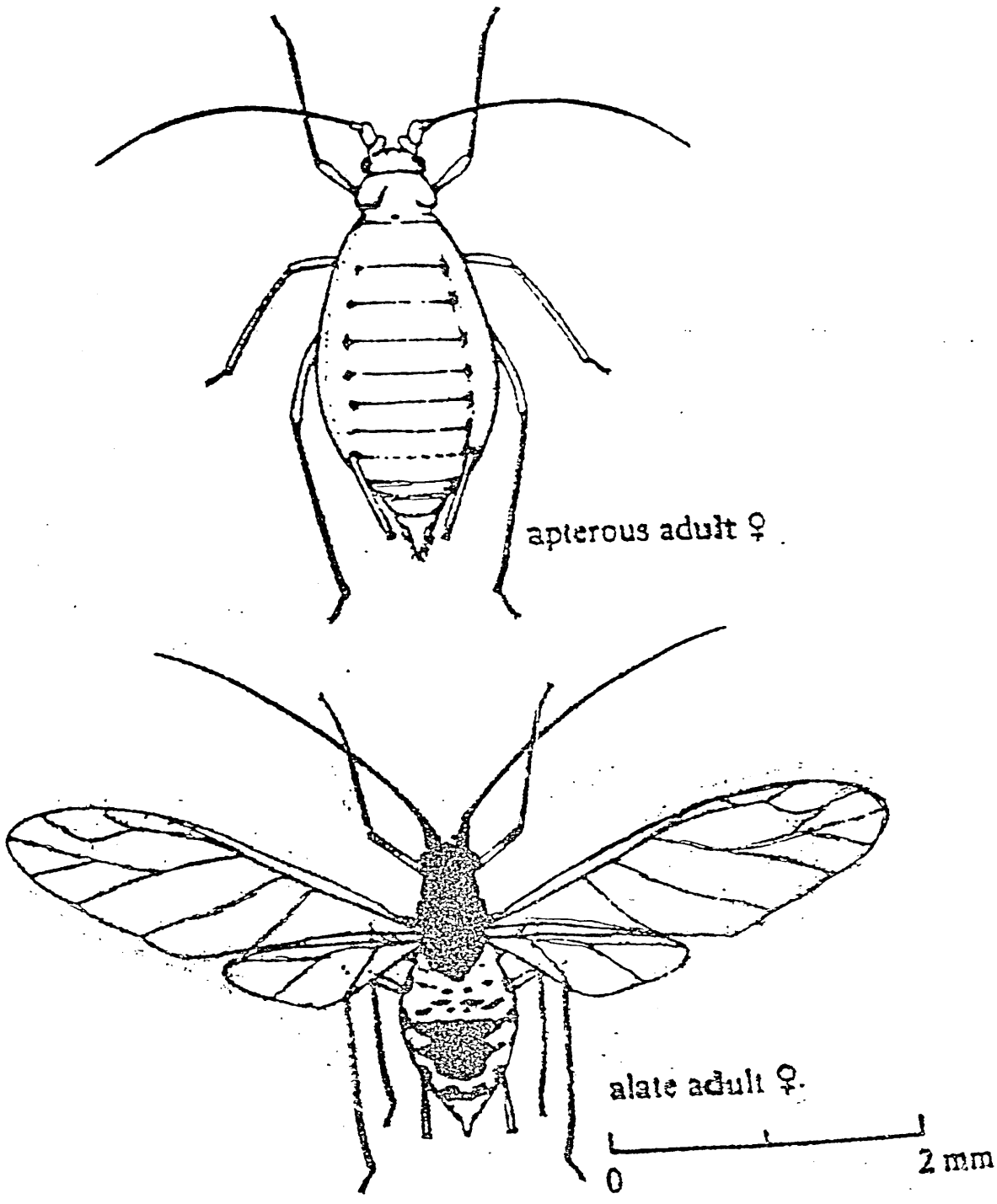


Figure 1.2 Myzus persicae Sulzer

tends to be yellower than the nutritionally poorer mature leaves (Kennedy, Booth & Kershaw, 1961). Despite the distinctive odour of many plants there is no unequivocal evidence that aphids are attracted by odour when locating their host plants (Dixon, 1985). The accumulation of aphids on their host plants is mainly due to a differential rate of departure with aphids staying longer on their host plants (Kennedy et al., 1959). The rate of departure is determined by the aphid response to contact with external and internal features of the plant (Dixon, 1985). So, the arriving alatae of most aphid species select plants in a particular stage of growth and leaves of an age characteristic for the species. They avoid mature tissue which is least active physiologically in terms of growth and senescence. M. persicae alatae alight on host and non-host plants with equal frequency and differentialiy retake off for further aerial dispersal and low level flight produce a redistribution of the initial settlings (Kennedy et al., 1959).

1.4.5 POLYMORPHISM

An aphid life cycle is made up of a sequence of morphs that differ in both their behaviour and structure. Polymorphism is characteristic of aphids and reaches its greatest development in host alternating species (Dixon, 1985). The eventual form of an aphid is the result of its genetic constitution and of the degree of character expression determined by the environment. Aphids often show striking environmental polymorphism (Hille Ris Lambers, 1946). Day length, temperature, nutrition and crowding may control the production of sexuals and of alate and apterous parthenogenetic nymphs in aphids (Lees, 1966). In temperate climates, in autumn most aphids produce sexual forms comprising wingless females and usually winged males (Dixon, 1985).

1.4.6 LIFE CYCLE

M. persicae reproduces continually by parthenogenesis over a large part of its range. While M. persicae is a well defined species, numerous

subspecies, races and biotypes have been recognized according to different criteria (van Emden et al., 1969). In the tropics there is no alternation of generations between different hosts and neither are there sexual forms. Males are never found. Females breed by parthenogenesis and vivipary and most individuals are apterous, but winged forms are produced at times for the dispersal of species (Lees, 1966; Hill, 1983).

In temperate climates, the life cycle can be very complex. Holocyclic and anholocyclic races exist. In holocyclic, winged immigrant gynoparae of M. persicae reach the primary host during the Autumn. The peach Prunus persica is the principal primary host of M. persicae in Britain and most of Europe. Success on colonizing a particular tree must depend on coincidence of the time of migration and the time where the leaves become physiologically suitable as they begin to senesce. Gynopara produce about 5-15 oviparae. The development of the male is triggered by day length. Each male can fertilize several oviparae. The oviparae cannot feed or develop once the tree becomes dormant. Those maturing in time each lay about 5-15 eggs in crevices and up to 4000 eggs per tree is found. The eggs overwinter in diapause. Hatching coincides closely with vegetational phenology and the newly hatched fundatrics feed on the buds of the primary host. The fundatrics produce 50-60 young and up to 8 apterous generations of fundatrigeniae have been recorded (Davis & Landis, 1951). There is a rapid and continuous decline in aphid reproduction as summer approaches associated with the decrease in nutrient status of the host plant and crowding of the aphids. An increasing proportion of individuals become alate. Migrant M. persicae from the primary host migrate to secondary plants, potato, brassicas, tobacco, etc. There they continue to reproduce parthenogenetically until autumn where winged gynoparae appear and migrate to primary hosts to repeat the cycle (Hille Ris Lambers, 1946; Davis & Landis, 1951; Lees, 1966; van Emden et al., 1969; Hodgson, 1977; Mackauer & Way, 1976; Dixon, 1985). In the anholocyclic life cycle M. persicae

overwinters as active stages on crops and weeds in regions of mild winters. Heie & Peterson (1961) suggest that M. persicae aptera can survive when the mean temperature remains above 4°C during the coldest months. M. persicae also overwinters readily in sheltered situations such as in glasshouses (van Emden et al., 1969). Anholocyclic overwintering of M. persicae has been observed in winter cabbage and spinach. The small population that survives where winters are mild start reproducing with the beginning of spring. These insects produce winged virginoparous females which disperse to secondary host plants together with the winged fundatrigeniae (Mackauer & Way, 1976). Anholocyclic forms in M. persicae occur in 3 main situations:

1. In areas with cold winters where the aphids survive only in sheltered sites, e.g. glasshouses or in the open during specially mild winters. The aphids may exist as races that do not normally respond to stimuli, e.g. shortening photoperiod and decreasing temperature which induce production of sexuals.

2. In more equitable areas where conditions may favour overwintering active stages and where both holocycly and anholocycly occur.

3. In warm temperate to tropical regions where M. persicae is exclusively anholocyclic (van Emden et al., 1969; Mackauer & Way, 1976).

The method of overwintering adopted either by parthenogenetic forms on secondary host plants or by fertilized ova on the primary host, holocycly, must have profound effects on the ecology and genetics of M. persicae populations (Mackauer & Way, 1976). From the arrival of the initially infesting alatae to the breakdown of the infestation, the host plant plays a key role in influencing all phases of the population dynamics of the aphid population. The effectiveness of natural enemies, for example, is very largely a function of the multiplication rate of the aphids which is in turn considerably influenced by the host plant. The selective advantage of

anholocycly has made parthenogenesis the sole form of reproduction in many parts of the world and it has been enhanced by agricultural and horticultural practices that provide nutritious crops throughout the year (Davis & Landis, 1951; Mackauer & Way, 1976).

1.5 EFFECT OF TEMPERATURE ON DEVELOPMENT, FECUNDITY AND SURVIVAL

Various intrinsic and extrinsic factors such as weather, population density, feeding site, food, etc., determine the rate of development, survival and fecundity of insects. Putman and Wratten (1988) stated that 'Abiotic relationships are the primary factors determining whether or not any organism can exist in a certain environment, and, while biotic interactions may later modify how an organism lives with that structural environment, may alter the fine details of its ecology, if the organism is not initially adapted to its physico-chemical environment, it cannot exist there in the first place'. To understand the behaviour and ecology of populations of an insect species, a knowledge of the reactions of the insect to temperature conditions is essential.

1.5.1 TEMPERATURE

Weather (temperatuure, humidity, rain, light, etc.), profoundly affect the physiology and behaviour of insects (Andrewartha & Birch, 1954; Wiggleworth, 1972). It is well known that day length and temperature influence the insect endocrine system which can act as a switch and determine whether the insect is active or goes into diapause; this is in turn modifies the effects of weather factors on survival, fecundity and speed of development. Weather affects insects as individuals independently of the population density so acts as a density independent factor. Temperature is regarded as one of the most important weather factors and the role it plays has been widely studied over the past two centuries. Temperature is a measure of intensity of heat

in terms of standardized units and is commonly expressed as degrees on either the Fahrenheit or Celsius scale. Heat is a form of energy and as such is necessary for the very existence of life. Each species has a wide range of temperature between cold stupor and heat stupor within which it can perform its normal functions. Towards the limits of this range, growth or reproduction or survival may be adversely affected and some point in the middle range is described as the optimum temperature. This point is frequently difficult to define and may vary with humidity. The resistance of insects to high temperature is altered by interaction of other factors, e.g. certain insects can survive in dry air at higher temperatures than in humid air by virtue of being able to cool themselves by evaporation.

1.5.2 EFFECT OF TEMPERATURE ON DEVELOPMENT

Development of most organisms follow a time scale which is temperature dependent. Attempts to integrate temperature over time date back more than two centuries (Allen, 1976). Most determinations of the temperature coefficients of development rate are carried out commonly at constant temperatures (Uvarov, 1931; Wiggleworth, 1972). As most insects develop naturally under conditions characterized by daily cycles of fluctuating temperatures, a question that arises is whether the development rate is directly related to thermal energy input or whether the change of temperature may also affect the rate. The literature is rich with conflicting reports of the increase or decrease of development rates by daily alteration of temperature (Pradhan, 1945; Cloudsley-Thompson, 1953; Messenger & Flitters, 1959; Bursell, 1964; Messenger, 1964a; Howe, 1967; Hagstrum & Hagstrum, 1970). Campbell, Frazer, Gilbert, Guitierrez and Mackauer (1974) did not find much difference in developmental rate between temperatures that were constant or fluctuating about the same average value provided that fluctuations do not extend below the threshold or above the upper limit.

The interest in temperature threshold dates back to the 17th century (Lin, Hodson & Richards, 1954). The temperature threshold is commonly defined as the temperature below which no development occurs. A more accurate definition is given as the lowest temperature at which a given physiological process or development through a given stage in the life history can be carried out through to completion (Lin et al., 1954). The amount of heat required over time to complete some aspect of development is considered to be a thermal constant (Andrewartha and Birch, 1954; Bursell, 1964). Various mathematical formulae have been used by ecologists from time to time to express the relationship between developmental rate and temperature in poikilotherm animals. The objective was to establish velocity constants which will give a quantitative expression for this relationship. The curve of velocity is S-shaped; it rises slowly at first, then steeply, then more slowly to a maximum and falls again to end suddenly at the lethal temperature. The curve represents the sum of chemical and physical reactions many of which must be differently affected by changes of temperature. Many formulae have been made :

1.5.2.1 THERMAL SUMMATION

The formula of the thermal summation of temperature have been widely used (Sanderson & Peairs, 1913; Uvarov, 1931; Andrewartha & Birch, 1954; Wiggleworth, 1972; Campbell & Mackauer, 1975a). The relationship between the activities of the organism and the temperature is expressed as follows :

$$y\ (x-t0) = k$$

Where y is the time required to complete development at temperature x, k is the thermal constant, t0 is the temperature threshold. The relationship can be re-expressed in another form:

$$v = k\ (x-t0)$$

Where v is the reciprocal of y. When v is plotted against x a straight line is drawn to intercept the temperature axis at point t0, the theoretical lower temperature threshold. This equation is valid when the velocity temperature curve is linear and the accelerating effect of temperature is the same at all stages in the development process. Where the linear relation between the velocity and temperature holds each developmental process will require a fixed number of degree days to bring it to completion. Therefore even if the temperature is changed in the course of development, it is theoretically possible to predict the time necessary for its completion by adding up the number of degree days contributed at each temperature.

1.5.2.2 THE LOGISTIC EQUATION

The formula represents a form of the logistic curve developed by Davidson (1944). The relationship between temperature and speed of development has been described by a particular sigmoid curve that is called the logistic curve:

$$1/y = k/(1+e^{a-bt})$$

1/y is the reciprocal of the developmental period at temperature t. k, a and b are constants. k represents the value of the upper asymptote towards which the curve is bending. a indicates the relative position of the curve on the abscissa. b represents the degree of acceleration of development in relation to temperature and determines the slope of the curve. e is the base of Napierian logarithms (Davidson, 1944).

1.5.2.3 THE POLYNOMIAL REGRESSION METHOD

Situations arise where the linear representation of the relationship between temperature and rate of development is inadequate, especially at extremes of temperatures. The rate of development increases with the

increase in temperature up to a certain level above which the rate decreases due to the deleterious effects of high temperature. In such situations more complicated functions of the independent variables must be considered. One of these functions is the polynomial. The regression equation, in general is as follows:

$$y = a + bx + cx^2 + dx^3 + ex^4;....$$

The fitting of a polynomial regression is similar to that of a multiple regression. Here the powers x^1, x^2, x^3 act the same role as x1, x2, x3 of the multiple regression equation. Tanigoshi, Hoyt, Browne and Logan (1975) in their constant temperature studies on the development of McDaniel spider mite Tetranychus mcdaniel McGregor, have found after evaluation of various methods for fitting developmental curves that the general method of polynomial regression analysis provided the flexibility required to determine the best fit curve for development. The polynomial regression analysis was recently used to predict development periods of 3 mealybug parasitoids. These predictions were found considerably more accurate than day degree predictions when substantial periods at extreme temperatures were involved, but not significantly different from degree days predictions under hot house conditions (Tingle & Copland, 1988).

1.5.2.4 RECENT ADVANCES

Insect population dynamics models have become more sophisticated. These new advances include a modified sine wave method for calculating degree days by using maximum and minimum temperatures to compute heat and cooling degree days between and below thresholds respectively (Allen, 1976). A second recent approach entailed the construction of a biophysical model of development known as stochastic based on concepts and techniques developed by Sharpe and Demichele (1977). This technique accounts for both linear and nonlinear effects while simultaneously incorporating the skewed distribution

of development times. Wagner, Sharpe, Wu & Coulson (1984) presented a modified approach to the stochastic model. Here a SAS computer programme was developed that uses the cumulative Weibull function to describe the probability distribution of normalized development times for individuals in a population. Future work will modify the current population dynamics models towards sound ones making use of recent advances in computer technology. So far simple methods may still be in common use since the complicated ones do not give significant improvement over them (Whalon and Smilowitz, 1979; Allsopp, 1981).

1.5.3 EFFECT OF TEMPERATURE ON LONGEVITY

As with all poikilothermic animals, temperature has a great influence upon longevity of insects. The distribution of species in time and space is frequently determined by limiting temperature factors. Most species live only in predominantly favourable temperatures. Thus, the life cycles of many species are synchronized with seasons and long periods of excessively high or low temperatures are often avoided either by entering a diapause or dormancy, or by migrating to more favourable areas. Despite this safeguard, high mortality rates can occur as a result of severe winters in which there is continuous snow. The direct harmful effects of temperature on survival of insects occur only with extreme conditions that are outside the range to which the species is adapted. Bodenheimer (1938) wrote: '...longevity is to a great extent inversely proportional to the intensity of life or metabolic rate of an insect'. The survivorship curve of an aphid population declines at a rapid rate at high temperature and senescence takes place within a short time for the entire population (Graham, 1959). Within the favourable range of temperature, however, temperature still has many indirect effects on survival. An inverse relationship between adult longevity and temperature is commonly acknowledged (Allsopp, 1981). But within a broad range of temperature above zero, a bell-shaped relationship was obtained

(Karandinos ; Axtell, 1967). Different methods are used to present longevity data. The classic method is the longevity mean value with its standard deviation (Graham, 1959). A second method is the survivorship curve in which the percentage survival of the original number is plotted against time from which 50% mortality or LT_{50} is produced (Hofsvang & Hagvar, 1975a). A third method uses age specific survival, Lx, which is the probability at birth that an individual will survive to age x or longer (Barlow, 1962; Messenger, 1964b; Deloach, 1974; Allsopp, 1981). It is especially useful when it is necessary to construct life table data to calculate intrinsic rate of increase. A recent method of representing longevity data uses the Weibull distribution for summarising survivorship data (Pinder, Wiener and Smith, 1978). The Weibull distribution is an extremely flexible frequency distribution which can possess either positive or negative skewness (Pinder et al., 1978). It has been widely used in engineering as a time-to-failure model and has previously been considered as a model of human survivorship (Gehan and Siddiqui, 1973). It has been used recently for summarising survivorship data for insects (Pinder et al., 1978). The Weibull frequency distribution is also used along with survival curves (Allsopp, 1981; Tingle and Copland, 1989). The proportion surviving at time (t) is given by:

$$Ft = 1 - \exp(-[(t/b)^c])$$

$$t, c, b > 0$$

Where b and c are respectively the scale and shape parameters of the Weibull distribution (Pinder et al., 1978).

1.5.4 EFFECT OF TEMPERATURE ON FECUNDITY

Cold-blooded animals are dependent on the right temperature for maximum reproduction. As with survival, reproduction may be directly impaired or enhanced by temperature. In insect species recruitment to the population by

egg laying or by birth often follow a daily variation in temperature. Under constant temperatures both of these curves would probably follow a normal or Gaussian distribution, i.e. a symmetrical bell-shaped curve, but this will be modified by temperature variations. Unfavourable temperature at the time of reproduction may greatly reduce the size of a population whilst population outbreaks may result from enhanced reproduction due to abnormal favourable temperatures. In most insect species, the pattern of reproduction per day by adults is characterized by a relatively rapid rise in the number of progeny produced per day until in a relatively short time a maximum rate of productivity is reached after which a gradual decrease occurs until reproduction finally ceases. These patterns are affected in both shape and magnitude by temperature (Messenger and Force, 1963). Differences in temperature influence many aspects of this basic pattern including the mean total fecundity and mean and maximum daily fecundity and the duration of the reproductive life of adults. Generally, there is also an optimal temperature range outside of which fecundity and oviposition are gradually decreased to zero (Greenfield and Karandinos, 1976). In insects the calculation of reproductive potential is complicated by the temperature mediated time scale experienced by insects as poikilotherms. This time scale is a fundamental driving variable in the population dynamics of insects and of special reference in the approach to an understanding of the population ecology of species through systems analysis and simulation modelling (Kitching, 1977). The fecundity data is usually presented as mean values with its standard deviation, and the mean daily production of eggs or progeny is plotted against time and presented graphically for each temperature (Graham, 1959). Another method used age specific fecundity rates, m_x, as the number of young born per female per day per female alive at the mid-point of each day (Barlow, 1962; Deloach, 1974).

1.6 INTRINSIC RATE OF INCREASE

Species of insects vary in numbers in different places at one time or in the same place at different times of year. They tend to increase under favourable conditions and to decrease under unfavourable conditions. Generally species with a high capacity for increase in numbers are likely to attain greater proportions than species with a lower capacity for increase (Barlow, 1962).

1.6.1 THEORY AND CONCEPT

Populations are usually changing continually under the impact of environmental factors which affect birth or death rates. To explain these changes in population rates of growth or decline quantitatively, one must measure population gains and losses. Gains occur from reproduction and immigration, while losses occur from mortality and emigration. In the highly hypothetical situation of unrestricted growth, the growth rate of an animal population is exponential or geometric. In this case the relationship between log population log (N) and time (t) is linear and the slope of the line is (r), where (r) equals births minus deaths, thus:

$$dN/dt = rN$$

The parameter r describes the rate of population growth in an ideal unlimiting environment. If the population has a stable age distribution, r is constant and is known as the potential rate of increase. Stable age distribution is important as age affects both reproduction and mortality rates. Generally the greater the number of generations which overlap in time, the more stable will be the age distribution of the population. Unrestricted growth of course is an unrealistic concept since all natural environments will limit population increase in some way. A more realistic concept is the maximum value of r which is possible for species under the influence of a particular environment. This is called the intrinsic rate of

increase (Lotka, 1925) or the innate rate of increase (Birch, 1948; Andrewartha & Birch, 1954) and usually denoted by the symbol rm. Lotka (1925) developed this function of intrinsic rate of increase which allowed for variations in birth rate and death rate with time in human populations. These methods were subsequently applied to insects (Birch, 1948). Birch (1948) described his method for determination of innate capacity of increase and applied his techniques to compare the effects of temperature and moisture conditions upon the population of 3 species of grain beetles. Birch (1948) defined the innate capacity for the increase of species under specified environmental conditions as the infinitesimal rate of increase which a population of stable age distribution would have when growing in a constant environment in which space is unlimited. The capacity is expressed as rm in the integrated formula:

$$Nt = No\ e^{rm\ t}$$

Where No is the number of animals in time zero. Nt is the number of animals in time t. rm is the innate capacity for increase. e is the base of the Naperian or natural logarthims .

1.6.2 ACCURATE METHOD FOR CALCULATING rm

An accurate estimate of rm may be determined from the age schedules of births and deaths for the species under the specified environmental conditions from the formula:

$$\Sigma\ e^{-rm\ x}\ Lx\ mx = 1 \qquad \text{(Birch, 1948).}$$

Where Lx is the probability at birth of a female being alive at age x. Mx is the mean number of female offspring produced in a unit of time by a female aged x.

The finite rate of increase is denoted by the symbol (λ) and defined as the multiplication per female per unit of time which a population of stable

age distribution would have when increasing in a constant environment in which space is unlimited. It is derived from the formula

$$\lambda = \text{anti log } e^{rm}$$

The generation time (T) is the mean time elapsing between birth of parents and birth of offspring and it is derived from the formula

$$T = \log Ro/rm$$

Where Ro is the net reproductive rate or the number of times an unhindered population will multiply in each generation.

1.6.3 SIMPLE METHODS FOR CALCULATING rm

Since Birch (1948) established the steps for determining the intrinsic rate of increase (rm) his methods have proved useful in biological and ecological studies. However, breeding insects under the required exacting conditions for collecting and making detailed life tables and the final rather complex trial and error calculations most frequently have deterred entomologists from carrying out such studies. Several authors have attempted to find simpler methods of determining the value of rm (Birch, 1948; Laughlin, 1965; Wyatt & White, 1977).

Birch (1948) gave an approximate method of calculating rm. This method still requires collecting and constructing detailed life tables but saves the complex trial and error calculations. First, the generation time T is calculated from the approximate formula:

$$T = \Sigma\, x\, mx\, lx / \Sigma\, mx\, lx$$

Then rm is calculated as follows:

$$rm = \log e\, Ro/T \qquad \text{(Birch, 1948).}$$

Laughlin (1965) showed the relationship between the rm and the capacity

for increase rc which is derived from the net reproductive rate Ro and the cohort generation time Tc by the equation:

$$rc = \log e\ Ro/Tc$$

Laughlin (1965) claimed that this approximation of rm is accurate enough for animals without overlapping of generations. Wyatt & White (1977) proposed a more simplified method for estimation of the intrinsic rate of increase. Having determined the prereproductive time d (birth to first reproduction), the number of progeny Md produced in an equal time is calculated and the rm is obtained from the equation:

$$rm = 0.74 \log e\ Md/d$$

The method has been shown to be reasonably accurate and to be applicable to animals with overlapping of generations such as aphids (Wyatt & White, 1977).

In a preliminary calculation, a comparison is made between the intrinsic rate of increase calculated from all these methods and one calculated from the accurate method of Birch (1948). The approximate method of Birch (1948) was found to be more accurate than the simple methods of both Laughlin (1965) and Wyatt & White (1977).

1.7 FUNCTIONAL RESPONSE AND AGGREGATIVE RESPONSE

Hassell, Lawton & Beddington (1976) have defined 3 basic parasite responses which are considered to be important in determining the outcome of an insect parasite interaction with its host population. They are the response to host density (the functional response), the response to host distribution (the aggregative response) and the response to parasite density (the interference effect). The quantitative effect of the reactions of predators and parasites on different densities of their prey or hosts still remains a topic of interest among ecologists, because these reactions are of

importance in regulating the numbers of prey or hosts. Therefore these reactions play an important role in some population dynamic theories and in biological control of pests. Solomon (1949) distinguished 2 types of response, the functional response in which the individual predator or parasite attacks more prey or host when prey or host density increases and the numerical response, in which, as a result of an increase in prey or host density the number of predators or parasites increases. The functional response has been classified into 3 basic types (Holling, 1959a). Type 1 where there is a linear rise to a maximum in the number of hosts attacked per parasitoid as host density increases. Type 2 where the response rises at a decreasing rate towards a plateau and type 3 where the response is sigmoid, is an S shaped rise again reaching an asymptote. Type 3 is more characteristic of vertebrate predators while type 1 or 2 is generally linked with invertebrate predators (Holling, 1959a, 1966). Type 3 responses are found more common in invertebrate parasitoids than previously thought (Hassell, Lawton & Beddington, 1977; Dransfield, 1979).

The importance of distinguishing between the type 2 and 3 functional response lies in their contribution to stability (Murdoch & Oaten, 1975). Sigmoid functional responses are density dependent up to some threshold prey density and may contribute to stability if average prey densities fall below this (Hassell, 1984). However, the type 2 response has received the most attention. The best known model for type 2 response is the disc equation of Holling (1959b). Holling (1959b, 1966) approached the predator-prey interactions as a system of behavioural components that could be partitioned and applied to predictive mathematical modelling. In predator-prey systems in which all available time is spent by the predator either in searching for prey or handling prey, the number of prey attacked Na is a hyperbola function of prey density N.

$$Na = a\,Tt\,N\,/(1 + a\,Th\,N)$$

The model assumes that the number of prey attacked is a function only of prey density (N), the predator rate of successful search (a), the length of time the predator and prey are exposed to one another (Tt) and the handling time per prey (Th). Holling's equation assumes that the predator searches at random at a constant speed for randomly distributed prey with a constant handling time for all predators and prey items. The model also presumes a fixed probability of prey encounter and does not allow for the outcome of prey consumption.

Messenger (1968), Royama (1971) and Rogers (1972) stressed the point that the disc equation does not permit the depletion of available prey during the course of predation. A later model of functional response possessing similar restrictive assumptions but allowing for exploitation of prey was developed by Messenger (1968), Royama (1971) and Rogers (1972). The model has become known as the random predator equation. It combines the immediate predation rate over the duration of experimental time presuming an exponential decline in prey density and is therefore relevant for long term close system experimental designs in which predators are not observed constantly.

$$Na = N\,[1-\exp(-\,a\,Tt\,/\,1\,+\,a\,Th\,N)]$$

A linearized form of the equation is:

$$\log_e [1 - Na/N] = a\,Th\,Na - a\,Tt$$

The validity of the random equation has been challenged. Fitting the random equation raises several difficulties, the most important of which is that it is impossible to isolate the dependent variable Na on the left side of the equation (Livdahl & Stiven, 1983; Houck & Strauss, 1985). The statistical grounds of the traditional linearization of the disc equation as put forward by Holling has also been subject to criticism. Holling's (1959b) linear transformation for fitting the disc equation is

$$Na/N = - a\ Th\ Na + Tt\ a$$

Livdahl & Stiven (1983) claimed that this equation breaks assumptions required by regression analysis. The independent variables are not independent. They suggest the use of an alternative linear transformation as a solution to this problem. A linearization is obtained by reciprocating both sides of the disc equation

$$N/Na = 1/ a\ Tt + Th\ N/Tt$$

The slope is the reciprocal of the attack rate and the intercept multiplied by the time of exposure gives the handling time.

The effects of parasitoid density have been examined by several authors (Hassell, 1971; Beddington, 1975; Hassell et al., 1976). Hassell et al., (1976) have shown that the searching efficiency decreases as parasite density increases. It has been shown that dispersal in pursuit of an optimal strategy should not be thought of as interference and it has been suggested that there might be selection for aggression which enables a parasite to drive others out of highly profitable areas. The response to host distribution has been considered separately by Hassell & May (1974) and called the aggregative response. A question of importance to ecologists is how foraging animals exploit prey populations which are patchily distributed in the environment. Orientation to hosts often involves responses to successive levels of environmental patchiness as is expressed in the classical description of a foraging process as one of host habitat finding followed by host finding (Flanders, 1953; Doutt, 1959). At each level in this process attractant stimuli may mediate orientation to host containing areas and arrestant stimuli elicit intensive search of these host areas which may be considered patches by virtue of this arrestment (Waage, 1978). Hassell & Southwood (1978) proposed 3 hierarchical levels, within the forager environment habitat, patch and host. The patch is defined as a

section of the parasitoid environment the borders of which when crossed by the forager elicit a change in its behaviour. The attractant stimuli involved in parasitoid foraging are those produced by the host and those produced by the immediate environment of the host. Visual and chemical stimuli from the host's immediate environment are often associated with a comparatively higher level of foraging. The stimuli associated with the presence of host or its excretion and secretion is connected to a lower level of foraging.

During the past few years spatial heterogeneity has emerged unequivocally as a crucially important factor affecting a population's dynamics (Hassell, 1982). The spatial distribution of parasites has often been viewed at a more behavioural level in which the aggregative response of the adult female parasitoid in patches of different host density is examined. Most theoretical models have assumed that the aggregative responses of the adult female is broadly of the same form as the relationship between per cent parasitism and host density per patch (Hassell & May, 1974). Morrison & Strong (1980) have shown that the spatial distribution of the searching adults need not necessarily reflect the same relative distribution of parasitism. This means that, it is quite probable to find a positive aggregative response leading to an inverse density dependent relationship between per cent parasitism and host density per patch. Natural selection should act on foraging behaviour as to maximize the rate of energy intake or prey capture if prey items are identical in energy value (Waage, 1979). Several models have been developed which suggest how animals might behave if they were to forage efficiently or optimally (Hassell & May, 1974; Murdoch & Oaten, 1975; Cook & Hubbard, 1977; Waage, 1978). Foraging theory suggests that host distribution should have a significant effect on the response of the parasitoid. The optimal patch use strategy for a parasitoid depends strongly on host distribution. A strategy that is advantageous with highly aggregated hosts may be poor with randomly distributed hosts.

Ecologists have long been concerned with determining whether populations are stable and if so what mechanisms are responsible. Stability in mathematical models implies a tendency to return to equilibrium after a perturbation and one approach has been to search in real systems for mechanisms shown to be stabilizing in models (Walde & Murdoch, 1988). Virtually all models of parasitoid-host interactions are based on Nicholson & Bailey models (1935) in which the host and the parasitoid have discrete generations almost always of the same length. Univoltine insects are perhaps the best suited for such models. Attacks are assumed to be distributed among hosts at random. Stability in such models depends on two criteria, the relationship between parasitism rate and parasitoid density and that between parasitism rate and host density. The Hymenoptera parasitoids are interesting subjects for the study of foraging mechanisms. Their hosts are small and widely dispersed in clumps associated with preferred food plants or microhabitat. The patterns of parasitism are important for the population ecology and biological control researcher because of their potential effects on population dynamics.

1.8 SEARCHING BEHAVIOUR

'The field observer can^not fail to be impressed by the ability of aphids to find even a single isolated host plant, and it was once generally supposed that the winged migrants must sense and direct themselves toward their specific host plants from a distance' (Kennedy, Booth & Kershaw, 1959). If so the ability of finding even a single isolated host aphid by a parasitoid should be even more impressive. Insect parasitoids undergo a series of distinct behavioural responses during the location and parasitization of their hosts. It is widely accepted that the parasitoid is initially attracted to the host habitat and then to the host (Salt, 1935). The host finding process often takes the form of a sequence of responses involving several levels of stimuli. Such sequences which lead to

successful location of hosts by parasitoids depends on a number of complex and interacting factors. Salt (1937) classified host selection into three broad categories which follow in proper sequence: 1. Ecological selection (host finding) then 2. Psychological selection (host selection) and finally 3. Physiological selection (host suitability). Doutt (1959) combined these into four consecutive steps: 1. Host habitat finding 2. Host finding 3. Host acceptance and 4. Host suitability. The first two are divisions of Salt's 'ecological selection' and step 3 and 4 are equivalent respectively to Salt's 'psychological' and 'physiological selection' (Doutt, 1964b). Vinson (1975) added host regulation as a fifth step in host selection. Limitation of the number of host species attacked by a species of insect parasitoid is determined by these steps. Aspects of host finding behaviour of many adult parasitoids have been investigated (Salt, 1935; Laing, 1937; Flanders, 1953; Doutt, 1959, 1964b; Kennedy, 1965, 1978; Brown, Eisner & Whittaker, 1970; Vinson, 1975, 1976; 1981, 1984; Waage, 1978; Arthur, 1981; Nordlund, 1981; Weseloh, 1981). The steps of host habitat finding and host acceptance are progressive and overlap one another when many host-parasitoid relationships are described (Arthur, 1981). In many insect parasitoids host finding is mediated by chemicals associated with the presence of host. The chemicals appear to play a major role in the sequence of events leading to host acceptance, physical factors may also be involved (Vinson, 1976). Responding to physical and chemical cues the forager is first attracted to one level and then arrested within it while seeking out lower level cues in pursuit of its prey (Waage, 1978). The search is thus gradually confined to successively smaller sections of the environment until the host is located. Involvement of chemicals in various stages of the host selection process of parasitoids is well documented (Vinson, 1976; Nordlund, 1981). Chemical stimuli odour perceived at a distance through the antennal chemoreceptors of the female parasitoid is one of the most common cues used during host habitat and host location. Odours emitted by damaged leaves or plants

attract parasitoids to the host infested area and stimulate them to change from random search to a host searching pattern (Bragg, 1974). The chemicals that mediate interactions between organisms were termed semiochemicals (semeon = signal) by Law & Regnier (1971). Semiochemicals are subdivided into two major - groups : pheromones and allelochemics depending on whether the interactions are intraspecific or interspecific respectively (Nordlund, 1981). A pheromone is a substance secreted by an organism to the outside that causes specific reaction in a receiving organism of the same species e.g. sex pheromones. Allelochemics were proposed by Whittaker (1970) to describe chemicals that mediate interspecific interactions and are subdivided in to:

1. Allomones are a substance produced by an organism which, when received by another species, evokes in the receiver a behavioural or physiological response that is favourable to the emitter but not the receiver e.g venom used in prey capture.

2. Synomones are chemicals that evoke in the receiver a behavioural or physiological response that is favourable for both the emitter and receiver.

3. Kairomones were proposed by Brown, Eisner and Whittaker (1970) and are defined as substances produced or acquired by an organism that when it contacts an individual of another species in the natural context, evokes in the receiver a behavioural or physiological response that is adaptively favourable to the receiver but not to the emitter.

During the past decade scientists have become increasingly aware of the importance of allelochemics particularly kairomones to the performance of parasitoids. In the immediate past it was generally believed that parasitoids efficiency was solely dependent on the ability of these organisms to randomly encounter hosts while being limited by the supply of

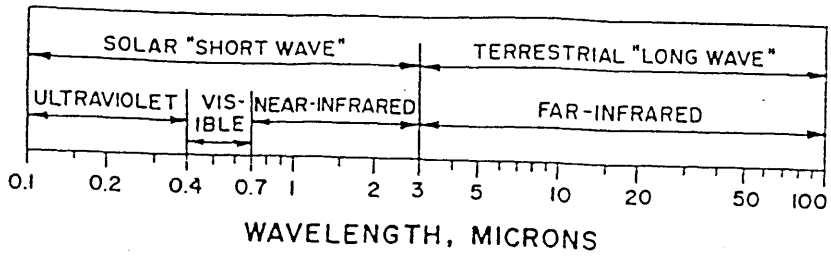
eggs. It is generally agreed now that the host finding efficiency of many parasitoids is determined mainly by their frequency of encounter with allelochemics emanating from the host, host secretions or excretions, host plants, by-products from damaged hosts of the target species etc. And by inherent parasite capacity to orient via allelochemics to a high host probability site (Gross, 1981).

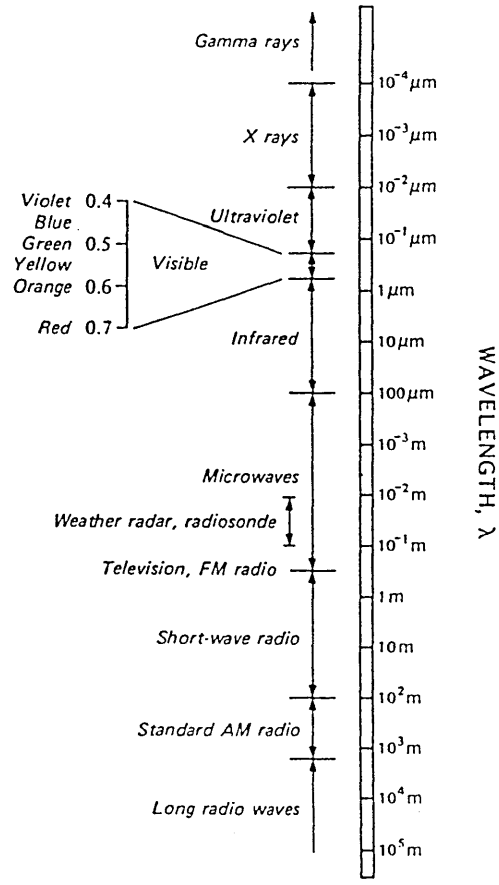
Read, Feeny & Root (1970) first demonstrated the attraction to synomones of mustard oil odour in crucifers for the aphid parasitoid Diaretiella rapae parasitizing Brevicoryne brassicae. Some aphid parasitoids are strongly responsive to aphid odours (kairomones) and do not react to odour of host plant (synomones) as Aphidius nigripes on the potato aphid Macrosiphum euphorbiae (Bouchard & Cloutier, 1985). Schlinger and Hall (1960) observed that Praon palitans a parasitoid of the spotted alfalfa aphid, Therioaphis maculata, was apparently able to detect its host only by contact. However, they proposed that some odour emitted by the aphid or by honeydew could act as a general attractant.

1.9 LIGHT AND COLOUR

All behaviour is the product of central nervous integration of different stimuli from both outside and inside the insect and likewise of different responses (Kennedy, 1978). Although the olfactory ecology of insects has received the most attention by researchers, the visual ecology may be no less important in locating resources. An insect foraging for its host most probably perceives the environment in a sequence of several hierarchial levels. Long distance orientation appears dominated by non-specific signals. Visual stimuli can be one of the cues used at certain levels for many species. The detectability of a host at any distance by an insect visual system is a function of the item's dimension, pattern, colour, intensity and contrast against the background. For insects in general, oriented movements to sources of light play a large part in their behaviour

(Wiggleworth, 1972). Responses to light may result from light intensity, specific visual pattern or wavelength. Some insects are positively phototactic, whereas others are negatively phototactic. Oke (1978) defined radiation as the transfer of energy by the rapid oscillations of electromagnetic fields. These oscillations may be considered as travelling waves characterized by their wave length (λ) (distance between successive wave crests). A researcher concerned with thermal radiation as a factor in the animal environment will usually consider radiation of wavelengths from 0.1 - 100 µm, where (1µm = 10^{-6} m), representing only a very small portion of the total electromagnetic spectrum (Figure 1.3). The visible portion of the spectrum to which the human eye is sensitive is an even smaller fraction extending from 0.36 - 0.75 µm. It is presumed that the eyes of animals are generally sensitive to this same range of wavelengths. Radiation is able to travel in a vacuum and all radiation moves at the speed of light (3×10^{8} m/s) = (3×10^{10} cm/s). Wave length and frequency are related by $\lambda v = c$, where c is the velocity of light, v is the frequency in cycles per second and λ is the wavelength in centimeters. Since c is constant a scale of wave number is often used and is defined as $1/\lambda$ cm^{-1}. If the wavelength is in microns, rather than centimetres the wave number is determined by $10.000/\lambda$. White light is a mixture of light rays of different wavelengths. If it is passed through a prism the rays are refracted to varying degrees according to their wavelength, and when arranged in this way there appears the coloured bands of the spectrum (Figure 1.3) as nature demonstrates it charmingly in a rainbow. To each wavelength there is a corresponding definite colour sensation. The longest wavelength is seen as red. Even the long light wave is still so small that they are measured in millimicrons (1 mµ (nm) = 1 millionth of a millimeter). The coloured bands extends from the red with a wave length of 800 mµ (nm) to the violet with a wavelength of 400 mµ (nm), where visibility for human eyes ceases. Sunlight contains still shorter wave lengths, ultraviolet rays. Bees are sensitive to ultaviolet





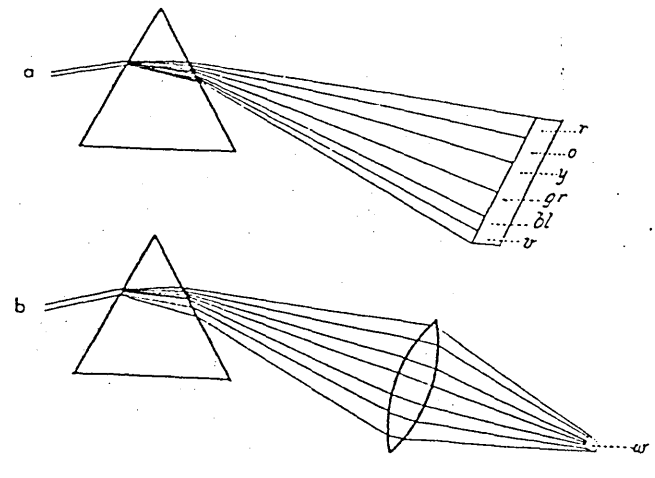


Figure 1.3 LIGHT RADIATION WITHIN THE ELECTROMAGNETIC SPECTRUM

(von Frisch, 1971). In nature the sun light caught in a mirror or on water is partly or completely polarized. The blue sky is full of polarized light, though human eyes do not notice it but for insects they can even distinguish the direction of its vibration which they use to help them in their orientation (von Frisch, 1971).

The general distribution of different colour receptors over the compound eye is known in some species. Green receptors are more frequent in the ventral side of eye, the part of the eye looking upward contains more ultaviolet sensitive receptors (Menzel, 1979). Different sensitivities of photoreceptors depend on the different absorption properties of retinal photopigments. Insects in general possess simple and compound eyes. Compound eyes are the main visual organs. The visual system of an insect is a fixed-focus type so that visual acuity, the ability to resolve patterns, is maximum at very close range (centimetres) and decreases rapidly with distance. The larger the compound eye the greater the acuity.

Colour is specifically defined by 3 attributes: hue, saturation (tint) and intensity. The hue is defined by the wave length in the spectrum, the tint means the amount of white added to hue and the intensity is the brightness which can be diminished by adding black (Moericke, 1969). A pure yellow of a petal reflects not only the special wavelength of this hue about 600 nm but nearly all wavelength from green 500 nm to red 700 nm. All these wavelengths when combined together by the human eye or insect (excluding red) give the impression yellow. A relatively simple measure of intensity is the percentage reflectivity of the peak of the curve compared with a white standard. A more exact measure is the total area under the reflectance curve. A saturated yellow attains about 80%. The more black added the lower is the intensity until nearly zero with deep black.

The importance of leaf colour as a determinant of the settling behaviour of flying aphids was described some 30 years ago by Kennedy et al., (1959).

Leaf colour is in the main determined by features of the interior of the leaf, the pigments and their arrangement but the reflectance will be influenced by the nature of the leaf surface, the cuticle, wax and pubescence (Southwood, 1986). Menzel (1979) defined true colour vision as the ability of an animal to distinguish spectral colours on the basis of wavelength differences only independent of brightness differences or absolute spectral distribution of the stimulus. This involves central integration of the output of photoreceptors with different spectral sensitivities. An insect with true colour vision can distinguish between a series of different wavelengths with a maximum discriminative ability falling between the peak sensitivities of the respective photoreceptors e.g. ants (Kretz, 1979). Among the insects, the honey-bee Apis mellifera is still the insect for which colour vision is well proved (Neumeyer, 1980). In insects other than bees and ants colour vision has been studied only qualitatively, only few have proved to have true colour vision (Menzel, 1979; Coombe, 1981). There is little information concerning colour responses among hymenopterous parasitoids. Whether or not Aphidiidae have colour vision is as yet not fully known. The hymenopteran ichneumonid Itoplectis conquisitor (Say) demonstrated a preferrence for blue (Arthur, 1966). Hollingsworth, Hartsack and Lingren (1970) found that the ichneumonid Campoletis perdistinctus (Vierick) and the braconid Apanteles marginventris (Cresson) were both attracted to green light. Goff & Nault (1984) showed that when the pea aphid parasitoid Aphidius ervi Haliday was given a choice to respond to a series of two or three monochromatic lights in series, the parasitoid always chose that light nearest green in the spectrum.

1.10 IMPACT OF PARASITISM

When attention is directed to the dynamics of glasshouse populations of aphids it is often necessary to ask whether parasitism could have accounted for the observed change in aphid numbers or to what extent parasitism contributed to a retarding of growth or population collapse. A variety of techniques were used for assessing parasitism on an aphid population. The need for a quantitative analysis for this kind of investigation is recognized as essential to the evaluation of parasitoid effectiveness. Several authors have studied this aspect of aphid-parasite relationship. Parasitized aphids showed a significant reduction in fecundity and longevity as compared to normal individuals, the degree of reduction varying with host age at the begining of parasitization (Hafez, 1961; Fox et al., 1967). Campbell & Mackauer (1975b) used the intrinsic rate of increase as an index in order to quantify the impact of the parasitoid Aphidius smithi on the pea aphid, Acyrthosiphon pisum (Harris), parasitized at various stages. Following the same methodology, Liu & Hughes (1984b) quantified the effect of host age at parasitization by Aphidius sonchi Marshall on the sowthistle aphid Hyperomyzus lactucae (L.). The same procedure demonstrated recently for Praon pequodorum Viereck on population growth of the pea aphid A. pisum (Sequeira & Mackauer, 1988).

SECTION 2 THE EFFECT OF CONSTANT TEMPERATURE ON DEVELOPMENT, FECUNDITY AND LONGEVITY OF BOTH M. persicae AND A. matricariae

2.1 INTRODUCTION

2.1.1 DEVELOPMENT

Generally numerical changes in an insect population is most strongly influenced by the duration of development from birth to first reproduction (Lewontin, 1965). Since the rate of development of most insects varies with temperature, a realistic measure of this relationship is fundamental to any study of the population dynamics. For each insect species temperature below which no measurable development occurs is its threshold of development. The thermal constant is the amount of heat required over time for an insect to complete some aspect of development (Andrewartha & Birch, 1954). The effect of temperature on insect development has been widely studied over the past century (Sanderson & Peairs, 1913; Uvarov, 1931; Davidson, 1944; Pradhan, 1946; Andrewartha & Birch, 1954; Messenger, 1964a). There is no single formula used to describe such a relationship. Day-degrees is widely used (Campell, Frazer, Gilbert, Gutierrez & Mackauer, 1974; Campell & Mackauer, 1975a). Logistic curve (Davidson, 1944; Liu Shu-sheng & Hughes, 1984a). Modified logistic curve (Pradhan, 1946; Deloach, 1974). Polynomial regression (Tanigoshi, Hoyt, Browne & Logan, 1975; Tanigoshi, Nishio, Moreno & Fargerlund, 1980; Tingle & Copland, 1988). There are several reports concerning the effect of constant temperature on development of M. persicae (Barlow, 1962; Harrison, 1969; Deloach, 1974), but few reports for A. matricariae (Rabasse & Shalaby, 1980). Such studies showed that the development of both species is greatly affected by temperature.

2.1.2 FECUNDITY

The rate of egg production is markedly influenced by temperature (Wiggleworth, 1972). Generally the number of eggs laid increases with rising temperature up to an optimum then declines rapidly as temperature increases still further (Bursell, 1964). The preoviposition period is also

reduced with increasing temperature. The effect of temperature on M. persicae fecundity has been studied by several workers (Barlow, 1962; Deloach, 1974). For A. matricariae the number of eggs laid depends on the egg production capacity of the female and on the location of suitable oviposition sites. As the ability to find hosts is involved, egg production rates and oviposition rates may be very different. It is the latter which is more important in determining the number of offspring produced by a given individual or generation. Both egg production and number of eggs laid are affected by temperature. Fecundity in A. matricariae varies from 100 - 400 eggs (Vevai, 1942), but few have demonstrated the effect of temperature on fecundity (Giri, Pass, Yeargan & Parr, 1982).

2.1.3 Longevity

Temperature also has a marked influence on survival and longevity of insects. Excessively high or low temperatures can be lethal to insects. An inverse relationship between temperature and longevity within an optimal range of temperature is a common phenomenon. Many reports were found concerning the effect of temperature on survival of M. persicae (Barlow, 1962; Deloach, 1974). Few were found describing such a relationship for A. matricariae (Giri et al., 1982). These measurements were in the form of average longevity or age specific survival curves. None was analysed by means of the Weibull function (Pinder, Wiener & Smith, 1978).

The aim of this study was to elucidate the influence of a series of constant temperatures on development, fecundity and longevity of both M. persicae and its parasitoid A. matricariae.

2.2 GENERAL MATERIALS AND METHODS

2.2.1 APHID CULTURE

The laboratory colonies were started with aphids collected from potato and turnip in the glasshouse. Colonies were maintained on turnip plant Brassica rapa L. variety Seven-Top as the principal host, inside ventilated perpex cages (610 x 400 x 530 mm), in the labaratory held at 20 ± 3°C with 12 - 18 hours photophase. Each week a few aphids from healthy colonies were transferred from old plants to young uninfested plants in a clean cage, the old colonies were discarded after one month. Thus aphids of about the same stage of colony development were constantly available and the danger and the possibility of deterioration was reduced. The aphid M. persicae used in the various studies were the progeny of apterous parthenogenetic viviparous females. To obtain 1st instar nymphs about 100 adult aphids were placed individually on brassicae seedlings and were allowed to deposit young for 24 hours at laboratory conditions indicated above. These progeny were the experimental subjects. In preliminary studies an attempt was made to rear aphids on leaf discs during the experiment. It was found that leaf-discs deteriorate rapidly and it was necessary to transfer aphids to fresh discs frequently which results in an increased mortality from handling in addition to other losses due to fungal infection and aphids wandering-off discs. Other limitations of discs were that to obtain leaf discs of sufficent size it was necessary to use mature leaves. Although these were accepted by aphids they did not represent their preferred feeding stages such as leaves near the growing point or senescent leaves. The physiology and nutrient status of detached leaf discs are not strictly comparable with the growing plant. Also the leaf discs were inverted, forcing the aphids to feed in an unnatural position. As a result, the aphids were exposed to direct radiation from the light whereas they frequently feed in diffused light.

A preliminary experiment was done to decide whether to use either whole plants or parts of plants or seedlings. As a result, seedlings were found

to be better than whole plants or parts of plants for several reasons. They conserve space within the incubator. They function with minimal changes in the CO_2 - O_2 balance. It is easy to standardize nutrition which consequently affects the physiology of aphids. Lighting within incubators could be insufficient for normal growth of whole plants. Seedlings of the same age and size with similar standard nutrient solutions are more comparable in different experiments and could be readily supplied when needed. Turnip seedlings were used because they are the principal host in laboratory culture, they thrive better on turnip and are easily seen. The method finally adopted was to rear aphids on 7 day old brassica seedlings of uniform size. These seedlings were pulled out underwater. Each seedling was then placed with its stem protruding into small glass vials through a hole in the plastic covers (Plate 2.1). The vials were filled with distilled water. A drop of standard plant nutrient solution (Long Ashton method) was added every week and distilled water added when needed. The distilled water together with nutrient solution was renewed completely once every two weeks. If seedlings appeared wilted, aphids were transfered to fresh seedlings.

The nutrient solution was prepared as a complete nutrient solution based on nitrate nitrogen as used by Long Ashton

Compound	g/l	ppm
kNO_3	0.404	4.00
Ca $(NO_3)2$ Anhy	0.656	4.00
Mg SO_4. $7H_2O$	0.368	1.50
Na H_2 PO_4.$2H_2O$	0.208	1.33
E D T A	0.0335	0.10
Mn SO_4.$4H_2O$	0.00223	0.01
Zn SO_4. $7H_2O$	0.00029	0.001
Cu SO_4. $5H_2O$	0.00025	0.001
H_3 BO_3	0.0031	0.05
Na_2 MO O_4. $2H_2O$	0.00012	0.0005
Na Cl	0.0058	0.10
Co SO_4.$7H_2O$	0.000056	0.0002

2.2.2 PROCEDURE

Light is provided in each incubator by six 8-watt fluorescent tubes giving an intensity of 25-30 W/m^2. Illumination was kept constant during experiments with a continuous photophase. No attempt was made to control humidity inside the incubators. Hydrometers showed that it varies between 60 and 80%. The temperature in incubators fluctuated within 0.5°C of the



Plate 2.1 Turnip seedlings with their stems in small glass vials placed inside a ventilated box used for rearing the aphid and parasitoid in incubators

required temperature. Temperatures at various positions within the incubators, determined by thermometers readings had a maximum variations of less than 1°C. With the use of continuous illumination and nutrient solutions it was possible to maintain the seedlings in a good condition for not less than 8 days at 30°C, and as long as 20 days at 12°C. The conditions under which the aphids were reared apparently were unfavourable for the production of alate forms. As a result all data here refers to apterous parthenogenetic females. To give reliable data, if some alate were produced in the experiment, they and their progeny were omitted from the analysis.

2.2.3 FORMULAS FOR DEVELOPMENT

The relationship between rate of development (reciprocals of developmental time in days at each constant temperature multiplied by 100) and temperature is tested for both M. persicae and A. matricariae using the following formulas:

2.2.3.1 : THE LOGISTIC CURVE

A curve of the form:

$$1/y = k / (1 + e^{a - bx})$$ (Davidson, 1944)

was used to describe the trend of acceleration. Where 1/y represents the reciprocal of time required for complete development to be achieved at a given temperature. 'k' represents the value of the upper asymptote of the curve. 'a' is the parameter which indicates the relative position of the origin of the curve on the abscissa. 'b' is the parameter representing the degree of acceleration of development of the insect in relation to temperature, it therefore determines the slope and course of the curve. 'e' is the base of the Napierian system of logarithms, 'x' is the given temperature.

2.2.3.2 THERMAL SUMMATION

When the rate of development is related to temperature by a linear equation ($y = a + bx$), the straight line is best characterized biologically in terms of temperature threshold (t0) and time to adult (k) which is the number of degree days above t0 required by an insect to complete development. 'k' in fact is the reciprocal of the slope 1/b of the straight line and $t0 = -a/b$ (Hughes, 1963; Campbell & Mackauer, 1975a). The rate of development, v, at any temperature, x, is given by:

$$v = k\,(x - t0)$$

2.2.3.3 POLYNOMIAL REGRESSION

When a linear relationship between rate of development and temperature does not fit, a polynomial in x should be developed:

$$y = a + bx + cx^2 + dx^3 + \ldots.$$

Higher powers of x are added until a sufficiently close fit is found. Such regression is used to predict the behaviour of y in relation to x.

2.2.4 WEIBULL CURVE FOR SURVIVAL

Adult longevity data for both M. persicae and A. matricariae is summarized by means of the Weibull frequency distribution, where the proportion surviving at time t is given by:

$$Ft = 1 - \exp(-[(t/b)^c])$$

Where b and c are the scale and shape parameters of the distribution (Pinder et al., 1978). These parameters were estimated by linear regression (Hahn and Shapiro, 1967). Lt_{50} values were then calculated using the relation:

$$Lt_{50} = b\, e^{(1/c \times \log \log 2)}$$

2.3 THE EFFECT OF TEMPERATURE ON DEVELOPMENT, FECUNDITY AND LONGEVITY OF *M. persicae*

2.3.1 MATERIALS AND METHODS Experiments at each temperature were begun with sixty 1st instar nymphs of aphids collected within 16 hours of birth. The nymphs were transferred using a fine moist brush to the undersides of 7 days old brassicae seedlings. They were first touched gently until they withdrew their mouthparts and started walking to avoid damaging their stylets. Two aphids were placed on each plant. The seedlings were transplanted into small plastic vials 50 x 25 mm. The vials were covered by plastic lids, petioles of seedlings protruded through a hole in the centre of the lid. The vials were held inside Stewart plastic boxes 173 x 115 x 63-mm, with ventilation supplied through rectangular opening 62 x 32 mm, cut in the sides and covered with nylon gauze 40 mesh/cm. Each box held five vials spaced 1 cm apart. These boxes were placed in six controlled environment incubators at 12, 16, 20, 24, 28 and 30°C, six boxes for each. Only the middle two shelves of incubators were used to minimize temperature variations. The arrangement of boxes was three in each shelf. The same arrangement was used on the two shelves. Boxes were placed in a corresponding positions in each incubator. All boxes were allocated at random to incubators. With these procedures, it is assumed that, all conditions in incubators except temperature are similar.

The aphids were checked every 24 hours during their nymphal development at midday until they produced their first progeny. Then they were examined daily at noon and records were kept on births and deaths in addition to length of adult life. The young that were produced each day during the life of an adult aphid were counted and removed from the seedlings so that the density of populations remained constant.

2.3.2 RESULTS

2.3.2.1 DEVELOPMENT

Table (2.1) shows the duration of development period for nymphs of M. persicae at various constant temperatures between 12 and 30°C. Time required for development decreased with an increase in temperature up to 24°C. Above 24°C, time required increased slowly up to 30°C. At 32°C they failed to complete development and none reached the adult stage. When rate of development is plotted against temperature a sigmoid curve is obtained (Figure 2.1).

THERMAL SUMMATION

The plot of temperature and rate of development has been checked for linearity. The highest values of temperatures 28 and 30°C had to be rejected because they did not fit the straight line through the other points. From the remaining data 12, 16, 20 and 24°C, the relationship can be represented by a straight line (Figure 2.2). The straight line when extended cuts the x-axis at the temperature threshold t0. The relationship is represented by the following linear equation:

$$y = -4.009 + 0.759625x$$

It is then possible to describe development with two parameters the theoretical temperature threshold (t0) and the thermal constant (k). The present results for M. persicae are 5.28 and 131.644 for t0 and k respectively. Using the formula:

$y\,(x - t0) = k$, the calculated values for development periods within 12 - 30°C are given in Table (2.2). The four observed values for developmental periods within 12 - 24°C, which is the linear portion of the curve of rate of development, were found to be a good fit to the calculated values. The difference between observed and calculated values

suggests that the deviation of any of the points from the calculated values does not exceed 3.3% of the appropriate calculated value. The greatest deviation is 0.6 at 12°C, which is 3.2% of the calculated value at 12°C. The root mean square deviation between the observed and calculated value is only 0.3 which is only 1.6% of the calculated value at 12°C. The observed values for development at temperatures above 24°C fall short of the calculated values. The difference increases as temperature increases. At 28°C the percentage deviation was about 38% and increased to about 70% at 30°C.

LOGISTIC CURVE

Data on rate of development at temperatures above the peak should not be included when calculating the formula for the temperature-velocity curve (Davidson, 1944). So the observed values for rate of development between 12 - 24°C have been fitted to a curve having the formula:

$$1/y = k / (1 + e^{a - bx})$$

The value of the parameter k is calculated from the following formula according to Davidson (1944):

$$k = 2\,p1p2p3 - p2^2(p1 + p3) \,/\, p1p3 - p2^2$$

Where p1, p2 and p3 are values for 100/y on the curve at three equally spaced temperatures on the abscissa. The following values for p1, p2 and p3 were selected for M. persicae:

y1 at 12°C p1 = 4.946

y2 at 16°C p2 = 8.197

y3 at 20°C p3 = 11.561

Substituting these values for p in the above formula, the calculated value for k, is found to be 17.152471. Values are then calculated for k - p / p for each of the four observed values of p at temperatures 12, 16, 20 and 24°C. When the values of log e k - p / p at each temperature 12, 16, 20 and 24°C is plotted against the appropriate temperature, the four points approximate closely to a straight line. The values of a and b are obtained directly from the equation of a straight line:

$$\log e \quad k - p / p = 3.2726 - 0.19858x$$

From which the calculated formula for the temperature-velocity curve for the development of M. persicae is obtained as follows

$$100/y = 17.152471 / 1 + e3.2726-0.19858x$$

The curve shown in Figure (2.3) has been calculated from this formula. The numerical values for development period being given in Table (2.3). The four observed values for development period at temperatures ranging from 12 - 24°C were a good fit to the calculated curve. The greatest deviation is 0.19 at 12°C. It is only 0.97% of the calculated value at 12°C. The observed values for development period at temperatures above 24°C, fall short of the calculated values. The difference increases as temperature rises. At 28°C the percentage deviation between the observed and calculated value is 24.9% of the calculated value whilst it goes up to 45.6% at 30°C.

POLYNOMIAL REGRESSION

The relationship between temperature and duration of development is well expressed by the polynomial curve. The best fit of polynomial regression found is polynomial order 4, (R^2 =,99 834), the equation is:

Table 2.1 EFFECT OF TEMPERATURE ON DEVELOPMENT OF M. persicae.

Temperature °C	Development time in days Mean	s.e.	l.s.d. 5% = 1.17
12	20.2	0.8	a
16	12.2	0.4	b
20	08.7	0.2	c
24	07.2	0.2	d
28	08.0	0.2	dc
30	09.1	0.2	c

Means not sharing the same letters are significantly different.

Table 2.2 DEVELOPMENT PERIOD OF M. persicae PREDICTED BY THERMAL SUMMATION.

Temp. °C	Observed	Calculated	Observed - calculated	% deviation
12	20.22	19.59	0.63	03.22
16	12.20	12.28	-0.08	00.65
20	08.65	08.94	-0.29	03.24
24	07.17	07.03	0.14	01.99
28	08.02	05.79	2.23	38.51
30	09.07	05.33	3.74	70.2

Table 2.3 DEVELOPMENT PERIOD OF M. persicae PREDICTED BY LOGISTIC CURVE

Temp. °C	Observed	Calculated	Observed - calculated	% deviation
12	20.22	20.02	0.2	00.99
16	12.20	12.24	-0.04	00.33
20	08.65	08.73	-0.08	00.92
24	07.17	07.14	0.03	00.42
28	08.02	06.42	1.6	24.9
30	09.07	06.23	2.84	45.6

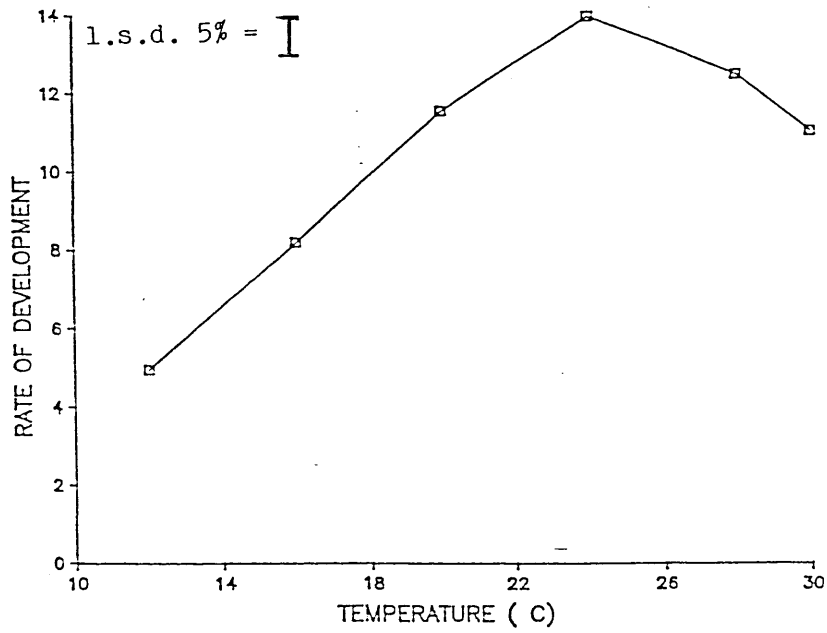


Figure 2.1 THE RELATIONSHIP BETWEEN TEMPERATURE AND RATE OF DEVELOPMENT FOR M. persicae (12-30C°)

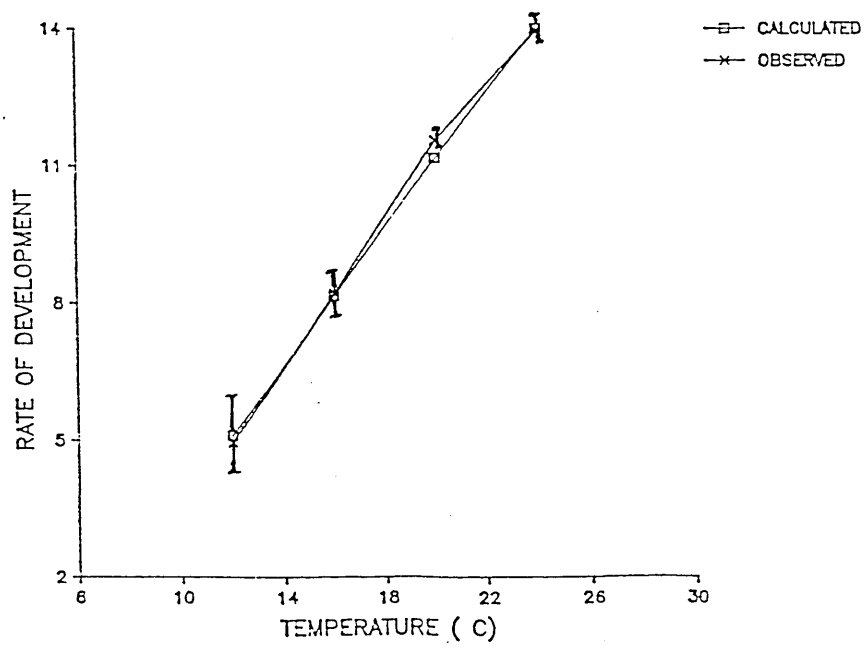


Figure 2.2 THE RELATIONSHIP BETWEEN THE RATE OF DEVELOPMENT OF M. persicae AND TEMPERATURE, WITH THE FITTED LINEAR REGRESSION (12-24°C)

Bars = standard errors

$$y = a + bx + cx^2 + dx^3 + ex^4$$

Where a = 105.502811

b = -13.5028429

c = 0.730417738

d = -0.018823957

e = 0.000196980505

Table (2.4) shows the predicted values of development period by using polynomial regression. The observed values within the whole range (12 - 30°C) were found to be an excellent fit to the calculated values (Figure 2.4). The deviation of any point from calculated value does not exceed 1.63% of the appropriate calculated value.

2.3.2.2 FECUNDITY

The relationship between temperature and the average total fecundity is shown in Table (2.5). M. persicae produced the greatest number of progeny at 20°C. At lower and higher temperatures, total fecundity was less, particularly at temperatures higher than 28°C. Age specific fecundity rates Mx are illustrated in Figure (2.5) as the number of young born per day per female alive at the mid-point of each day. As temperature was increased up to 24°C, the number of progeny produced per day also increased. The number of progeny laid per female per day reached a peak earlier at higher temperatures. The peak was followed by an equally rapid decline. Temperature also influenced the length of reproductive period. Generally between 12 - 30°C, the higher the temperature the sooner larviposition began and the shorter the reproductive period.

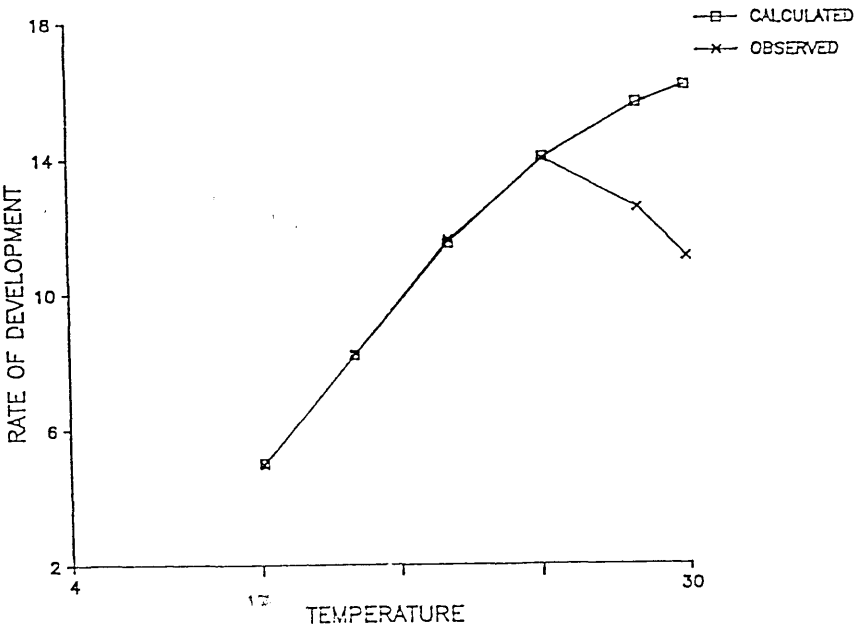


Figure 2.3 THE RELATIONSHIP BETWEEN THE RATE OF DEVELOPMENT OF M. persicae AND TEMPERATURE AS CALCULATED FROM THE LOGISTIC EQUATION

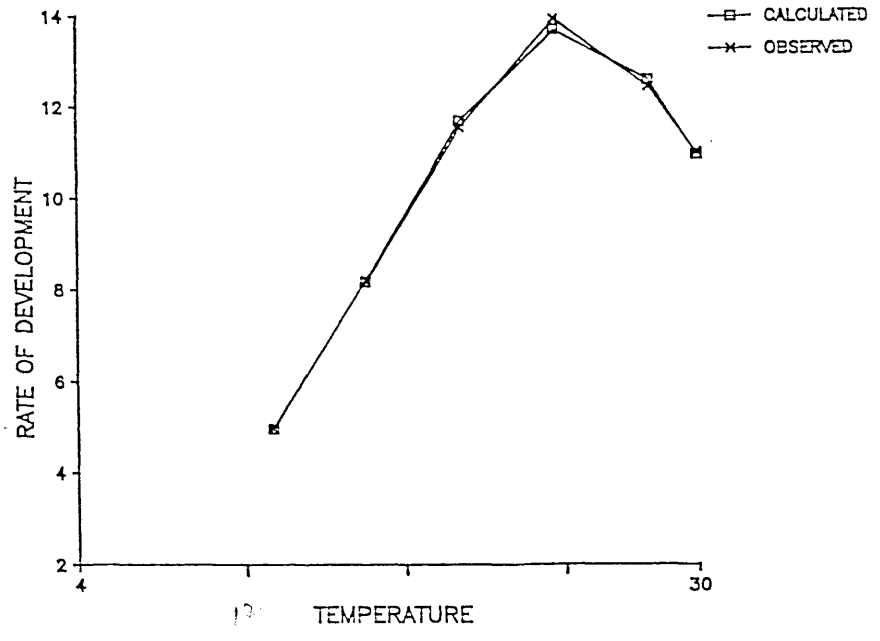


Figure 2.4 THE RELATIONSHIP BETWEEN THE RATE OF DEVELOPMENT OF M. persicae AND TEMPERATURE CALCULATED FROM POLYNOMIAL REGRESSION

Table 2.4 DEVELOPMENT PERIOD OF M. persicae PREDICTED BY POLYNOMIAL REGRESSION.

Temp. °C	Observed	Calculated	Observed - calculated	% deviation
12	20.22	20.20684	0.01316	0.07
16	12.20	12.25225	-0.05225	0.4
20	08.65	08.54027	0.10973	1.28
24	07.17	07.28861	-0.11861	1.63
28	08.02	07.92526	0.09474	1.2
30	09.07	09.10385	-0.03385	0.37

Table 2.5 EFFECT OF TEMPERATURE ON FECUNDITY OF M. persicae.

Temperature °C	Fecundity Mean	s.e.	l.s.d. 5% = 7.91
12	43.9	1.8	c
16	52.0	1.6	b
20	64.1	5.3	a
24	36.3	2.1	c
28	20.5	2.1	d
30	11.2	1.5	e

Means not sharing the same letters are significantly different.

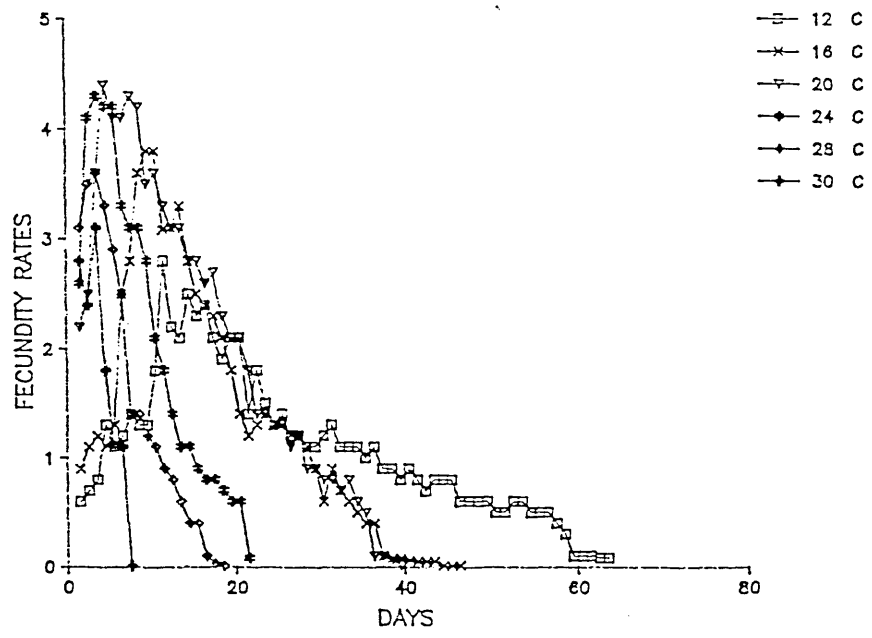


Figure 2.5 AGE SPECIFIC FECUNDITY OF M. persicae AT VARIOUS CONSTANT TEMPERATURES (12-30°C)

2.3.2.3 LONGEVITY

The relationship between temperature and mean adult longevity is shown in Table (2.6). The longevity of M. persicae decreased as temperature increased from 12 to 30°C. The maximum longevity was about 63 days at 12°C. The shortest was about 7 days at 30°C. Longevities of the populations are presented as survival rates in Figure (2.6). The number of aphids alive at the mid-point of each day is plotted as a proportion of the original 60 aphids with which the experiment was begun. The resulting line Lx, age specific survival, gives the propability at birth of being alive at age x. The survival curves for M. persicae, the proportion surviving at each time interval, along with the fitted Weibull curves are shown in Figure (2.7). Table (2.7) shows the value of the two Weibull parameters and the calculated LT_{50} for M. persicae at the six constant temperatures. The value of LT_{50} generally decreases with rising temperature. The value of the c parameter is bigger than 1 at all temperatures. The value of b generally decreases with increase in temperature being significantly greater ($P<0.05$) at 12°C than at any other temperature and greater at 16°C ($P<0.05$) than at 20, 24, 28 and 30°C and being greatly less at 30°C ($P<0.05$) than at any other temperature.

2.3.3 DISCUSSION

The present results on development agree well with those of Barlow (1962), but disagree in completing their development at 30°C where those of Barlow died rapidly none reaching the adult stage. The results are in line with DeLoach (1974) results, especially at 30°C where his M. persicae survived and completed development in 9.2 days. The period of development at 16 and 20°C is comparable to those of Rabasse & Shalaby (1980) at 15 and 20°C which had been 11.48 and 8.76 respectively.

The results and analysis suggest that the rate of development of M.

Table 2.6 EFFECT OF TEMPERATURE ON LONGEVITY OF M. persicae.

Temperature °C	Longevity in days Mean	s.e.	l.s.d. 5% = 8.31
12	63.8	3.3	a
16	47.7	2.5	b
20	37.0	3.4	c
24	24.0	3.3	d
28	18.2	3.1	d
30	07.7	2.4	e

Means not sharing the same letters are significantly different.

Table 2.7 ADULT LONGEVITY OF M. persicae: WEIBULL PARAMETERS FOR SURVIVAL CURVES AT VARIOUS CONSTANT TEMPERATURES.

	Temperature (°C) 12	16	20	24	28	30
b	42.02 a	24.28 b	17.86 c	13.45 d	10.75 d	4.29 e
c	01.81	01.90	01.71	01.86	01.72	2.64
Lt_{50}	34.32	20.02	14.41	11.05	08.69	3.73

Numbers followed by the same letter not significantly different at the 5% level (tables of Thoman & Bain, 1969).

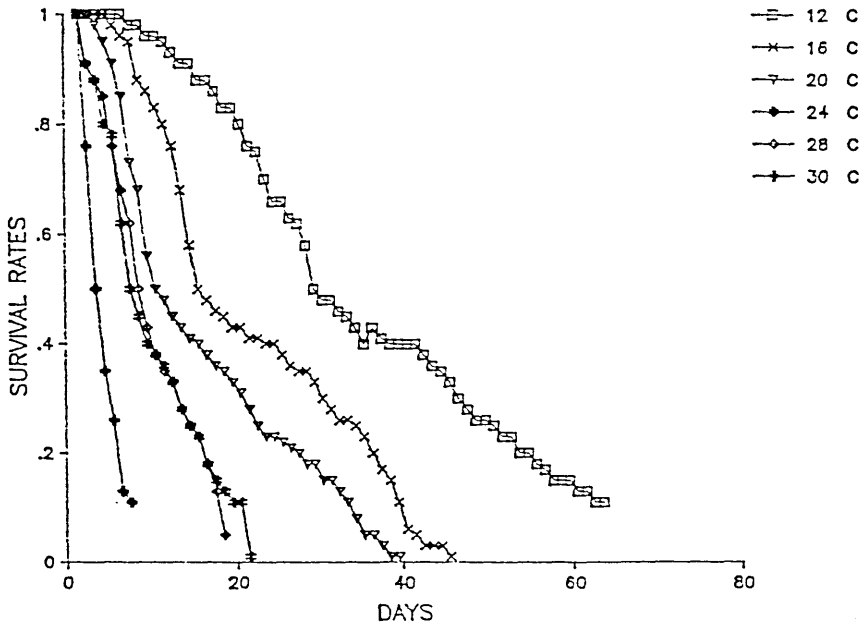


Figure 2.6 AGE SPECIFIC SURVIVAL OF M. persicae AT VARIOUS CONSTANT TEMPERATURES (12-30°C)

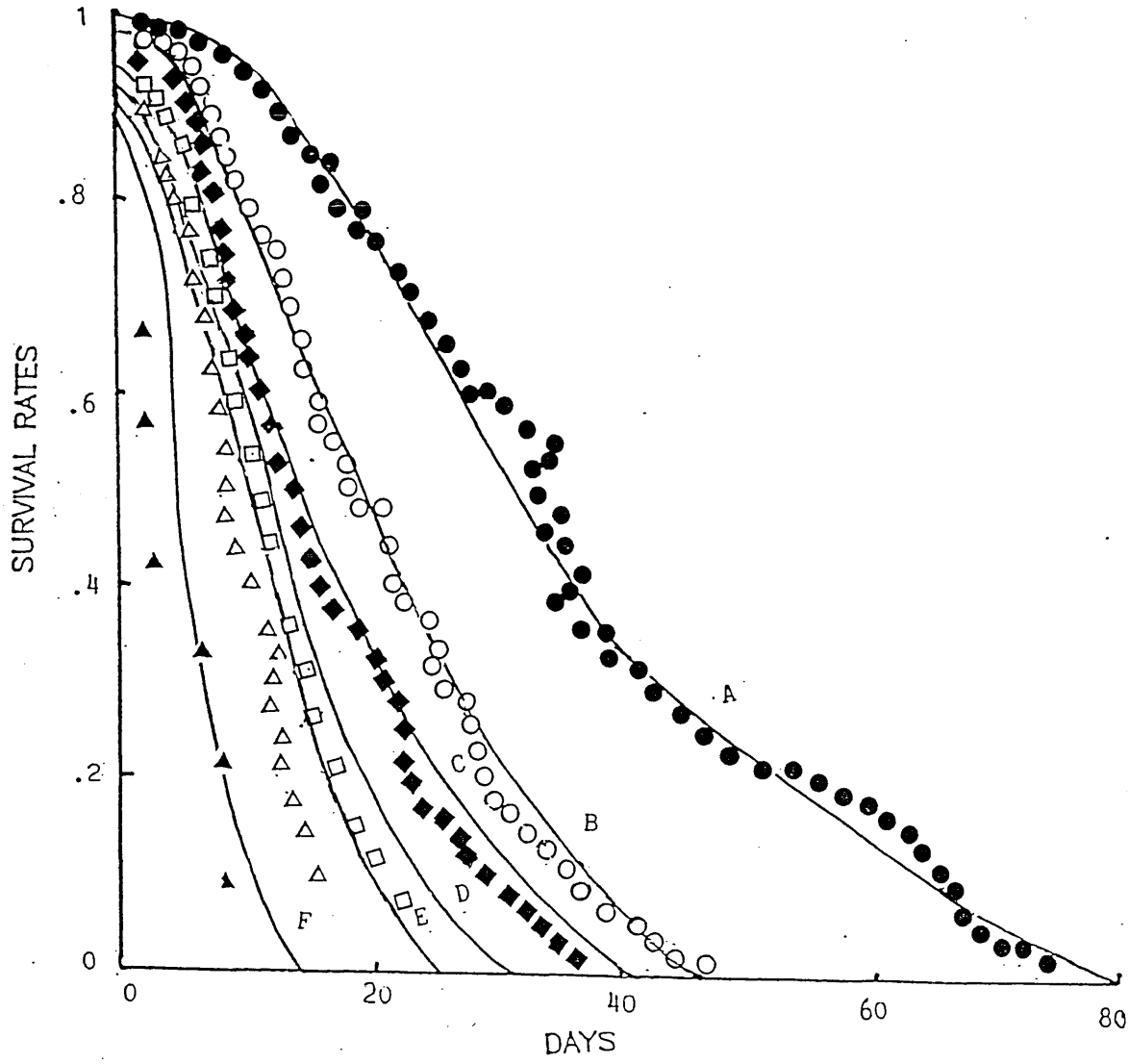


Figure 2.7 THE SURVIVAL DATA FOR M. persicae AT CONSTANT TEMPERATURES ALONG WITH THE FITTED WEIBULL CURVES

Fitted Weibull curves

A (12°C) $F(t) = 1 - \exp(-[(t/42.02)^{1.81}])$

B (16°C) $F(t) = 1 - \exp(-[(t/24.28)^{1.9}])$

C (20°C) $F(t) = 1 - \exp(-[(t/17.86)^{1.7}])$

D (24°C) $F(t) = 1 - \exp(-[(t/13.45)^{1.86}])$

E (28°C) $F(t) = 1 - \exp(-[(t/10.75)^{1.72}])$

F (30°C) $F(t) = 1 - \exp(-[(t/4.29)^{2.64}])$

persicae can be expressed as a sigmoid curve Figure (2.1) within 12 - 30°C. It is similar to the sigmoid curve obtained by Messenger (1964a) for the spotted alfalfa aphid Therioaphis maculata Buckton when a wide range of temperatures was used. However, the sigmoid logistic equation described the developmental period only within 12-24°C. Above 24°C the calculated values deviate steadily from the observed ones, due to deleterious effects of high temperatures.

The relationship between temperature and development period was found to be hyperbolic within the range 12-24°C, therefore a linear relationship was obtained for the relationship between temperature and rate of development within the same range. The estimated temperature threshold and thermal constant under the present study were found to be 5.28°C & 131.6 D° respectively, as calculated from linear regression (R^2 = 0.9947). The results are comparable with that found in the literature for M. persicae. Van Emden et al. (1969) considered t0 to equal 4.3°C, Rabasse & Shalaby (1980) considered it to be 4.8°C for t0 and 124.5 D for K. The differences in thresholds might be expected. Morris (1971) and Campbell et al. (1974) declared that populations in different areas might have different thresholds. They have shown differences of 1 - 2°C over the 1300 km difference in latitude between Berkeley and Vancouver in their work with five aphid species and their aphidiid parasitoids. So, the differences in results of temperature threshold 1-2°C from other workers may be due to the above mentioned reason or may be due to higher temperature requirements of M. persicae in the present studies than those of van Emden et al. (1969) and Rabasse & Shalaby (1980). A possible explanation is that the temperature requirements of M. persicae in this study have been adjusted to suit the local climatic conditions of the laboratory 20 ± 3°C. Such adaptation may result from continuous breeding for successive generations over a long period of time in laboratory conditions. This very reason may explain why M. persicae under this study survived and completed their development at

30°C while those of Barlow (1962) failed to do so at the same temperature.

The linear portion of the curve of rate of development calculated from the thermal summation formula was found to be a good fit to the observed values. The observed values for rate of development at temperatures above 24°C fall short of the calculated values. The difference increases as temperature rises, with the percentage deviation reaching about 70% at 30°C. The values of rate of development calculated from the logistic curve followed the same trend only the percentage deviation was much less reaching about 45% at 30°C. No significant improvement over thermal summation was achieved by using the logistic curve of Davidson (1944). Because both models are based upon linear assumption of the temperature-velocity curve, they were reliable only within the linear portion of the relationship. The polynomial model was found to give an excellent fit to the observed values within the whole range (12 - 30°C) covering linear and nonlinear portions of the temperature-velocity relationship. The polynomial regression model can be safely used to predict developmental periods on the basis of a reasonable number of observations. If the number of observations are quite small, this may be dangerous, especially to predict what might happen outside the range of observations actually made.

The pattern of reproduction per day by adult M. persicae at almost all temperature levels studied is characterized by a relatively rapid rise in numbers of progeny produced per day until, in a relatively short time, a maximum rate of productivity is reached, after which a gradual decrease occurs until reproduction finally ceases. At 16°C, a maximum daily production of 3.8 progeny per female is reached after the 9th day. At 20°C, a peak of 4.4 progeny per day is reached on the 4th day, while at 28°C a maximum of 3.6 is achieved on the 2nd day. Reproductive times were prolonged by low temperature. The duration of the reproductive period at 20°C is not much different from Barlow (1962), Harrison (1969), DeLoach

(1974) and Wyatt & Brown (1977). The results are comparable with those of Barlow (1962), they differ in reproducing at 30°C while those of Barlow did not survive to reach adult stage. The total fecundity of about 64 progeny attained, under this experiment, at 20°C is much more than that obtained by Whalon & Smilowitz (1979) which was about 28 at 21.1°C. However, all these tests were under different conditions and such variations in results would be expected. So, the variations in results could be attributed to differences in races of M. persicae, host plants and rearing methods. The differences in biotypes due to different geographical distribution may result in differences in fecundity and longevity. The difference in host plants, where brassica plants were used in the present study, while Barlow (1962) and Whalon & Smilowitz (1979) used potato, Harrison (1969) used tobacco, DeLoach (1974) used cabbage and Rabbase & Shalaby (1980) used egg plants. It is a fact that different plants have different nutritional values and different susceptibility to attack which in turn affect fecundity and longevity. There is a difference in rearing methods, as Barlow (1962), Wyatt & Brown (1977) and Rabasse & Shalaby (1980) used leaf discs while the present experiment used growing seedlings. The leaf discs of sufficient size usually obtained from mature leaves did not represent the preferred feeding sites which are senescent or young growing leaves. Besides the physiology and nutritional status of growing young seedlings are not comparable with detached leaves. Finally the difference in light intensity could also be a possible reason for the difference in fecundity. Wyatt & Brown (1977) pointed out that low light intensity greatly impaired reproduction especially when combined with high temperatures. This very reason could be attributed to the low fecundity obtained by Whalon & Smilowitz (1979) in comparison to present results.

The results show that longevity is strongly temperature dependent, and adversely affected by an increase in temperatures. The populations of M. persicae under the present study seem more adapted to higher temperatures

than those of Barlow (1962). M. persicae populations survived longer than those of Barlow (1962) at higher temperatures of 28 and 30°C. Barlow's aphids survived up to 70 days at 10°C with 50% death after 42 days which is comparable to the present results at 12°C which survived up to 63 days with 50% death after 34 days. They are in line with DeLoach's (1974) results whose aphids survived for about 40 days at 20°C and 10 days at 30°C. The present corresponding results were 37 and 7 days at 20 and 30°C respectively. LT_{50} is a measure of average life span but gives no further information about the shape of survival curve. The same is true of other measures of mean longevity. The results are best described and summarized according to Weibull frequency distribution. There have been no data in the literature, about M. persicae longevity summarized by means of the Weibull function, to compare it with the present obtained b and c parameters. The value of c was bigger than 1 for all temperatures indicating type 1 survivorship curve (Pinder et al, 1978) in which mortality is increasing function of age. The advantage of the Weibull distribution as a description of longevity data is that it summarizes all the information contained in an age specific survival curve using two parameters b & c scale and shape respectively. This gives all the important information about the number of individuals dying over a given period of time and is something the other methods fail to do.

2.4 THE EFFECT OF CONSTANT TEMPERATURES ON DEVELOPMENT, LONGEVITY AND FECUNDITY OF A. matricariae

2.4.1 THE EFFECT OF CONSTANT TEMPERATURE ON DEVELOPMENT

2.4.1.1 MATERIALS AND METHODS

To study development time several parasitoids of both sexes not more than 24 hours old were kept in ventilated plastic boxes 175 x 155 x 55 mm with 50% honey solution streaks on sides for food. A day later the parasitoids were released to oviposit freely on an excess of M. persicae aphids distributed on 5 potted turnip plants Brassica campestris rapa L. placed inside ventilated perspex cages 610 x 400 x 530 mm at a laboratory temperature of 20 ± 4°C. The following day at the same time, all parasitoids were removed. The exposed aphids were then transferred using a fine moistened paint brush onto the undersides of 7 day old turnip seedlings, 3 aphids per seedling. Seedlings were placed in vials filled with tap water and provided with standard nutrient solution (Section 2.2). Seedlings with aphids were put inside plastic boxes with rectangular openings on dorsal side covered by 40 mesh/cm gauze for ventilation. Each box contained 5 seedlings with total of 15 aphids. Six replicate boxes were placed inside incubators at 6 different constant temperature regimes 12, 16, 20, 24, 28 and 30°C. A 24 hour constant illumination of 25-30 W/m^2, was provided by 6 8-watt fluorescent tubes. Relative humidity ranged between 60-80%. Each day the seedlings were examined for mummified aphids and then were checked daily at midday for adult parasitoid emergence. Each adult was then recorded and removed. Any non-emerged mummies were dissected at a later stage. From these recordings the mean duration of development from egg to mummification and from mummification to adult was computed. The percentage mortality during pupal development under each temperature was recorded. In the last analysis development was measured as the time to adult which is defined as the period from oviposition to emergence and

includes, egg, larva and pupal period. Newly emerged parasitoids from different temperature regimes were sexed. The sex was identified by the shape of pointed abdomen and ovipositor for females. The overall sex ratio was recorded for 3 replicates for each temperature. Each replicate composed of only one box.

2.4.1.2 RESULTS

Table (2.8) shows the mean periods of development for Aphidius matricariae at various constant temperatures. The total development period given in the table is also divided into the period from the oviposition to aphids mummification and from mummification to parasite emergence from the cocoon. The development period decreased as temperature increased from 12 to 24°C but increased above 24°C. Means were calculated from the pooled data of male and female developmental times. The percentage emergence of adults was fairly high and consistent at temperatures between 12-24°C but greatly declined ($P<0.05$) at 28 and 30°C (Table 2.9). Table (2.9) also reveals that the overall sex ratio over the different temperatures is relatively consistent 1:1 but the ratio is significantly ($P<0.05$) altered in favour of males at 30°C.

THERMAL CONSTANTS

The relationship between rate of development and temperature within the range 12-24°C (Figure 2.8) is described by a linear regression equation of the form:

$$y = -3.4435 + 0.54625\ x$$

From the equation the lower threshold, t0 is calculated as 6.30 and the thermal constant, k as 183.066.

Table 2.8 EFFECT OF TEMPERATURE ON DEVELOPMENT OF A. matricariae.

Temp. °C	Development period Egg-mummification l.s.d. 5% = 0.50 Days	s.e.		Mummific.-adult l.s.d. 5% = 0.39 Days	s.e.		Total development l.s.d. 0.1% = 1.25 Days	s.e.	
12	21.82	0.35	a	11.25	0.19	A	33.07	0.51	U
16	13.18	0.13	b	06.07	0.09	B	19.25	0.14	V
20	08.37	0.11	d	04.27	0.11	D	12.58	0.20	Y
24	07.17	0.08	e	03.48	0.12	E	10.65	0.11	Z
28	08.15	0.12	d	04.08	0.13	D	12.23	0.14	Y
30	09.18	0.11	c	05.15	0.16	C	14.33	0.09	X

Means within columns sharing the same letters are not significantly different

Table 2.9 EFFECT OF TEMPERATURE ON SEX RATIO AND PERCENTAGE EMERGENCE FROM COCOONS for A. matricariae

Temp. °C	% emergence from cocoons	s.e	l.s.d. 5% = 8.83	% female	s.e	l.s.d. 5% = 6.88
12	97.0	1.46	a	50.67	2.89	A
16	95.67	0.99	a	58.7	4.51	A
20	94.33	1.54	a	55.83	3.11	A
24	91.3	1.89	ab	50.3	3.37	A
28	82.0	4.46	b	53.17	4.85	A
30	69.33	5.41	c	37.33	4.84	B

Means within columns sharing the same letters are not significantly different, l.s.d. and analysis is on the basis of arc-sine transformation.

THERMAL SUMMATION

The calculated values for development of A. matricariae within 12-30°C according to the thermal equation: $y\ (x-t0) = K$ are given in Table (2.10). The four observed values for development at temperatures ranging from 12-24°C were a good fit to calculated values. The deviation of any of the points from the calculated values does not exceed 5.8% of the appropriate calculated value. The observed values for developmental times at temperatures above 24°C fall short of the calculated values. The difference increases as temperature rises. At 28°C the deviation was 45%, increased up to 85% at 30°C.

LOGISTIC CURVE

The velocity-temperature curve was fitted to the logistic equation:

$$y = K / 1 + e^{(a-bx)} \quad \text{(Davidson, 1944)}$$

k is calculated by:

$$k = 2p1p2p3 - p2_2\ (p1+p3) / p1p3 - p2_2$$

The values for p1, p2 and p3 were selected for A. matricariae which represent values for y on the curve at 3 equally spaced temperatures on x-axis as follows:

p1 = 3.024 at 12°C

p2 = 5.195 at 16°C

p3 = 7.947 at 20°C

By substituting these values for p in the above formula, the calculated value of k was found to equal 15.693952. The values of log k - p / p at each of temperatures 12-24°C were plotted against the appropriate temperature. The constants a and b were derived from linear regression

equation working in Naperian logarithms:

$$\log k - p / p = 3.228 - 0.1556x \qquad (R^2 = 97.1)$$

By substituting the values of constants a, b and k the calculated formula for logistic curve is obtained as

$$y = 15.693952 / [1 + e(3.228-0.1556x)]$$

The numerical values for development period, the calculated from logistic and the observed ones are given in table (2.11). The observed values of development within (12-24°C) were a good fit to calculated values. The deviation of any points from the calculated curve does not exceed 7% of the appropriate calculated value. The observed values of development at temperatures above 24°C fall short of the calculated values. The difference increases as temperature rises. At 28°C the difference between the calculated and observed value was about 45% of the calculated value, it raised to about 82% of the calculated value at 30°C.

POLYNOMIAL REGRESSION

The best maximum possible fit was found to be a polynomial order 4. The co-efficient of determination, R^2 was found to be.99 999. The quartic parabola curve is shown in Figure (2.9). The quartic equation is as follows:

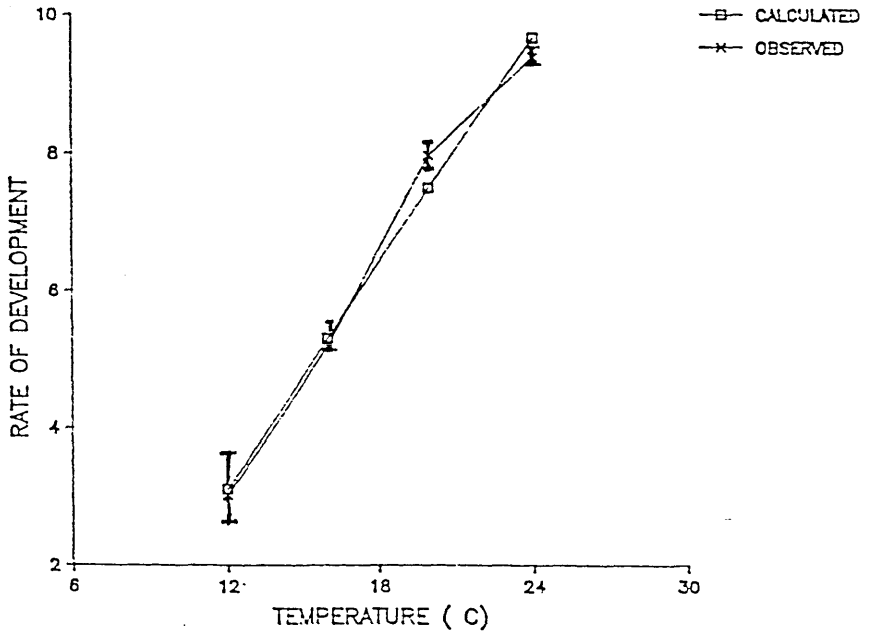


Figure 2.8 THE RELATIONSHIP BETWEEN THE RATE OF DEVELOPMENT OF A. matricariae AND TEMPERATURE, WITH THE FITTED LINEAR REGRESSION (12-24°C)

Bars = standard errors

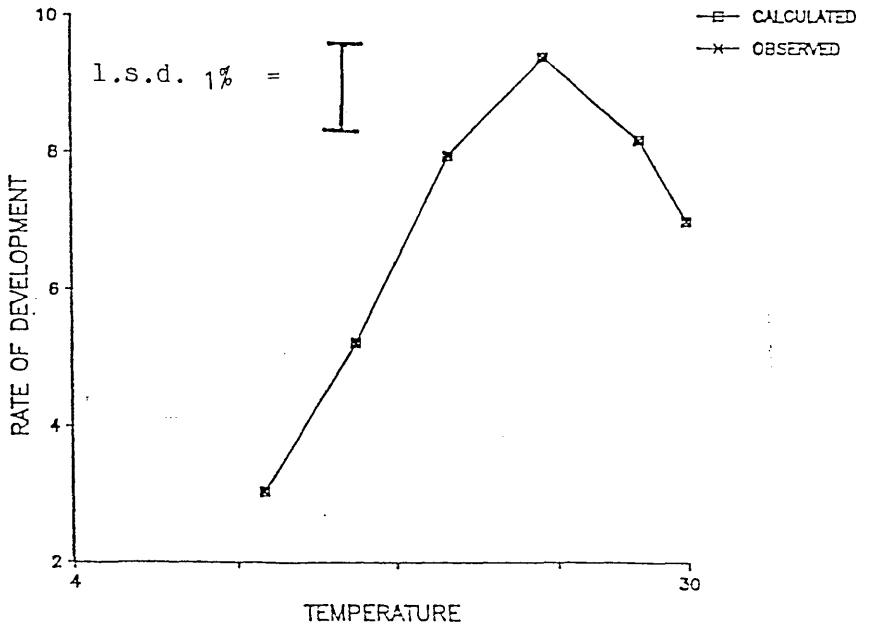


Figure 2.9 THE RELATIONSHIP BETWEEN THE RATE OF DEVELOPMENT OF A. matricariae AND TEMPERATURE CALCULATED FROM POLYNOMIAL REGRESSION

$$y = a + bx + cx^2 + dx^3 + ex^4$$

where

a = 160.746133

b = -18.9775654

c = 0.9183977

d = -0.0210875038

e = 0.000204592138

The whole observed values for development rates at temperatures (12-30°C) were found to be a good fit to the calculated curve from the quartic equation (Figure 2.9). Table (2.12) shows the observed and calculated periods of development. The greatest deviation from the appropriate calculated value is 0.00499 at 24°C which is only 0.047 of the calculated value. The root mean square deviation between the observed and calculated values is 0.000203 which is 0.019% of the calculated value at 24°C.

2.4.1.3 DISCUSSION

The rate of development of A. matricariae was influenced by temperature. In general, the mean developmental time decreased with an increase in temperature. At 28-30°C, the rate of development declined suggesting that the upper limit or upper temperature threshold was being approached. The percentage emergence from cocoons was drastically reduced at 30°C, indicating the upper thermal limit is approached. The results show that with exception of 30°C the overall sex ratio was relatively consistent 1:1. The dominance of males at high temperature of 30°C may be due to death of sperms or paralysis of spermatheca muscles. Such information is valuable for construction of life table data.

Table 2.10 DEVELOPMENT PERIOD OF A. matricariae PREDICTED BY THERMAL SUMMATION.

Temp. °C	Observed	Calculated	Observed - calculated	% deviation
12	33.07	32.12	0.95	02.96
16	19.25	18.87	0.38	02.01
20	12.58	13.36	-0.78	05.84
24	10.65	10.34	0.31	03.0
28	12.23	08.43	3.8	44.9
30	14.33	07.72	6.61	85.62

Table 2.11 DEVELOPMENT PERIOD OF A. matricariae PREDICTED BY LOGISTIC CURVE.

Temp. °C	Observed	Calculated	Observed - calculated	% deviation
12	33.07	31.22	1.85	05.93
16	19.25	19.71	-0.46	02.33
20	12.58	13.53	-0.95	07.02
24	10.65	10.21	0.44	04.31
28	12.23	08.43	3.8	45.07
30	14.33	07.88	6.45	81.9

Table 2.12 DEVELOPMENT PERIOD OF A. matricariae PREDICTED BY POLYNOMIAL REGRESSION.

Temp. °C	Observed	Calculated	Observed - calculated	% deviation
12	33.07	33.06741	0.00259	0.0078
16	19.25	19.24788	0.00212	0.011
20	12.58	12.58744	-0.00744	0.059
24	10.65	10.64501	0.00499	0.047
28	12.23	12.23670	-0.0067	0.055
30	14.33	14.33149	0.00149	0.010

The results are very close to the ones obtained by Rabasse & Shalaby (1980) for A. matricariae on M. persicae in the range 10-20°C. They found A matricariae completed development in 43.20, 22.19 and 12.88 days at 10, 15 and 20°C respectively. The present corresponding values being 33.067, 19.25 and 12.583 days at 12, 16 and 20°C. The present results are also comparable to the ones found for other aphidiids. Liu Shu-sheng & Hughes (1984a) have found developmental periods for Aphidius sonchi Marshal parasitizing sowthistle aphid Hyperomyzus lactucae L. are 12.5 days at 20°C and 10.1 days at 24°C and increased slightly to 10.2 days at 28°C which is comparable to our results.

The temperature requirements of the parasitoid was found to be a little higher than that of its host. The lower temperature threshold for A. matricariae was 6.30 while it was 5.28 for M. persicae. Campell et al., (1974) suggested that higher temperature requirements of parasites than their hosts have two fold effect on the host-parasite complex. First, ensuring that in a temperate climate parasites do not appear before their hosts early in the season. Secondly, that a continued minimum host supply is available throughout the season. It would be expected that because of differences in threshold values, the parasitoid appear shortly after the fundatrix generation of M. persicae in the spring. Care was taken to ensure that hosts used in the laboratory are similar to those in the field.

Some limitation may arise from the use of constant versus variable temperature (Pradhan, 1945; Messenger, 1964a). However, Campell et al., (1974) have not found much difference in development rates between temperatures that were constant or fluctuating about the same average value provided that fluctuation do not extend below the threshold.

There was a definite relationship between time taken for an insect to develop and the temperature at which development occurs. Since the 18th century, numerous attempts have been made to describe this relationship

using mathmatical models, but none have met with universal acceptance.

The theory of summation of temperatures has been widely used by entomologists, once the t0 and k have been determined from constant temperature data, the development period under any regime may be determined by a simple summation method. Unit day degrees above t0 are accumulated until the value of k is reached at which point development is complete. It implies that the temperature-time curve is a hyperbola and its reciprocal a straight line. It represents the development-temperature sufficiently accurately on the linear portion of the curve from 12-24°C. It is obvious that temperature summation is satisfactorily only for the linear portion of development rate. It has inherent faults. Firstly the assumed linear relationship is known to hold as an approximation for the median portion of the temperature range (Campell et al., 1974). Towards temperature extremes the relationship deviates from linear and estimates therefore become inaccurate. Secondly, the lower threshold on which the thermal summation is based is a purely theoretical point determined by extrapolation of the linear portion of the relationship into where the relationship is not linear. Thus, temperature summation is an unsatisfatory representation for the whole data from 12-30°C.

A logistic equation fitted to the data as described by Davidson (1944) did not conform closely to the observed values. The trend of rate of development from 1st instar to adult for A. matricariae suggests that the relative rate of acceleration of development gradually increases with a rise in temperature until the inflexion of the curve at 20°C is reached. At temperatures above the inflexion of the curve, the relative rate of acceleration decreases until the peak temperature is reached 24°C. This is the temperature at which the development proceeds at the fastest average rate. At temperatures above the peak 28-30°C relative rate of acceleration of development declines. The mathematical formula of the logistic curve

implies that, under the given conditions, A. matricariae has the inherent power of achieving the average rate of development represented by the value of the parameter k which is 15.69395. The temperature at which this rate of development would be approached is 65°C based on The formula :

$$x = 1/b\ (a - \log_e k-p\ /\ p)$$

In reality A. matricariae can not attain this rate of development because its development would be inhibited at much less than this value at about 32°C. So, the parameter k may be looked upon as only a theoretical biological constant. This value is different for different insects and different stages of the same insect and subject to alteration by change in surrounding conditions which lead to differences in the rate of development. However, the logistic curve described under this study gave an empirical representation of the trend in rate of development from 12°C to peak temperature of about 24°C. Above the inflexion, the retarding forces of heat slow down the speed of development. Above the peak 24°C, these forces are intensified and the observed values for speed of development fall significantly below computed ones. Logistic curve represents data only within linear portion up to the peak temperature 24°C. So, no significant improvement of using logistic over summation is obtained.

Although a number of equations have been proposed to describe developmental curves, polynomial regression analysis was found to be the more accurate method of determining and describing the temperature-development relationship. From the calculated curve of polynomial, the minimum developmental period was found to be 10.65 days. Temperature corresponding to the minimum developmental period is considered to be optimum for development which is 24°C, although deleterious effects not related to speed of development may occur at this temperature. Any fluctuation from this optimum temperature (24°C) will cause an increase in developmental time. The results and analysis showed that the polynomial

regression equation faithfully represented the data over the whole range of temperature (12-30°C) with negligible maximum deviation from the calculated values. This is made possible by obtaining the best fit (R^2 = 99.999). If the deviations from a computed curve appear to be more or less random fitting a higher degree curve is usually useless. If the deviations are systematic or in definite groups as to sign it is generally advantageous to introduce a higher degree. The polynomial is by far the most widely used expression for describing the relation between two variables. It is so flexible and easily handled mathematically. It is possible to calculate a polynomial curve that will almost exactly fit every point on condition there is only one value for the dependent y for each value of the independent x. The degree of polynomial required to do this is at most one less than the number of pairs of observations. In reality, it is seldom more than a fourth degree is needed especially when R^2 = 99.99, the calculations beyond this are formidable and the results are not worthwhile.

2.4.2 THE EFFECT OF CONSTANT TEMPERATURE ON LONGEVITY

2.4.2.1 MATERIALS & METHODS

Longevity was studied by means of 50 x 25 mm glass tubes. The glass tubes had plastic lids with approximately 50 small air-holes and one central hole of 10 mm in diameter. An inverted 50 x 10 mm glass vial containing 50% honey solution held in by moistened cotton plug was placed in the large hole for the parasitoid to feed on. A small strip of Whatman's no. 1 filter paper was placed in the tube to absorp any drips from the solution above. One male and one female were placed in each tube. The parasitoids were never more than 6 hours old when the experiment started. The glass tubes were placed inside incubators with continuous light provided by 6 8-watt fluorescent tubes giving an intensity of 25-30 W/m^2. Relative humidity ranged between 60-80%. The tubes were checked once a day as long as the parasitoids lived. Longevity was determined for 36 parasitoids at each of the following constant temperature regimes 12, 16, 20, 24, 28 and 30°C. A group of 3 tubes with 6 parasitoids were enclosed together inside plastic boxes 175 x 155 x 55 mm. The number of replicates were 6 per incubator. The 6 replicates were distributed equally to 2 shelves at random.

THE EFFECT OF FOOD ON LONGEVITY

Adults of A. matricariae of less than 6 hours old were placed in glass tubes with the same specifications as mentioned above. The inverted vials were provided either with 50% honey solution or 50% honey-dew or only water. A group of 3 tubes, each contained one male and one female parasitoid were put together inside a plastic box. The number of parasitoids used for each kind of food, treatment, was 36 in 6 boxes. Each treatment was represented by six replicates, 6 boxes divided equally between the 3 shelves. The boxes were placed at random inside incubator at constant temperature of 20°C. Photoperiod and relative humidity was the same as mentioned above. The

tubes within each box were checked daily until the death of all individuals. The time of death for each individual was recorded.

THE EFFECT OF HOST PLANT

Parasitoids of less than 6 hours old, emerging from 3 groups of plants namely potato Solanum tuberosum, turnip Brassica campestris rapa and broad bean Vicia faba were used. The number of parasitoids used for each group was 36, distributed equally to 18 tubes of the same specifications mentioned above. Each tube contained one male and one female. Each group of 3 tubes were enclosed inside a plastic box as one replicate. The number of replicates was 6. The 6 boxes were distributed equally to the 3 shelves. Boxes within each shelf were allocated at random. All boxes were placed in an incubator at constant temperature of 20°C. Photoperiod and relative humidity was the same as mentioned above. The parasitoids were checked and counted daily until the death of all individuals.

2.4.2.2 RESULTS

Table (2.13) shows that average longevity is strongly temperature dependent ranging from about 2.1 days to 16.97 days over a temperature range of 18°C for pooled sexes. The survival increased gradually when temperature fell from 30 to 12°C. The number of parasitoids alive at the mid-point of each day is plotted as a proportion of the original 36 parasitoids with which the experiment was begun. The age specific survival rates are illustrated in Figure (2.10). The results for separate sexes (Table 2.14) shows that obvious differences in longevity of males and females were observed at lower temperatures. For females survival increased as temperature fell from 30 to 12°C. For males survival increased as temperature fell from 30 to 16°C, at 12°C survival again decreased but slightly. Males lived longer than females at 16°C. Thus about 16°C seems to be an optimum temperature for survival of this species.

Table 2.13 EFFECT OF TEMPERATURE ON LONGEVITY OF SEX POOLED A. matricariae.

Temperature °C	Mean in days	s.e.	l.s.d. 5% = 0.548
12	16.97	0.21	a
16	14.63	0.20	b
20	13.07	0.14	c
24	08.00	0.12	d
28	04.20	0.15	e
30	02.07	0.28	f

Means sharing the same letters are not significantly different.

Table 2.14 EFFECT OF TEMPERATURE ON LONGEVITY OF MALE AND FEMALE OF A. matricariae

Temperature °C	Female l.s.d. 5% = 1.11 Mean	s.e		Male l.s.d. 5% = 1.66 Mean	s.e		t test significance between male and female
12	14.0	0.37	a	14.98	0.78	A	NS
16	13.17	0.48	b	16.1	0.44	A	**
20	11.0	0.26	c	12.67	0.42	B	**
24	07.83	0.40	d	08.83	0.60	C	NS
28	04.0	0.37	e	04.17	0.65	D	NS
30	02.17	0.40	f	02.2	0.48	E	NS

Means within columns sharing the same letters are not significantly different. ** = significant at the 1% level, NS = not significant.

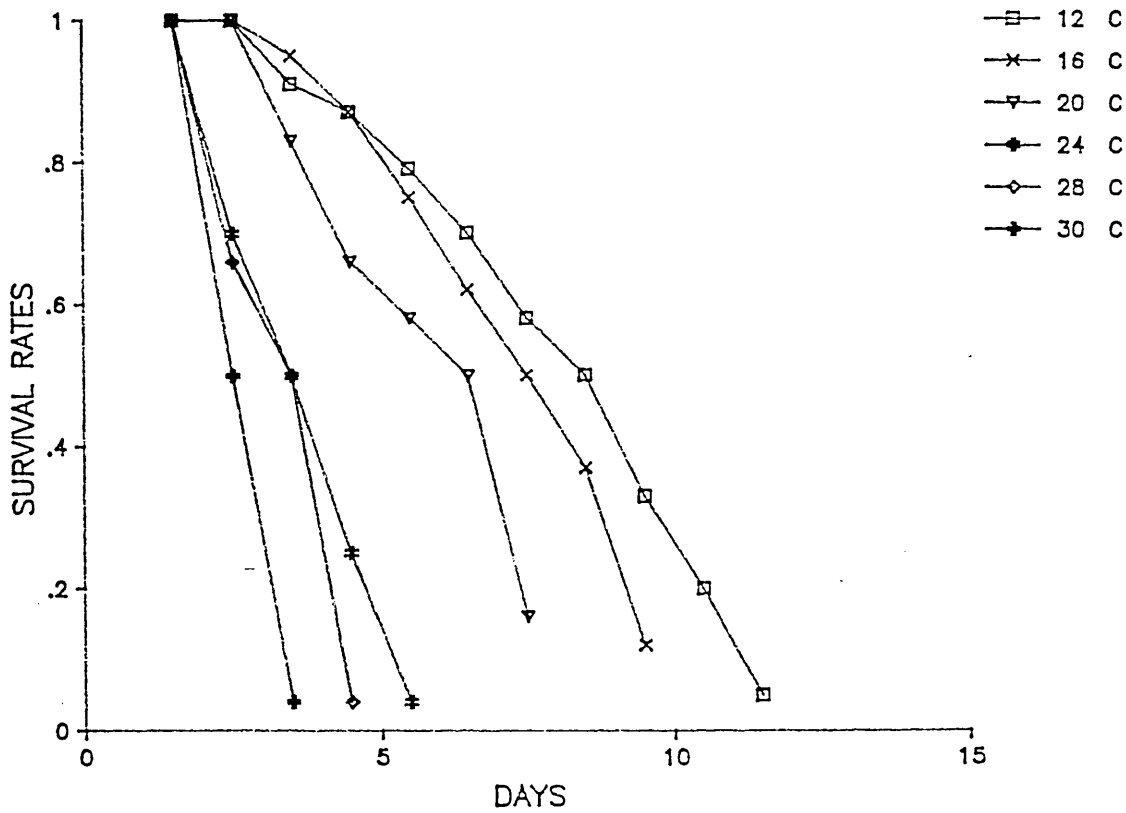


Figure 2.10 AGE SPECIFIC SURVIVAL OF A. matricariae AT VARIOUS CONSTANT TEMPERATURES (12-30°C)

The survival curves for pooled sexes, the proportion surviving at each time interval, along with the fitted Weibull curves are shown in Figure (2.11). The values of the two Weibull parameters and the calculated Lt_{50} for pooled sexes, males and females at six constant temperatures are presented in Tables (2.15, 2.16 & 2.17). The value of the shape parameter 'c' is bigger than 1 for pooled sexes, males and females at all temperatures. The value of b generally decreases with rising temperature being significantly greater ($P<0.05$) at 12°C than at any other temperature for pooled sexes and for females. The b value is significantly greater ($P<0.05$) at 12°C than at any other temperature except 16°C for males. The value of the b parameter reaches its maximum at 16°C for males. The value of b was significantly less ($P<0.05$) at 28 and 30°C than at any other temperature for pooled sexes and for males and females.

Average time to 50% mortality Lt_{50}, Tables (2.15,2.16 & 2.17) decreased with increase in temperature for pooled sexes and for females within (12-30°C) and within (16-30°C) for males.

The results of effects of temperature on longevity led to a number of small experiments to investigate the effect of further factors on longevity.

The longevity of adults is strongly influenced by food conditions (Table 2.18). Longevity was only 1-3 days when supplied with only water. When honey-dew was provided it increased to 5-8 days. Longevity reaches its maximum of 11-14 days when provided with honey solution.

Longevity of individuals emerged from mummies taken from turnip, potato and broad bean plants is shown in Table (2.19). Longevity was not significantly influenced ($P>0.05$) by different host plants during parasitoid development. Although there was a tendency for parasitoids emerged from turnip to live slightly longer than those emerged from potato or broad bean.

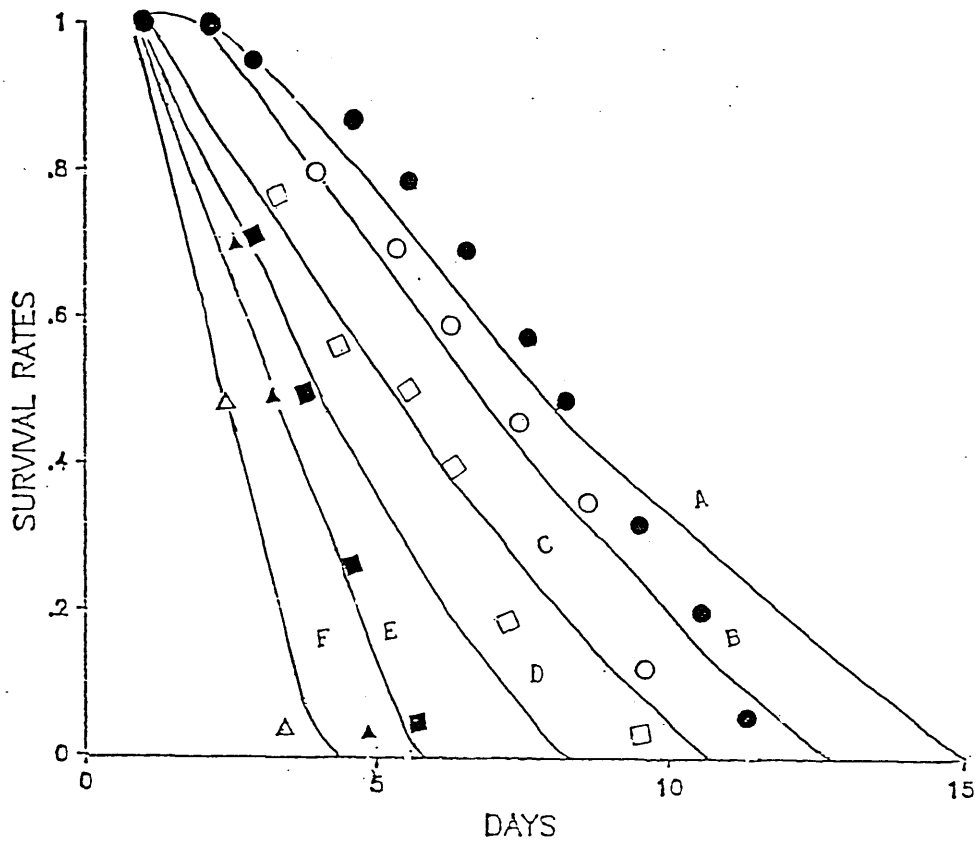


Figure 2.11 THE SURVIVAL DATA FOR A. matricariae AT CONSTANT TEMPERATURES WITH THE FITTED WEIBULL CURVES

Fitted Weibull curves

A (12°C) $F(t) = 1 - \exp(-[(t/13.01)^{2.01}])$

B (16°C) $F(t) = 1 - \exp(-[(t/10.87)^{2.14}])$

C (20°C) $F(t) = 1 - \exp(-[(t/9.92)^{1.91}])$

D (24°C) $F(t) = 1 - \exp(-[(t/5.86)^{2.39}])$

E (28°C) $F(t) = 1 - \exp(-[(t/3.79)^{3.31}])$

F (30°C) $F(t) = 1 - \exp(-[(t/2.2)^{3.77}])$

Table 2.15 ADULT LONGEVITY OF POOLED SEXES A. matricariae : WEIBULL PARAMETERS FOR SURVIVAL CURVES AT VARIOUS CONSTANT TEMPERATURES.

	Temperature °C											
	12		16		20		24		28		30	
b	13.01	a	10.87	b	09.92	c	5.86	d	3.79	e	2.20	f
c	02.01		02.14		01.91		2.39		3.31		3.77	
Lt_{50}	10.85		09.16		08.19		5.03		3.40		2.00	

Numbers followed by the same letter not significantly different at the 5% level (tables of Thoman & Bain, 1969).

Table 2.16 ADULT LONGEVITY OF A. matricariae MALE : WEIBULL PARAMETERS FOR SURVIVAL CURVES AT VARIOUS CONSTANT TEMPERATURES.

	Temperature °C											
	12		16		20		24		28		30	
b	12.29	a	12.65	a	9.20	b	5.82	c	3.39	d	2.20	e
c	02.11		02.14		2.39		2.47		2.37		3.77	
Lt_{50}	10.33		10.66		7.89		5.02		2.90		2.00	

Numbers followed by the same letter not significantly different at the 5% level (tables of Thoman & Bain, 1969).

Table 2.17 ADULT LONGEVITY OF A. matricariae FEMALE : WEIBULL PARAMETERS FOR SURVIVAL CURVES AT VARIOUS CONSTANT TEMPERATURES.

	Temperature °C											
	12		16		20		24		28		30	
b	12.42	a	10.13	b	8.34	c	5.82	d	3.33	e	2.20	f
c	02.13		02.20		2.16		2.54		2.56		3.77	
Lt_{50}	10.45		08.57		7.04		5.04		2.88		2.00	

Numbers followed by the same letter not significantly different at the 5% level (tables of Thoman & Bain, 1969).

Table 2.18 EFFECT OF DIFFERENT DIET ON LONGEVITY OF SEX POOLED *A. matricariae*.

Diet	Mean in days	s.e.	l.s.d. 0.1% = 2.98
Water	02.67	0.21	a
Honey-dew	07.33	0.67	b
Honey	12.5	0.56	c

Means sharing the same letters are not significantly different.

Table 2.19 EFFECT OF DIFFERENT HOST PLANTS ON LONGEVITY OF SEX POOLED *A. matricariae*.

Host plant	Mean in days $F_{2,15} = 0.725$ NS	s.e.
Turnip	13.35	0.496
Potato	12.433	0.714
Broad bean	12.283	0.789

NS = nonsignificant at the 5% level

2.4.2.3 DISCUSSION

Temperature has a profound effect on survival. The lethal effects of temperature on insects is well documented (Andrewartha & Birch, 1954; Bursell, 1964). The results and analysis show that, there is a definite relationship between longevity and temperature, within the favourable range. In general longevity decreases with increasing temperature. Longevity data was described by different methods. The mean longevities and the Lt_{50} are measures of average life span and gave no further information about the survival curves. Two insects with exactly the same mean longevity may have different shapes of survival curves. Thus important information is lost when longevity is merely represented by the mean or Lt_{50}. Figure (2.11) shows that temperature strongly affect the survival curves of the parasitoids. The form of survivorship curve is determined entirely by c. Survival curves are classified into type 1, 2 or 3 according to their shape (Pinder et al., 1978). The results show that all values of c are greater than 1 indicating type 1 survivorship curve in which the age specific mortality is an increasing function of age, increases with age (Pinder et al., 1978).

Temperature also influences the scale of curve. The survival period of the population decreases with increase in temperature. Generally, at low temperature, a large number of individuals survive for relatively long periods of time and the death rate is increasingly function of time. As the temperature rises the survival period decreases but the death rate is also increases with time. At high temperature the shape of survival curve changes, c is much bigger than 1, the majority of parasitoids die over a short period of time and the death rate as an increasing function of age is accelerated. The shape of the curve is important in terms of population dynamics of insects. A population with survival curve of type 1 has potentially very different dynamics from one with the same mean longevity

but with a type 3 survival curve. The Weibull curve did not give an exact fit to observed data, but still the parameters provide absolute values for the shape and size of the curve, which can be statistically analysed. This gives a standardizing method which allows differences between survival curves to be tested. The results in general demonstrate that the value of b declines with rising temperature, whilst the c value remains relatively constant until temperature reaches 30°C at which point it increases markedly. There are some similarities with previous work. The values of b for survival of false wireworms Pterohelaeus darlingensis and P. atternatus also declined fairly evenly with temperature, but that c values were less consistent, although they were always low at high temperatures (Allsopp, 1981). No data were available for A. matricariae which is summarised using Weibull function to allow comparison with the results obtained herein.

So, the comparison was based on mean longevities. The results are comparable with previous studies. Giri et al., (1982) found that A. matricariae longevity decreased as temperature increased within (7-32°C). They found mean longevity periods of 14, 10, 5 and 3 days at 15, 20, 25 and 30°C respectively. The present corresponding ones were 14.63, 13.07, 8 and 2.07 days at 16, 20, 24 and 30°C respectively. It is apparent that A. matricariae lived much longer under the present study at 20°C.

The results of effects of temperature on longevity led to a number of small experiments to investigate the effect of further factors on longevity.

The results demonstrate that the effect of temperature on longevity of A. matricariae depends on the sex at low temperature. Males tend to live significantly longer at 16°C. Giri et al., (1982) reported that differences in mean longevity between sexes for A. matricariae occured, but significant differences were found at 10 and 15.6°C in favour of males. The results are somewhat comparable with other aphidiid species. Shirota et al., (1983) found that Aphidius rhopalosiphi attacking cereal aphid S.

avenae lived for 13.1 days at 18°C. Mackauer (1983) found that A. smithi on A. pisum lived an average of 7 days at 20.5°C. Hagvar & Hofsvang (1975a) showed for E. cerasicola parasitizing M. persicae that longevity decreased gradually from 2.8 days at 32°C to 26.2 days at 15°C and decreased again to 16.9 days at 12°C. Stary (1964) found that in Aphidius megourae the males were more resistant to low temperature . Hagvar & Hofsvang (1975b) have found in A. ervi, females lived for 15.4 days and males 13.1 days at 21°C. The same authors (1975b) have found females of A. platensis tend to live longer than males at 15°C with the opposite relation at 21 and 24°C.

The results show that longevity of honey fed A. matricariae was significantly higher than that fed on water or honey-dew ones. Several authors have demonstrated the importance of honey for longevity of adult parasitoids (Schlinger & Hall, 1960; Stary, 1962, 1964; Wiackowski, 1962; Hagvar & Hofsvang, 1975b). Stary (1962) proposed that the most suitable food for adult A. ervi was honey and longevity was more than doubled when honey was added to water. In A. smithi the greatest effect of honey on longevity was at 15°C was 5.8 times, the lowest effect at the extreme temperature being 1.5 to 2 times (Wiackowski, 1962). Longevity in A. platensis increased slightly when an aphid infested leaf was added to water but maximal longevity obtained with water and honey which was 12 days for females and 13.4 days for males at 21°C (Hagvar & Hofsvang, 1975b). However, Stary (1970) states that honey-dew from aphids is probably the main natural source of food for adult parasites and should theoretically satisfy both carbohydrate and protein needs.

The results indicated that no significant difference ($P>0.05$) between parasitoids emerged from turnip, potato and broad bean existed with respect to longevity. But those emerged from turnip lived slightly longer than those of broad beans and potato. Hagvar & Hofsvang (1975b) have found no significant influence of different host plants during parasite development

on longevity of A. platensis on paprika and pepper. The effect of host plant in longevity has in general not been extensively examined but some influence is likely through the production of different sized aphids which in turn produce different sized parasites (Hagvar & Hofsvang, 1975b). The danger of dehydration is relatively greater in small parasitoids (Fox et al., 1967). It is most likely that the more resistant potato and the less preferred broad bean plants for M. persicae could be a reason for producing smaller sized individuals of aphids. This in turn may lead to production of smaller sized parasitoids. This may explain the slightly shorter longevity of species emerged from mummies taken from potato and broad beans. Xia & Tingey (1986) found that removal of glandular trichomes from Solanum tuberosum ssp. tuberosum (L.) x S. berthaultii Hawkes hybrid improved aphid survival nearly two fold compared with survival on foliage with intact trichomes. M. persicae mean body weight of nymphs was significantly lower on foliage bearing intact trichomes than on foliage lacking trichomes and replaced at 48 hours interval.

Under the present experimental set-up, males and females were confined in small glass tubes, deprived of energy demanding activities such as flying, searching for mates, hosts and oviposition. Therefore little energy is used and longevity is probably near the maximum for the species at the experimental conditions. Survivorship curves obtained for confined parasitoids at 16 and 20°C indicate that little mortality occurs in the first 2 days. This is a reflection of the conditions under which the species were living protected in tubes, boxes with ample food and no crowding, no mortality factors from external sources. These conditions allow the full display of survival power inherent in the species. Such survivorship curves are characteristics of organisms living to the full physiological longevity (Bodenheimer, 1958).

2.4.3 THE EFFECT OF CONSTANT TEMPERATURE ON FECUNDITY

2.4.3.1 MATERIALS AND METHODS

OVIPOSITIONAL BEHAVIOUR

A number of parasitoids males and females were confined in a plastic box with streaks of 50% honey solution on sides as food. A day later, they were transferred into an experimental arena of 21 cm high, 14 cm wide of clear acetate sheet containing one potted turnip plant with an excess of M. persicae aphids. Close observations for successive 4 hours were made through the transparent walls. The observations were repeated 5 times on different separate days and at different times of day at laboratory conditions of temperature 20 ± 4°C and 60-80% r.h..

POTENTIAL FECUNDITY

Potential fecundity was determined by dissecting 25 female parasitoids soon after emergence and before egg-laying, after being preserved in 80% ethanol. Counts of initial eggs in ovaries was done under a binocular microscope.

REALIZED FECUNDITY

Realized fecundity was determined by transferring 90 M. persicae aphids to 6 turnip seedlings of 7 days old. Seedlings with aphids were placed inside a plastic box 175 x 155 x 55 mm with a 40/cm gauzed mesh window on top to allow aeration. A single mated female parasitoid of less than 6 hours old was introduced into the box. After 24 hours the parasitoid was transferred to a fresh seedlings in another box, also with 90 aphids. The process was repeated daily until the death of the parasitoid. The boxes were placed inside incubators at constant temperatures of 12, 16, 20, 24, 28 and 30°C. A 24 hour photoperiod was provided by 6 8-watt fluorescent tube giving an intensity of about 25-30 W/m^2. Relative humidity ranged between 60-80%.

The transferrence of parasitoids and ovipositional activity was carried out inside incubators. The parasitoids were fed with 50% honey solution on glass slides placed inside boxes every 2 days. Each experiment started with only 3 parasitoids at a time as a replicate, each for a certain series of boxes with fresh aphids. The number of replicates was 6. The time elapsed between any two replicates is between 1-20 days. In total 18 parasitoids were used for each temperature regime. After the death of parasitoids, the old boxes were moved out of incubators and kept on a side bench at laboratory conditions of temperature 20 ± 4°C and 60-80% r.h.. Each day thereafter, the seedlings in old boxes were examined for mummified aphids and then for parasitoid emergence. Counts of mummified aphids and emerged parasitoids was recorded for each box.

THE EFFECT OF PARENTAL AGE ON DEVELOPMENT TIME

Certain boxes which had been parasitized at 20°C were removed daily and kept separately for each age group of parasite parent until the death of parasitoid. The developmental time for progeny up to emergence of adults were recorded for each parent age group. The number of replicates was 6, each replicate composed of only one box for each age group of parasitoid. The time elapsed between replicates was 1-20 days.

THE EFFECT OF PARENTAL AGE ON SEX RATIO OF OFFSPRING

The sex of progeny for each parental age group was determined on emergence from cocoons. The number of replicates was 3. Each replicate composed of only one box per age group of parasitoid. The time elapsed between replicates was 1-20 days.

2.4.3.2 RESULTS

OVIPOSITIONAL BEHAVIOUR

During the 1st hour of release the parasitoids were excited and very active in search for aphids. They stab different objects, they try to strike moving aphids as well as dead and mummified ones. Oviposition immediately took place whenever an aphid was encountered irrespective of place and in any position and on any part of the aphid. During the process of egg-laying the female bends its abdomen under the thorax and between legs and pointed it forward towards the target aphid. Time taken for actual process of egg-laying is not more than 2 seconds. Some made repeated attacks on the same aphid. The ovipositional activity pattern occurs in cycles. It starts with active ovposition period in which successive ovipositions may take place in a very short time moving from one host to another. This may go on for up to about one hour in which about 30 stabs are made. After this period a period of rest follows which includes preening and cleaning and feeding and resting, this may last for up to 30-40 minutes. Then another period of activity follows but of a shorter time, which may last for about 30 minutes. Then a non-activity period follows of about 30-50 minutes, followed by a lesser period of activity and so on. Then the time of non-activity become dominant with casual attacks.

POTENTIAL FECUNDITY

The potential fecundity, the number of eggs in ovaries was found to be 81 ± 7.2 of which 43 ± 6.3 mature eggs.

REALIZED FECUNDITY

The number of progeny produced by A. matricariae under the various temperature regimes is given in Table (2.20). The ovipositional period decreased as temperature increased from 12-30°C. The number of progeny

produced per day also increased up to 20°C, then decreased with rise in temperature up to 30°C. The maximum progeny from a single female was 228 and the greatest mean number of progeny was 208, both were produced at 20°C. The mean number of progeny produced by female at 28 and 30°C were significantly less than the rest ($P<0.05$). The age specific fecundities, the mean daily production of eggs that resulted in mummies, are illustrated throughout the parasitoids lives in Figure (2.12). The females of A. matricariae oviposited throughout most of their lives. The oviposition period differs according to temperature from 2 days at 30°C to 11 days at 12°C. The basic pattern of egg laying was consistent for all temperatures. The daily fecundity increased rapidly to reach its maximum on 2nd day, followed by a rather rapid gradual decline in the number produced per female per day.

Table (2.21) shows no significant difference ($P>0.05$) between developmental times of progeny resulted from different parental age groups.

The effect of parental age on sex ratio is shown in Figure (2.13). Mated females of one day old produce progeny of 49.6% females. Mated females of 2, 3 and 4 day old produced progeny of 60.6, 47.2 and 45.7% females respectively. Older mated females of 5, 6 and 7 days old produced 39.3, 30.3 and 17.7% females respectively. The overall sex ratio was 41.48% females which means an approximate sex ratio of 1:1.

The relationship between sex ratio and parental age was tested for linearity, by constructing a 2 x 7 contingency table (Table 2.22). The regression coefficient of proportion of female p_i on the score (X_i) is tested. On the null hypothesis, no relation between p_i and X_i is assumed. Each p_i is distributed about the same mean, estimated by P with variance Pq/n_i. The regression coefficient b is calculated as usual except that each p_i must be weighted by the sample size n_i on which it is based (Snedecor & Cochran, 1980). The numerator and denominator of b are computed as follows:

Table 2.20 EFFECT OF TEMPERATURE ON FECUNDITY OF A. matricariae.

Temperacture °C	Mean fecundity	s.e.	l.s.d. 5% = 19.576
12	121.83	5.677	c
16	152.16	9.995	b
20	208.33	5.352	a
24	113.8	8.935	c
28	34.00	5.716	d
30	10.5	1.565	e

Means sharing the same letters are not significantly different.

Table 2.21 EFFECT OF PARENTAL AGE OF A. matricariae ON DEVELOPMENT PERIOD OF ITS PROGENY AT 20°C.

Parental age	Mean time in days $F_{6,35} = 0.566$ NS	s.e.
1	12.166	0.477
2	12.50	0.563
3	13.00	0.577
4	11.833	0.47
5	12.00	0.632
6	12.33	0.494
7	12.67	0.501

NS nonsignificant at the 5% level.

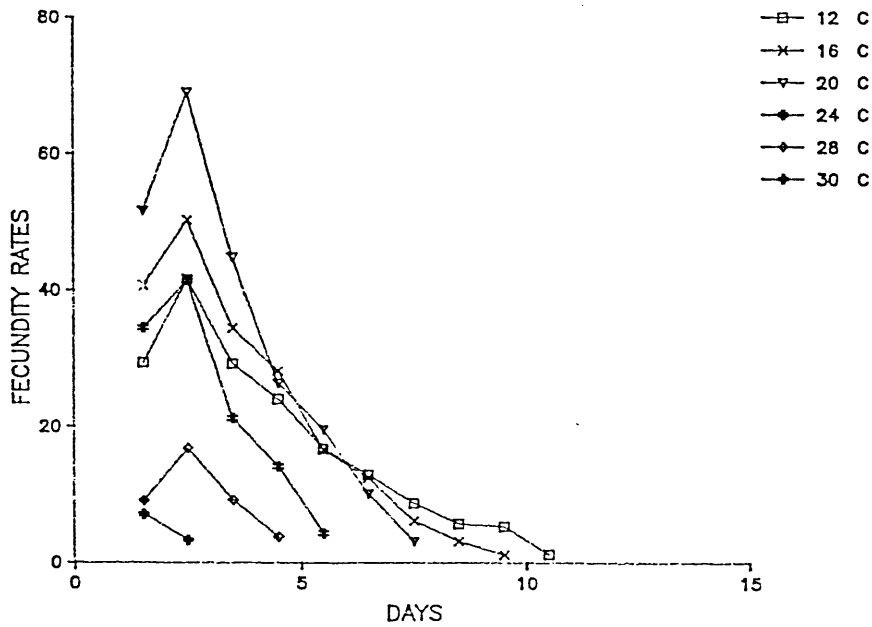


Figure 2.12 AGE SPECIFIC FECUNDITY OF A. matricariae AT VARIOUS CONSTANT TEMPERATURES (12-30°C)

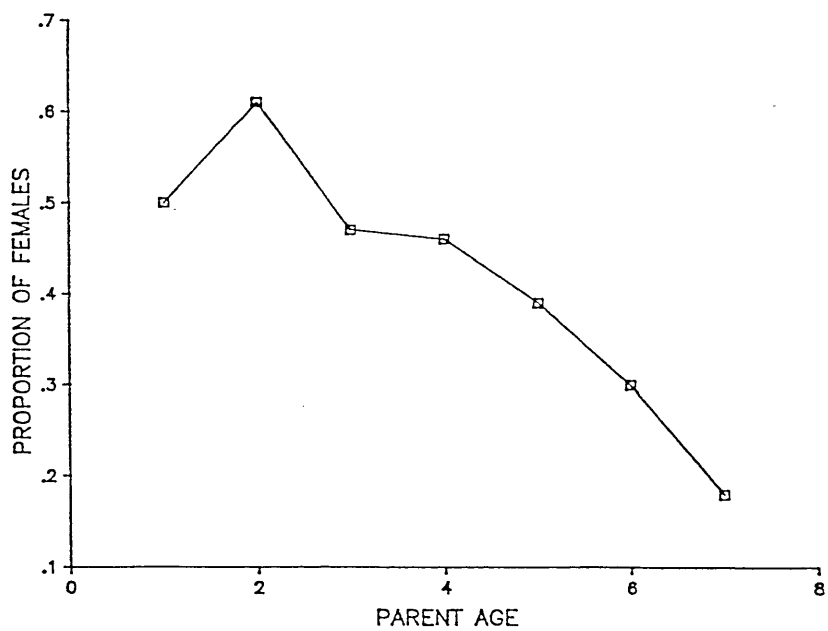


Figure 2.13 THE RELATIONSHIP BETWEEN PARENTAL AGE OF A. matricariae AND SEX RATIO OF ITS PROGENY

Table 2.22 TESTING A LINEAR REGRESSION OF PROPORTION OF FEMALES (p_i) ON THE SCORE (X_i) FOR THE RELATION BETWEEN SEX RATIO AND AGE OF PARENT FOR A. matricariae

								Total
Male	69	74	66	44	34	23	14	324
Female, a_i	68	114	59	37	22	10	3	313
Total, n_i	137	188	125	81	56	33	17	637, N
$p_i = a_i/n_i$	0.4964	0.6064	0.472	0.4568	0.3928	0.3030	0.1765	0.414835, P
Score, X_i	1	2	3	4	5	6	7	
Age of parent	1	2	3	4	5	6	7	

Data taken from total of 3 replicates.

num. = $\Sigma\, a_i X_i - (\Sigma a_i)(\Sigma n_i X_i)/N$

= 812 - (313) (1809)/637

= -76.881

den. = $\Sigma\, n_i X_i^2 - (\Sigma\, n_i X_i)^2 /N$

= 6731 - $(1809)^2$ /637

= 1593.66719

Then b = -76.881/1593.66719 = - 0.048241565

On null hypothesis its standard error is

s_b = square root of Pq/den. = (0.414835)(0.585165)/1593.66719 = 0.012341787

The normal deviate for testing the null hypothesis $\beta = 0$ is therefore

$Z = b/s_b$ = - 0.048241565/0.012341787 = 3.91 $\quad$ p = 0.0001

This indicates a highly significant inverse linear relationship between age of parent and percentage of female in progeny.

2.4.3.3 DISCUSSION

The pattern of oviposition behaviour observed under this study agree fairly well with previous studies. It is more or less similar to what described by Vevai (1942) for A. matricariae and that reported by Sekhar (1957) for Aphidius testaceipes (Cresson) and to that mentioned for A. smithi by Fox et al., (1967). Mating does not appear to be a prerequisite for oviposition and may take place within hours of emergence irrespective of presence of males.

The potential fecundity found under this study is much less than the

realized fecundity obtained at 20°C, indicating that further eggs mature in the ovaries during life. This confirms that A. matricariae is a synovigenic species which continues to produce eggs throughout its life. The potential fecundity for A. matricariae found under this experiment was somewhat different from that reported in the literature for other Aphidiidae. Dransfield (1979) proposed that the mean potential fecundity of Aphidius urticae reared on cocksfoot aphid Hyalopteroides humilis was 257 ± 8.5 of which 88 ± 3.4 were mature ova. Shirota, Carter, Rabbinge & Ankersmit (1983) suggested the mean potential fecundity for A. rhopalosiphi reared on cereal aphids Sitobion avenae to be 144 ± 17.8 for 18 parasitoids which is significantly less than the realized fecundity of 212.4 ± 49 found in 14 parasitoids. However, dissection of ovaries for potential fecundity is appropriate only for pro-ovigenic in which oogenesis is largely complete before oviposition begins (Flanders, 1950). In synovigenic species such as Aphidiidae oogenesis is a continuous process and therefore dissection is not a reliable method for the estimation of life time fecundity (Force & Messenger, 1964).

The results indicated that oviposition is adversely affected by temperature extremes. Temperature affects the pattern of egg-laying with a higher proportion of the eggs being laid sooner at higher temperatures. The results of realized fecundity showed that A. matricariae has a regular oviposition pattern with one peak in oviposition the second day followed by a gradual decline in the number produced per female per day. The results are comparable with previous studies. Vevai (1942) found that the activities in oviposition reaches its maximum on 2nd and 3rd day for A. matricariae. Giri et al., (1982) have found that the production of progeny for A. matricariae was most intensive during the 2nd day. The results are somewhat different from that found in other aphidiids. Clouteir, McNeil & Regnieve (1981) found that the mean daily fecundity for A. nigripes increases rapidly to reach a maximum on day 2 but remains at this level

until day 10 then gradually decreases. Egg-laying for A. rhopalosiphi was most intensive during the first week but then declined rapidly such that it stopped by the end of the second week (Shirota et al., 1983). This regular pattern of oviposition differs somewhat from some other aphidiids. Hafez (1961) reported an irregular oviposition pattern in A. rapae with a number of peaks. A similar pattern was found for Ephedrus cerasicola on M. persicae with several peaks in egg laying during the female life span (Hagvar & Hofsvang, 1975a).

The results demonstrate that oviposition is strongly influenced by temperature. In the temperature range 16-20°C the number of eggs produced daily increased with increase in temperature, but the adult parasitoid longevity decreased resulting in a more or less similar net reproduction. The average life span corresponded to the period of reproduction. The post reproductive period was very short. The post reproductive period was also very short for other aphidiids (Force & Messenger, 1964; Mackauer, 1983).

Age specific fecundity curves when compared with age specific survival ones reveal that the maximum daily egg-laying of parasitoids precedes most of the mortality. As time passes, fewer eggs are laid per day by each of the decreasing number of survivors. The curves therefore show the contributions to the populations by females of various ages. Old females contribute an insignificant number of progeny because they represent only a small fraction of the original number of females and because their rate of egg-laying is reduced.

The maximum number of progeny produced by a single female was 228 at 20°C. It is still less than 350 previously reported for A. matricariae (Vevai, 1942). And very much less than 392 and 407 progeny reported by Giri et al., (1982) and Shalaby & Rabasse (1979) respectively. It should be noted that the net reproduction in those experiments has been measured by counts of number of eggs by dissection of aphids 2-3 days after parasitization, whilst

the present study was based on counts of mummified aphids. This may be the reason for relatively small net progeny under this study. Force & Messenger (1964) pointed out that because of the chance of some superparasitization or egg and larval mortality the resulting number of mummified aphids expresses a minimum value of female fecundity. So, the present results may underestimate total fecundity in terms of total eggs laid, because more than one egg may have been laid per mummified aphid. But at least they can be regarded as a measure of effective fecundity. There is still greater variations in the number of progeny when compared with other aphidiids. Hagvar & Hofsvang (1975a) found an average fecundity of 68 mummies at 21°C for E. cerasicola parasitizing M. persicae. Dransfield (1979) proposed the realized fecundity to be 270 for A. urticae reared on the cocksfoot aphid. The fecundity was quite variable ranging from fewer than 100 to over 600 mummies for A. nigripes on potato aphid Macrosiphum euphorbiae (Cloutier et al., 1981). A. rhopalosiphi on cereal aphid S. avenae produced 212 offspring at 18°C, in one case 509 (Shirota et al., 1983). Mackauer (1983) found that A. smithi on pea aphid A. pisum produced an average of 870 eggs at 20.5°C.

The results illustrated that the development rate is independent of parantal age. A similar result obtained for E. cerasicola by Hagvar & Hofsvang (1975a). The results also showed that the sex ratio of the progeny is influenced by the age of parents. Females were obtained from the eggs laid in the first day of adult life. This indicates that mating can take place soon after emergence. Stary (1970) states that females of Aphidiidae mate only once in their lives, whereas males can mate several virgin females. Because females copulate only once and usually soon after emergence, the dominance of male progeny after the 5th day implies that the sperm supply in female spermatheca is probably exhausted by then. A similar decrease in percentage of female offspring according to increasing age of parents has been put forward by several authors. Messenger (1964b) in his

study on Praon palitans on Therioaphis maculata found that adult female age at the time of oviposition has a marked effect on the sex of the eggs laid. Young mated females produce progeny with a sex ratio in the order of 4 females:1 males but older females produce more and more males until the sex ratio eventually declines to around 1:4. Rogers, Jackson, Eikenbary & Starks (1972) state that the sex ratio favoured males in ageing E. plagator. Dransfield (1979) in his study on the sex ratio of A. urticae parasitizing Hyalopteroides humilis found that, as the age of female increased, the percentage of female progeny decreased in a linear manner. The proportion of female progeny produced by A. nigripes generally decreased with the age of parasitoid regardless of host potato aphid age (Cloutier et al., 1981).

2.5 THE EFFECT OF CYCLING AND FLUCTUATING TEMPERATURES ON DEVELOPMENT OF *M. persicae* AND *A. matricariae*

2.5.1 INTRODUCTION

The ability to predict host and parasitoid development period is crucial to placing the parasitoid in proper temporal relationship with its host. This requires first to determine rates of development of both species under a wide range of constant temperature as well as variable temperatures likely to be experienced under glasshouse conditions. Once this relationship has been identified it can be used to predict how development will proceed under the fluctuating conditions of the glasshouse. Tingle & Copland (1988) used thermal summation and polynomial regression techniques to predict mean developmental periods of 3 encyrtid mealybug parasitoids under glasshouse conditions.

The aim of the present work is to study the effect of fluctuating temperature on development of both *M. persicae* and *A. matricariae* and to compare day degrees and polynomial models when predicting development time under glasshouse conditions.

2.5.2 MATERIALS AND METHODS

Two general types of variable temperature patterns were studied :

1. A series of artifically constructed patterns in which temperature alternates between two constants in succession.
2. The natural temperature patterns actually encountered in the glasshouse at Wye College.

2.5.2.1 CYCLING REGIMES

The first set was under 12/12 hour cycling regimes with the first 12 hours at 20C in each case and the second 12 hours at 4, 6, 8, 32, 34 and 38°C for *M. persicae* and at 6, 8, 10, 32, 34 and 38°C for *A. matricariae*. The experimental procedure is similar to the one carried out in constant temperature regimes (Sections 2.3.1 & 2.4.1). It was performed in laboratory incubators provided with a timeswitch for providing alternating

temperatures. A constant photoperiod of 24 hours provided by 6 8-watt fluorescent tubes giving an intensity of 25-30 W/m^2. For the M. persicae experiment, 60 newly born aphids of less than 6 hours old were transferred to turnip seedlings inside 6 ventilated Stewart boxes (173 x 115 x 65 mm). Each box contained 5 seedlings with a total of 10 aphids. For A. matricariae, 6 female parasitoids of less than 3 days old were each introduced into a ventilated Stewart box containing 5 brassica seedlings with 10 aphids. The parasitoids were allowed to oviposit for a period of 4 hours, in each of 6 boxes before being removed. The boxes were then transferred to laboratory incubators, 6 boxes in each.

2.5.2.2 FLUCTUATING REGIMES

For glasshouse experiments, the same method was followed to prepare 6 boxes of newly born aphids, 10 aphids per box as well as 6 boxes of newly parasitized aphids, 10 per box. The boxes used were ventilated plastic boxes (173 x 115 x 65 mm) from which the top and bottom had been removed and replaced with 40 mesh/cm nylon gauze to allow free passage of air. Boxes were then suspended from the branches of trees and bushes in the conservatory at Wye by means of ventilated nets surrounding the boxes which permit free movement of air (Plate 2.2). The boxes were located as near the temperature sensors as possible so that ambient temperature was similar to that being recorded. The number of replicates for each species was six. A daily observation was carried out from the third day on. Aphids completing development and emerging parasitoids were counted daily. Data were recorded as the total development period for each individual in days from oviposition to adult emergence for A. matricariae and from the first instar to adult for M. persicae. Temperature in the conservatory was monitored constantly by electronic sensors in aspirated screens and hourly mean temperatures were recorded and stored on floppy disk using a microcomputer. Experiments were carried out at 5 different times of year, October, 1988; January-February, 1989; March, 1989; May, 1989 and June, 1989.





Plate 2.2 Ventilated plastic boxes used for determination of developmental rates under glasshouse conditions in the Wye College conservatory

2.5.2.3 DETERMINATION OF LOWER THRESHOLD FROM CYCLING TEMPERATURE

The lower threshold is known as developmental zero (Sanderson & Peairs, 1913). It is possible to determine the lower threshold from experimental data under cycling temperature regimes using thermal summation on an hourly basis (Tingle & Copland, 1988). The concept is that when the lower threshold temperature is cycled for 12 hours with 12 hours at 20°C for example, the developmental period will not be significantly different from twice that at constant 20°C. In order to locate these thresholds, a series of experiments were carried out where 12 hours at 20°C are cycled with progressively lower temperatures.

2.5.2.4 DETERMINATION OF CONSTANT TEMPERATURES FROM CYCLING

Since development could be incremented on an hourly basis assuming that the contribution made by an hour at any given temperature may be derived from constant temperature data. It follows that the reverse process is valid and that development rates under constant temperatures can be deduced from cycling temperature data (Tingle & Copland, 1988). This allows estimates to be made of development rates at temperatures which are outside favourable range which are lethal or time consuming to measure at constant temperatures.

2.5.2.5 DAY-DEGREE PREDICTIONS

These were achieved by a simple programme written in 'BASIC' for a microcomputer (Appendix 2.1). The inputs were the lower threshold (t0) and the thermal constant (k) calculated previously from constant temperature data (Sections 2.3.1 & 2.4.1). The day-degree predictions were carried out using the temperature data recorded on disk. The hourly temperatures were read off disk and any temperature over the lower threshold summed until the total reached the value of thermal summation (k). The time at which this happens is the predicted developmental period.

2.5.2.6 POLYNOMIAL REGRESSION PREDICTIONS

With access to a microcomputer program, polynomial regression analysis was used to select the best fit regression line to the data on development rates. The mean developmental rates at six constant temperatures in the laboratory were calculated for M. persicae and A. matricariae (Sections 2.3.1 & 2.4.1). In addition the mean rate of development at 4, 6, 8, 32, 34 and 38°C for M. persicae and at 6, 8, 10, 32, 34 and 38°C for A. matricariae was calculated from cycling data. The equation for this best fit line, was then fed into a second programme (Appendix 2.2), which would compute the proportion of the total life cycle completed in an hour at any given temperature. These proportions were summed until they reached unity, at which point development was complete. Development was not incremented at any temperature outside the 4°C to 38°C range for M. persicae or outside the 6°C to 38°C for A. matricariae. Hourly temperatures were read from disk as for the day degree predictions. The number of days to complete development is given in a print out. Significant differences in the methods of predictions were tested using data pooled across species by means of an F-test.

2.5.3 RESULTS

Data on development periods under various cycling and fluctuating temperature regimes are given in Table (2.23). Constant temperatures of 32, 34 and 38°C cause 100% mortality for both M. persicae and A. matricariae. But cycling 12 hours at 20°C with 12 hours at 32 or 34 or 38°C seems to allow development to go through to completion. The lower thresholds calculated from cycling were 4°C and 6°C for M. persicae and A. matricariae respectively. These temperatures of 4 and 6°C when cycled for 12 hours with 12 hours at 20°C gave a development period of twice that at 20°C for M. persicae and A. matricariae respectively.

Table (2.24) shows the procedure of calculation and the calculated developmental rates at each constant temperature, which were difficult to

Table 2.23 DEVELOPMENT PERIOD UNDER VARIOUS CYCLING AND FLUCTUATING REGIMES FOR *M. persicae* AND *A. matricariae*

Temperature °C	Mean development period *M. persicae* Mean	s.e.	*A. matricariae* Mean	s.e.
Cycling in lab.				
20/4	16.083	0.27	---	---
20/6	15.08	0.32	24.55	0.55
20/8	13.633	0.42	22.4	0.79
20/10	- - -	----	18.68	0.40
20/32	09.333	0.12	13.616	0.22
20/34	10.733	0.10	14.35	0.28
20/38	11.133	0.21	15.63	0.25
Fluctuating in glasshouse				
October, 1988	08.74	0.29	14.1	0.13
Jan./Feb., 1989	10.56	0.3	16.34	0.4
March, 1989	07.4	0.33	10.74	0.34
May, 1989	08.38	0.6	12.38	0.67
June, 1989	08.4	0.3	12.5	0.2

Cycling regimes alternating 12 hours at each temperature

measure or lethal when held constant, as deduced from cycling regimes.

Figure (2.14) illustrates the best fit linear regression line from which the thermal constant and lower threshold were calculated for M. persicae as 131.6 D.D. and 5.3°C. Figure (2.15) illustrates the best fit linear regression line from which the thermal constant and lower threshold were obtained for A. matricariae as 183.1 D.D. and 6.3°C.

Polynomial predictions were based on the following best fit regression lines:

A. matricariae : polynomial order 6 (R^2 =,99.170)

$y = -0.918334024 + 0.32354772\,x - 0.0443131659\,x^2 + 0.00306768763\,x^3 - 0.000111680536\,x^4 + 0.00000203738073\,x^5 - 0.0000000146909901\,x^6$

M. persicae : polynomial order 5 (R^2 =,99 283)

$y = -0.0522587776 + 0.0258665253\,x - 0.00367472692\,x^2 + 0.000275501649\,x^3 - 0.00000860192545\,x^4 + 0.0000000915551651\,x^5$

Regression lines for predicting development of M. persicae and A. matricariae from constant and cycling temperature data are also illustrated in Figures (2.14 & 2.15) respectively.

Table (2.25) shows the predicted and observed development times under fluctuating glasshouse temperatures measured at 5 different months of year. There was a significant difference between the residuals from the polynomial predictions and those from day degrees ($F_{1,18} = 6.18$ $P<0.05$), residuals pooled across species. The polynomial method was the more accurate. All the predicted values for both methods were less than the observed ones indicating strong tendency for underpredicting for both models. When temperature remains for substantial periods outside the linear range as occurs with exceptional hot summers encountered during May and June, 1989, weaknesses show up in the day degree method. This occurs due to deviation of the temperature-development relationship from linear at extreme temperatures.

Table 2.24 CALCULATION OF THE DEVELOPMENTAL RATE AND DEVELOPMENTAL PERIOD AT CONSTANT TEMPERATURE FROM ALTERNATING TEMPERATURE DATA.

Regime °C	dx	1/dx	d20	1/d20	1/d20*1/2	1/dx-1/d20*1/2	1/dc	dc
M. persicae								
20/4	16.083	0.621774	8.65	0.115606936	0.057803468	0.004373932	0.008747864	114.31
20/6	15.08	0.0663129	8.65	0.115606936	0.057803468	0.008509432	0.017018864	58.76
20/8	13.633	0.0733514	8.65	0.115606936	0.057803468	0.015547932	0.031095864	32.16
20/32	09.333	0.1071466	8.65	0.115606936	0.057803468	0.049343132	0.098686264	10.31
20/34	10.733	0.09317059	8.65	0.115606936	0.057803468	0.035367122	0.070734244	14.14
20/38	11.133	0.0898230	8.65	0.115606936	0.057803468	0.032019532	0.064039064	15.62
A. matricariae								
20/6	24.55	0.0407331	12.583	0.079472303	0.039736151	0.000996949	0.001993898	501.53
20/8	22.40	0.0446428	12.583	0.079472303	0.039736151	0.004906649	0.009813298	101.92
20/10	18.68	0.0535331	12.583	0.079472303	0.039736151	0.013796949	0.027593898	36.24
20/32	13.616	0.0734430	12.583	0.079472303	0.039736151	0.033706849	0.067413698	14.83
20/34	14.35	0.06968641	12.583	0.079472303	0.039736151	0.029950259	0.059900518	16.69
20/38	15.633	0.06396724	12.583	0.079472303	0.039736151	0.024231089	0.048462178	20.63

dx = development period under cycling regime.

d20 = development at constant temperature 20°C.

dc = calculated developmental period at constant 4°C, 6°C, 8°C, 10°C, 32°C, 34°C & 38°C depending on cycling regime used.

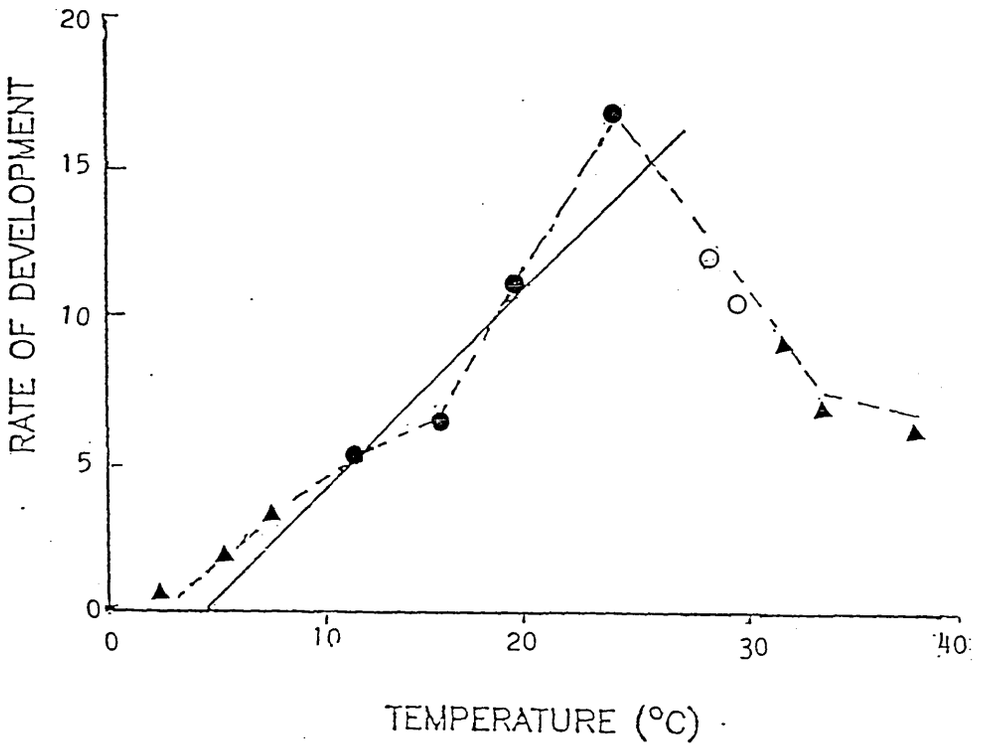


Figure 2.14 THE BEST FIT LINEAR REGRESSION ALONG WITH POLYNOMIAL REGRESSION LINES FOR PREDICTING DEVELOPMENT FROM CONSTANT AND CYCLING TEMPERATURES FOR M. persicae

Points represent mean development rates.

O = points not used in fitting regression lines.

▲ = points estimated from experiments using cycling temperatures; not used in fitting regression line.

Solid line = best fit linear regression line.

Dashed line = best fit polynomial regression line (all points used).

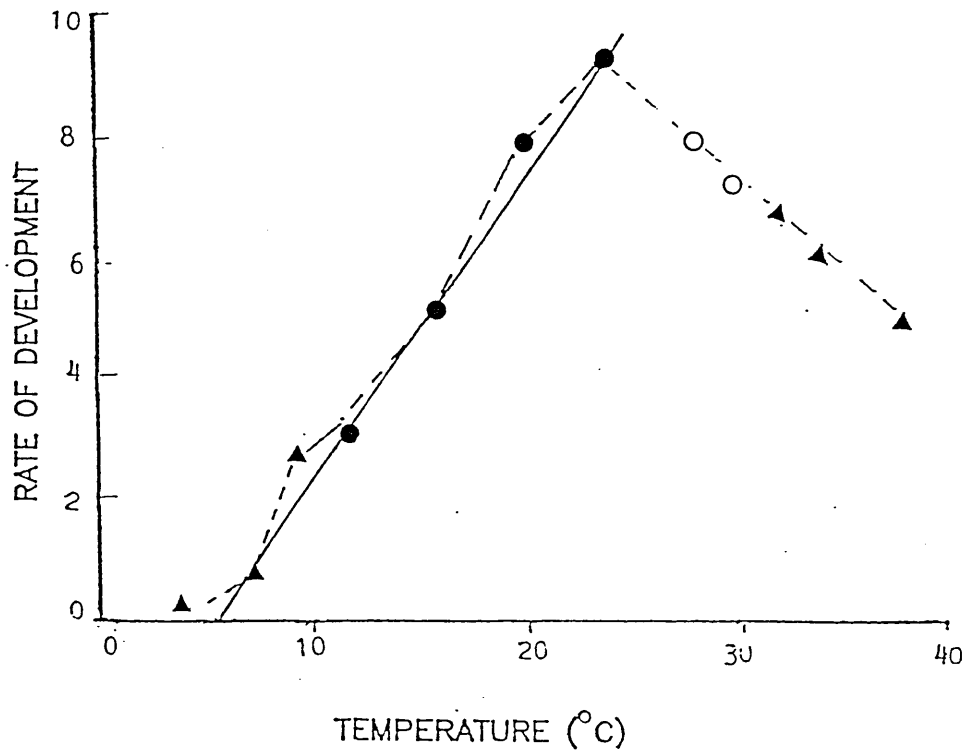


Figure 2.15 THE BEST FIT LINEAR REGRESSION ALONG WITH POLYNOMIAL REGRESSION LINES FOR PREDICTING DEVELOPMENT FROM CONSTANT AND CYCLING TEMPERATURES FOR A. matricariae

Points represent mean development rates of males and females combined.
O = points not used in fitting regression lines.
▲ = points estimated from experiments using cycling temperatures; not used in fitting regression line.
Solid line = best fit linear regression line.
Dashed line = best fit polynomial regression line (all points used).

Table 2.25 DAY DEGREE AND POLYNOMIAL PREDICTIONS OF DEVELOPMENTAL PERIODS OF THE APHID AND THE PARASITOID UNDER GLASS HOUSE FLUCTUATING CONDITIONS.

Regime °C	Actual emergence Mean ± s.e.	Polynomial prediction Develop. period	Residual	Day degrees Develop. period	Residual	Observed Rate of development	Predicted rate of develop. from polynomial
M. persicae							
October 1988	08.74 ± 0.28	8.26	-0.48	8.16	-0.58	0.114	0.120
Jan-Feb 1989	10.56 ± 0.21	8.69	-1.87	8.96	-1.60	0.090	0.115
March 1989	07.40 ± 0.33	7.15	-0.25	6.73	-0.67	0.135	0.139
May 1989	08.38 ± 0.40	7.62	-0.76	5.87	-2.51	0.119	0.130
June 1989	08.40 ± 0.33	8.33	-0.07	5.65	-2.75	0.119	0.120
A. matricariae							
October 1988	14.10 ± 0.13	12.9	-1.2	12.20	-1.9	0.07	0.077
Jan-Feb 1989	16.34 ± 0.37	13.1	-3.24	13.29	-3.05	0.06	0.076
March 1989	10.74 ± 0.34	10.6	-0.14	09.90	-0.84	0.093	0.094
May 1989	12.38 ± 0.60	11.8	-0.58	08.40	-3.98	0.0807	0.084
June 1989	12.50 ± 0.20	11.8	-0.70	08.43	-4.07	0.08	0.084

Temperature during May and June reached up tp 38°C for a number of days.

2.5.4 DISCUSSION

The results show that the lower thresholds obtained from cycling regimes using the techniques of Tingle & Copland (1988) reduce the lower threshold by about 1°C for both species than those obtained from linear regression of constant temperature data. This reduction in threshold value could be attributed to more accurate determination of lower threshold (Tingle & Copland, 1988) or probably explained by Messenger & Flitters (1959) statement that variable temperatures reduce the lower threshold. Attempts to examine the effects of temperature fluctuation have often been made by comparing results with those at constant temperatures equal to the daily mean of the fluctuations. As a result reports for acceleration or deceleration have been given (Huffaker, 1944; Pradhan, 1945; Cloudsley-Thompson, 1953). Little significance can be given to results of such direct comparisons. The absence of any effect of temperature fluctuations upon the relationship between temperature and rate of development means that laboratory data can be used safely to predict the development of insects under field or glasshouse conditions. The question is not only if there is an effect coming from fluctuating temperature but also if the effect is real. Pradhan (1945) explained that such effect may be due to interpretation of temperature-development relationship as linear and it does not necessarily mean a real effect on development processes. Messenger & Flitters (1959) put forward that a comparison between the two sets of curves, the theoretical and the empirical at any temperature level, gives a direct measure of the increased rate of development caused by variable temperature environments relative to rates occuring under constant temperature conditions. Where occuring this is a true accelerative effect due to variable temperatures, regardless of possible causes. Messenger (1964 a) used the constant temperature-development relationship to calculate the hourly increments of development expected at various temperature levels. Developmental periods estimated on the basis of this summing procedure are

compared with the developmental time actually observed under fluctuating conditions. A real evidence for an acceleration effect of fluctuating conditions could be shown if the observed developmental rate under fluctuating conditions was greater than that calculated from the hourly increments of constant data. From such comparisons under the present study (Table 2.25, with polynomial predictions) it can be seen that such accelerative effects on development are not present throughout the range of temperature encountered in glasshouse for both species, instead a tendency for retardation was evident. It is not in every case that the exposure to fluctuating or cycling conditions caused development to proceed faster than is predicted from the constant temperature response. Pradhan (1945) demonstrated that the development is quicker under variable temperature than under constant temperatures at lower degrees but the effects are just reversed at higher temperatures when development is slower under variable temperatures than under constant temperatures. Most probably the temperature encountered under the present study was not low enough to show such acceleration effect. So, most likely, the high temperatures experienced in the glasshouse during those months were responsible for the slower development found for both species. The results are in agreement with those of Tingle & Copland (1988) who reported that there is no evidence of an accelerating effect of fluctuating temperatures on developmental rates using hourly increments for 3 encyrtid mealybug parasitoids. Apart from acceleration or retardation effects of fluctuating temperature a more important aspect remains as the fact that the thermal limits to development are widened considerably under such conditions.

Day degree models seem to predict fairly well except in May and June, 1989. This is can be explained by the fact that in May and June, 1989 there were exceptionally high temperatures. Daily temperature fluctuations did go outside the middle range for long periods. Therefore, a linear extrapolation seems not valid. Still, Goodenough, Hartsack & King (1983)

reported that the poikilotherm model of Sharpe, Curry, Demichele and Cole (1977) was found not to give any great improvement in accuracy over day degree models when predicting development rates of the parasitoid Trichogramma pretiosum Riley on eggs of 40 host species. The day degree model was much easier to use and develop and appears acceptable for prediction in field conditions (Goodenough et al., 1983). However, when temperatures remain for substantial periods outside the linear range as was the case in the present study in glasshouse conditions in late May and June, 1989 predictions become less accurate irrespective of degree of accuracy with which the lower threshold has been determined. This is the result of assuming a linear temperature velocity curve for insect development which has been warned against by earlier workers (Davidson, 1944; Pradhan, 1946). The poor prediction of day degrees at high temperatures means that day degrees technique is relatively limited in its application. However, the day degree method would be more reliable to use during winter or mild summers.

Anyway, the cycling techniques used in this study while serving to provide information relating constant and variable temperatures, still remains an artificial approximation to natural conditions and involves sudden changes in thermal conditions and overextended periods in extreme temperatures rarely encountered in natural conditions.

The results show that polynomial regression does predict development reasonably accurately at all seasons throughout the year. Therefore, where temperature extremes are common, a precise curvilinear relationship can be used along with hourly temperature data. Tingle & Copland (1988) stated that the polynomial method, however, remains reasonably consistent under all conditions tested and should thus prove useful for predicting development in temperate glasshouses, where night time temperatures during the winter and midday temperatures during the summer reach opposite extremes.

Thus, the polynomial model may provide an important tool in understanding

the biology of both the aphid and the parasitoid over a broad range of temperature. Such models can be useful for planning and scheduling rearing times and sampling. Another important use of such a model is that it can be used as a basis for a computer forecast system to predict M. persicae population development in glasshouse using weather forecast data. And to predict the population dynamics of A. matricariae which can be used in augmentative release and to time such releases.

SECTION 3 CALCULATION OF INTRINSIC RATE OF INCREASE FOR Myzus persicae AND Aphidius matricariae

3.1 INTRODUCTION

The intrinsic rate of increase is a basic parameter which an ecologist may wish to establish for an insect population (Birch, 1948). The innate capacity for increase of a species of animal depends on its fecundity, longevity and speed of development which in a populaton are reflected by birth rate and death rate.

Valid conclusions concerning the abundance of species in nature can be made only by considering the sub-total effect of these characteristics on the birth rate and death rate in a population (Barlow, 1962). The intrinsic rate of increase has been used to compare the responses of different species to various environmental conditions (DeLoach, 1974). Messenger (1964b) used rm as an index of rate of population growth, response to temperature and potential effectiveness of parasite. The aim of this study was to establish the intrinsic rate of increase for both M. persicae and A. matricariae for use as an index of population performance and potential effectiveness of the parasitoid.

3.2 MATERIALS AND METHODS

Life tables for the aphid host M. persicae and its associated parasitoid A. matricariae were constructed by determining for each age interval the fraction of the initial population of individuals still alive, and the mean number of female progeny produced by these adult females at each age interval. This information was obtained from daily fecundity and survival data (Section 2). For M. persicae whose progeny are exclusively female the recorded progeny was used without correction. In such a table, the first column gives the age (x) of the cohort in days from birth. The second column lists the fractions (Lx) of the initial population still alive at the

end of each age interval (x). The third column gives the mean number (Mx) of progeny produced per day per female still alive at age x. In A. matricariae life tables, two sets of Mx columns were prepared which take into consideration sex ratio. One column takes sex ratio as 1:0 progeny all females to estimate a theoretical maximum rm. The second column takes sex ratio as 1:1 which gives a realistic estimate based on the ratio determined in an earlier experiment (Section 2). For each life table the following statistics were computed. The net reproductive rate or rate of replacement for the species, Ro, measured as female offspring per female parent per generation. In practice this is given by the sum of products LxMx for each age group. The intrinsic rate of increase, rm, is derived by iterative substitution of values of rm into the following equation

$$\Sigma\ lx.mx\ e^{-rm\ x} = 1 \quad \text{(Birch, 1948)}$$

x is the age of individuals in days. Lx is the age specific survival rate. Mx is the age specific fecundity rate or the average number of female offspring born to female of age x during the interval $x-\frac{1}{2}$ to $x+\frac{1}{2}$ e is the base of natural logarithms. The values of rm which best satisfies the equation is found by trial and error substitution of rm values in the equation. To simplify the whole procedure, it may be convenient to multiply both sides of the equation by a factor e^k in order to work with powers of e (Birch, 1948). Thus in the present study, k was taken as 5:

$$e^5\ \Sigma\ e^{-rm\ x}\ lx.mx = e^5$$

$$\Sigma\ e^{5-rm\ x}\ lx.mx = 148.4131591$$

A value of rm was then sought which would make the left hand side of this expression equal to 148.4131591. The process of carrying out this computation is made by iterative computing achieved with a microcomputer (Appendix 3.1). The mean generation time, T, which is defined as the time

elapsing from birth to weighted mean reproductive age is given for approximate purposes by

$$T = \Sigma x\, lx\, mx / \Sigma lx\, mx \qquad \text{(Birch, 1948)}$$

The accurate value is calculated from the formula

$$T = \log e\, Ro / rm$$

The finite rate of increase, λ which is the number of times a population multiplies for unit of time, day, is computed from the relation

$$\text{finite rate of increase } (\lambda) = \text{anti log } e\, rm \qquad \text{(Birch, 1948)}$$

The contribution of each age group to the value of rm varies. Certain age groups will have smaller influence than others in deciding the intrinsic rate of increase according to survival rates and birth rates at the different ages of individuals in the population. The relative contribution of each age groups to the value of rm are obtained by the products

$$lx\, mx\, e^{5-rm\, x}$$

2.3 RESULTS

The age specific fecundity (Mx) and survival rates (Lx) for the aphid reared at six constant temperatures of 12, 16, 20, 24, 28 and 30°C are presented (Appendices 3.2 - 3.7). The age specific survival and fecundity rates of both sex ratios of the parasitoid at the six constant temperatures are shown (Appendices 3.8 - 3.13). The values of Ro net reproductive rates are shown for M. persicae and A. matricariae. Comparisons of populations by means of their net reproductive rates may, however, be misleading unless the length of their generation time are the same (Birch, 1948). However Ro does give some insight into the reproductive rate of any population under one set of conditions (Barlow, 1962). Tables(3.1, 3.2 & 3.3) list the various population growth statistics for the host M. persicae and both sex ratios

Table 3.1 DEMOGRAPHIC STATISTICS FOR Myzus persicae AT SIX CONSTANT TEMPERATURES.

Growth parameters	Temperature °C 12	16	20	24	28	30
Developmental time (days)	20.21	12.20	08.65	07.17	08.02	09.07
Gross reproductive rate (f/f)	68.56	63.38	79.15	43.68	27.24	12.29
Net reproductive rate (f/f)	46.33	40.89	43.11	26.04	19.63	06.72
Innate rate of increase	00.1167	00.1826	00.2863	00.3148	00.2731	00.1815
Generation time (days)	32.87	20.32	13.15	10.36	10.90	10.50
Finite rate of increase	01.124	01.200	01.331	01.370	01.314	01.199
Doubling time	05.94	03.80	02.42	02.20	02.54	03.82

Table 3.2 DEMOGRAPHIC STATISTICS FOR Aphidius matricaricae AT SIX CONSTANT TEMPERATURES (SEX RATIO 1:1)

Growth parameters	Temperature °C 12	16	20	24	28	30
Developmental time (days)	33.07	19.25	012.58	10.65	12.23	14.33
Gross reproductive rate (f/f)	87.35	96.35	112.3	57.75	19.45	05.2
Net reproductive rate (f/f)	75.28	86.26	096.1	38.89	12.47	04.38
Innate rate of increase	00.1185	00.2023	000.311	00.3005	00.1766	00.0939
Generation time (days)	36.47	22.03	014.68	12.18	14.29	15.72
Finite rate of increase	01.13	01.22	001.37	01.35	01.19	01.10
Doubling time	05.85	03.43	002.23	02.31	03.92	07.38

Table 3.3 DEMOGRAPHIC STATISTICS FOR Aphidius matricariae AT SIX CONSTANT TEMPERATURES (SEX RATIO 1F:0M)

Growth parameters	Temperature °C 12	16	20	24	28	30
Developmental time (days)	033.07	019.25	012.58	010.65	12.23	14.33
Gross reproductive rate (f/f)	147.7	192.7	224.6	115.6	38.9	10.4
Net reproductive rate (f/f)	150.56	172.52	192.20	077.78	24.94	08.75
Innate rate of increase	000.1377	000.234	000.3589	000.3575	00.2254	00.1382
Generation time (days)	036.42	022.01	014.65	012.18	14.27	15.70
Finite rate of increase	001.15	001.26	001.43	001.43	01.25	01.15
Doubling time	005.03	002.96	001.93	001.94	03.08	05.02

(1f:1m and 1f:0m) of parasitoid A. matricariae respectively. Values of rm were computed on a daily basis. The figures were converted to the finite rate of increase. Finite rates of increase at all temperatures are illustrated in Figure (3.1). Values of, λ, increased with rising temperature up to 24°C for M. persicae but dropped as temperature increases further, whereas it is increased up to 20°C for A. matricariae then declined. At 32°C the results are not shown in the graphs, populations of both species were unable to maintain themselves and died out within the first generation, none completed development. The value of generation time, T, obtained from the accurate values of rm, (Tables 3.1, 3.2 & 3.3), are always shorter than those computed by the approximate method of Birch. This implies that the appropriate method for determining the T value overestimates this parameter and consequently underestimates the rm for the same species. For example at 20°C, for M. persicae the approximate generation time is 16.5 days and approximate rm is 0.2276 while the computed one is 13.15 and 0.2863 for generation time and rm respectively. For A. matricariae at 20°C, the approximate generation time is 14.9 days and the approximate rm is 0.3629 while the computed one is 14.65 and 0.3589 for generation time and rm respectively for the 1:0 sex ratio. Values calculated for the mean lengths of generation (Tables 3.1, 3.2 & 3.3) show that as temperature increased between (12-24°C) the mean lengths of generations of both species decreased. Further, at any temperature the mean length of generation was shorter for M. persicae than for A. matricariae. These facts could be guessed from the lengths of developmental periods which behave similarly relative to temperature. The value of the relative weights with which the different age groups contribute to the value of rm for M. persicae and A. matricariae at different temperatures are listed (Appendices 3.14 - 3.25). The results show that the value of rm was largely determined in most cases by the first few days of adult life. In addition this phenomenon became more obvious at higher temperatures. The

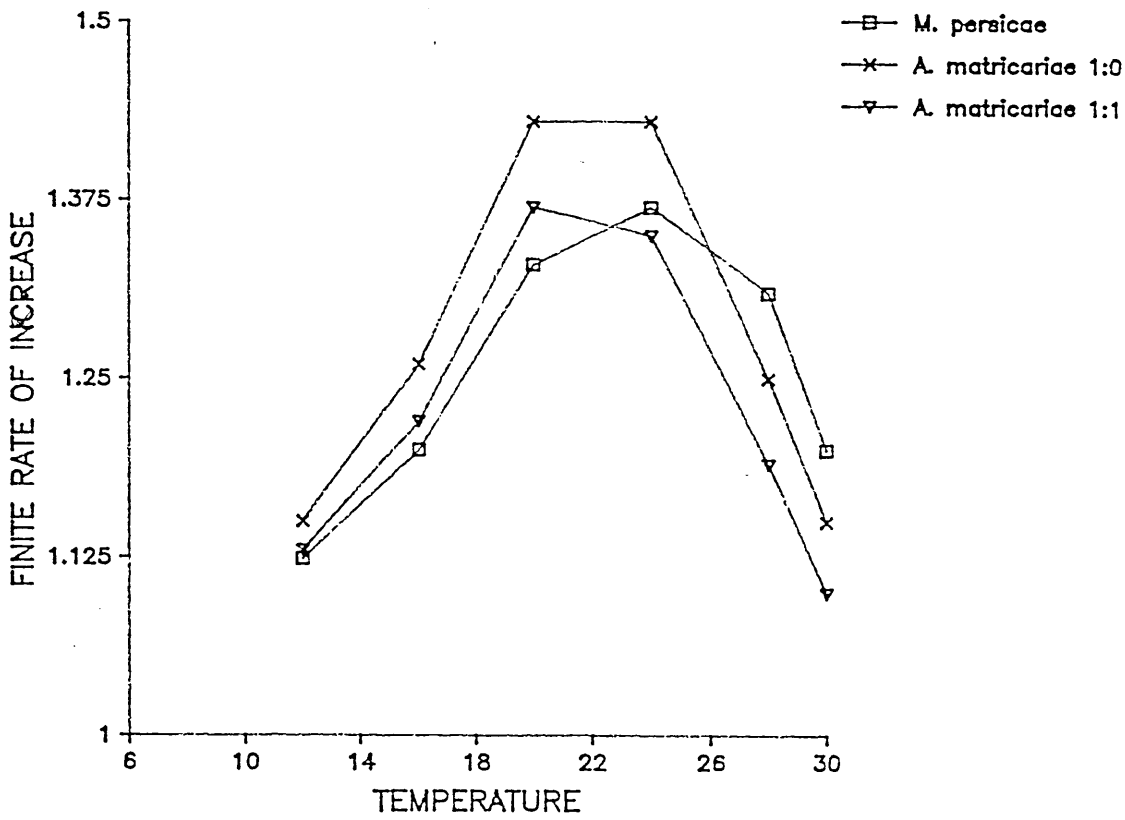


Figure 3.1 FINITE RATES OF INCREASE OF M. persicae AND BOTH SEX RATIOS OF A. matricariae AT CONSTANT TEMPERATURES OF 12-30°C

values of rm for M. persicae at 16°C was 90% accounted for in the first 11 days of adult life, but 90% of total young were not produced until the 27th day of adult life. The value of rm for A. matricariae at 16°C was 92% accounted for in the first 4 days of adult life even though only 79% of the total number of progeny was produced during this time.

3.4 PREDICTIVE MODELS FOR INTRINSIC RATE OF INCREASE

3.4.1 SIDDIQUI ET AL MODEL

3.4.1.1 INTRODUCTION, MATERIALS & METHODS

Siddiqui, Barlow and Randolph (1973) developed a predictive equation for rm by combining the equation of Pradhan (1946) (which describes the relation between rate of development and temperature), with the regression equation for the relationship between 1/rm and developmental time. The relationship between development rate and temperature could be defined empirically by the Pradhan equation as follows

$$y = y0\ e^{-a(t0 - t)^2}$$

where y = development rate at time t

y0 = the highest value of rate of development

e = constant 2.718 a = constant

t0 = temperature corresponding to y0

Derivations of these values are described by Pradhan (1964) (Appendices 3.26 & 3.27). The relationship between 1/rm and developmental time can be described by linear regression within certain temperature limits. By combining these two equations, predictive explanatory models expressing rm at constant temperatures were obtained for both M. persicae and A. matricariae according to Siddiqui et al., (1973).

3.4.1.2 RESULTS

Pradhan equations were obtained of the form

$y = 13.4626^{-0.00641768(24.585-t)^2}$ for M. persicae (Appendix 3.26)

and

$y = 9.0639^{-0.00749583(24.24-t)^2}$ for A. matricariae (Appendix 3.27)

The Pradhan exponential function closely describes the relation between temperature and development time for both the host and the parasitoid M. persicae and A. matricariae (Tables 3.4 & 3.5) respectively. The greatest deviation from calculated values was 0.31 at 12°C which is 1.5% of the calculated value at 12°C for M. persicae. Reciprocal values of rm within (12-24°C) temperature range were highly correlated with developmental time for M. persicae $r^2 = 0.9964$ (Figure 3.2). The greatest deviation from calculated value was 0.9 at 16°C which is 4.9% of the calculated value at 16°C for A. matricariae. Reciprocal values of rm were also highly correlated with developmental time for A. matricaricae, sex ratio 1f:0m $r^2 = 0.9964$ (Figure 3.3) as well as sex ratio 1:1 $r^2 = 0.9974$ (Figure 3.4). By combining Pradhan and linear equations for M. persicae and both sex ratios of 1:1 & 1:0 of A. matricariae the following predictive models were derived

M. persicae

$$rm = 1/0.0734309 + 0.423382\ (7.428\ e^{0.00641768\ (24.585-t)^2}$$

$r^2 = 0.9932 \qquad r = 0.9966$

$y = a + bx \quad a = 0.0734309 \qquad b = 0.423382$

Table 3.4 DEVELOPMENT PERIOD PREDICTED BY PRADHAN EQUATION FOR Myzus persicae

Temperature °C	Observed days	Calculated days	Observed-calculated	% deviation
12	20.22	20.53	-0.31	1.51
16	12.20	11.92	0.28	2.35
20	08.65	08.50	0.15	1.76
24	07.17	07.44	-0.27	3.63
28	08.02	08.01	0.01	0.12
30	09.07	08.97	0.1	1.01

Table 3.5 DEVELOPMENT PERIOD PREDICTED BY PRADHAN EQUATION FOR Aphidius matricariae

Temperature °C	Observed	Calculated	Observed-calculated	% deviation
12	33.07	33.92	-0.85	2.51
16	19.25	18.35	0.9	4.9
20	12.58	12.62	-0.04	0.32
24	10.65	11.04	-0.39	3.53
28	12.23	12.27	-0.04	0.33
30	14.33	14.15	0.18	1.27

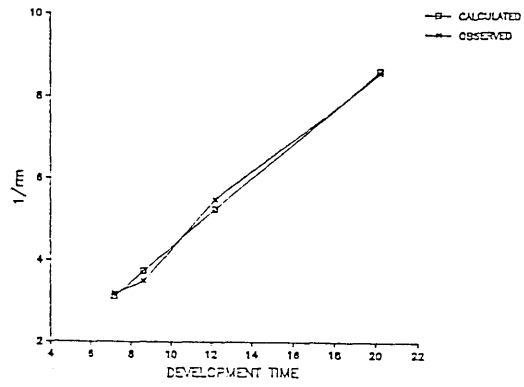


Figure 3.2 THE RELATIONSHIP BETWEEN THE INTRINSIC RATE OF INCREASE OF M. persicae AND DEVELOPMENT TIME

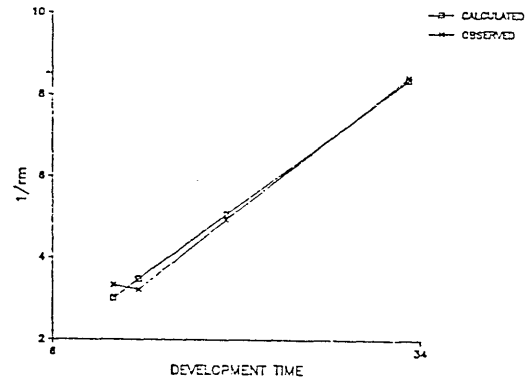


Figure 3.3 THE RELATIONSHIP BETWEEN THE INTRINSIC RATE OF INCREASE OF A. matricariae (1f:0m) AND DEVELOPMENT TIME

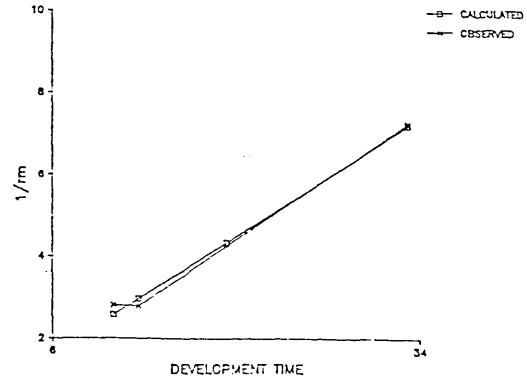


Figure 3.4 THE RELATIONSHIP BETWEEN THE INTRINSIC RATE OF INCREASE OF A. matricariae (1f:1m) AND DEVELOPMENT TIME

A.matricaricae (sex ratio 1:0)

$rm = 1/0.370274+0.206987\ (11.033\ e^{0.0074958(24.24-t)^2}$

a = 0.370274 b = 0.206987

r^2 = 0.9929 r = 0.9964

A. matricariae (sex ratio 1:1)

$rm = 1/0.469107+0.238896\ (11.033\ e^{0.0074958(24.24-t)^2}$

a = 0.469107 b = 0.238896

r^2 = 0.9894 r = 0.9947

These equations predicted the values of rm for M. persicae as well as for both sex ratios of A. matricariae satisfactorily within 12-24°C temperature range but tended to overestimate the true values at 28 & 30°C especially for A. matricaricae (Tables 3.6, 3.7 & 3.8; Figure 3.5)

3.4.2 POLYNOMIAL MODEL

Under the present study, a simple direct polynomial method is proposed. Since developmental period and 1/rm are closely related and so are developmental period and temperature there is a close correlation between temperature and rm. This relationship between rm and temperature can be expressed directly as the regression of rm on temperature. Since the relationship between development and temperature was a curvilinear one, then a curvilinear relation is also expected from the relation between rm and temperature.

3.4.2.1 MATERIALS & METHODS

The intrinsic rate of increase at each temperature for M. persicae and A. matricariae for both sex ratios 1f:1m & 1f:0m female:male was plotted

Table 3.6 rm PREDICTED BY PRADHAN SIDDIQUI EQUATION FOR Myzus persicae

Temperature °C	Observed rm	Calculated rm	Observed-calculated	% deviation
12	0.1167	0.1141	0.0026	02.28
16	0.1826	0.1953	-0.0127	06.50
20	0.2863	0.2723	0.014	05.14
24	0.3148	0.3101	0.0047	01.52
28	0.2731	0.2888	-0.0157	05.44
30	0.1815	0.2584	-0.0769	29.76

Table 3.7 rm PREDICTED BY PRADHAN SIDDIQUI EQUATION FOR Aphidius matricariae (SEX RATIO 1:1)

Temperature °C	Observed rm	Calculated rm	Observed-calculated	% deviation
12	0.1185	0.1167	0.0018	01.54
16	0.2023	0.2060	-0.0037	01.80
20	0.311	0.2869	0.0241	08.40
24	0.3005	0.3220	-0.0215	06.68
28	0.1766	0.2942	-0.1176	39.97
30	0.0939	0.2598	-0.1659	63.86

Table 3.8 rm PREDICTED BY PRADHAN SIDDIQUI EQUATION FOR Aphidius matricariae (SEX RATIO 1:0 F:M)

Temperature °C	Observed rm	Calculated rm	Observed-calculated	% deviation
12	0.1377	0.1353	0.0024	01.77
16	0.234	0.2398	-0.0058	02.42
20	0.3589	0.3352	0.0237	07.07
24	0.3575	0.3767	-0.0192	05.10
28	0.2254	0.3437	-0.1183	34.42
30	0.1382	0.3031	-0.1649	54.40

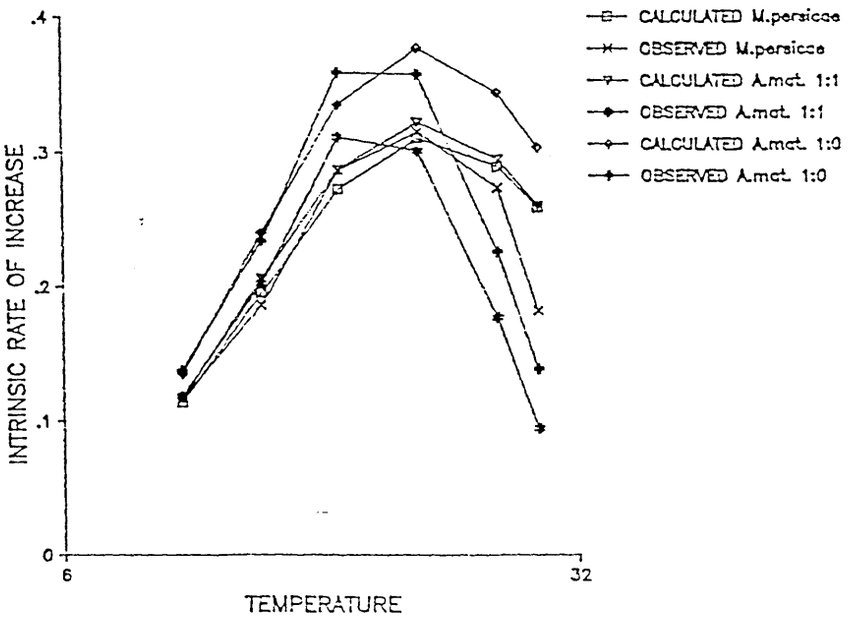


Figure 3.5 OBSERVED VALUES OF rm AND VALUES OF rm PREDICTED BY THE EQUATION OF SIDDIQUI et al., (1973)

against temperature. Curvilinear data of rm that do not fit or approach linear is fitted to a polynomial of the form:

$$y = a + bx + cx^2 + dx^3 + \ldots$$

The model can be changed into quadratic, cubic, etc.,. . to obtain better results

3.4.2.2 RESULTS

Polynomial regression analysis was carried out to determine the rm curve on temperature. The analysis was performed using a microcomputer as the regression of rm on temperature. The best curve was selected on the ground of significant improvement in fit. The best fitting curve selected for M. persicae was order 3. The best possible fit curve obtained for A. matricariae for both sex ratios were polynomial order 4. The regression equations that describe these relationships between temperature and rm for M. persicae and both sex ratios of A. matricariae were given in Table (3.9), as well as r^2 values. The calculated values for rm within (12-30°C) for M. persicae and both sex ratios of A. matricaricae are given in Tables (3.10, 3.11 & 3.12). The observed values of rm at temperatures ranging from (12-30°C) were a good fit to calculated values for both species (Figure 3.6). The difference between the observed and calculated values show that the deviation of any points from the calculatd curve does not exceed 0.00936 which is only 3.4% of the appropriate calculate value for M. persicae which occured at 20°C. The greatest deviation for A. matricariae found at 28°C which was 1% for 1:1 sex ratio and 0.5 for 1f:0m sex ratio.

Maximum rm for M. persicae and for both sex ratios of A. matricariae 1:0 and 1:1 were 0.3148, 0.3589 and 0.311 respectively. Temperatures corresponding to those maximum rm were (24, 20 & 20°C) respectively. These temperatures are considered as optimum for intrinsic rate of increase for respective species.

Table 3.9 COEFFICIENTS OF POLYNOMIAL REGRESSION FOR Myzus persicae AND Aphidius matricariae

Species	R^2 (%)	a	b	c	d	e
M. persicae	98.1285	0.594160	-0.11307	0.007956	-0.00015	
A. matricaria (1:1)	99.8108	3.120783	-0.68622	0.054643	-0.00762	0.00001
A. matricariae (1f:0m)	99.9443	3.495271	-0.766312	0.060888	-0.00195	0.00002

Table 3.10 rm PREDICTED BY POLYNOMIAL MODEL FOR Myzus persicae

Temperature °C	Observed rm	Calculated rm	Observed-calculated	% deviation
12	0.1167	0.115539452	0.001160548	1.00
16	0.1826	0.187814808	-0.00521480	2.78
20	0.2863	0.276931744	0.009362558	3.38
24	0.3148	0.323450468	-0.00865046	2.67
28	0.2731	0.267931184	0.005168816	1.93
30	0.1815	0.183332354	-0.00183235	0.999

Table 3.11 rm PREDICTED BY POLYNOMIAL MODEL FOR Aphidius matricariae (SEX RATIO 1:1)

Temperature °C	Observed rm	Calculated rm	Observed-calculated	% deviation
12	0.1185	0.118298949	0.000201051	0.170
16	0.2023	0.20333397	-0.00103397	0.509
20	0.311	0.308828657	0.002171343	0.703
24	0.3005	0.302912593	-0.00241259	0.796
28	0.1766	0.174790538	0.001809462	1.04
30	0.0939	0.094635249	-0.00073524	0.777

Table 3.12 rm PREDICTED BY POLYNOMIAL MODEL FOR Aphidius matricariae (SEX RATIO 1:0 F:M)

Temperature °C	Observed rm	Calculated rm	Observed-calculated	% deviation
12	0.1377	0.137586068	0.0001139322	0.083
16	0.234	0.234585927	-0.000585926	0.250
20	0.3589	0.357669546	0.0012304507	0.344
24	0.3575	0.358867162	-0.0013671617	0.381
28	0.2254	0.224374619	0.00102538144	0.457
30	0.1382	0.138616644	-0.0004166440	0.301

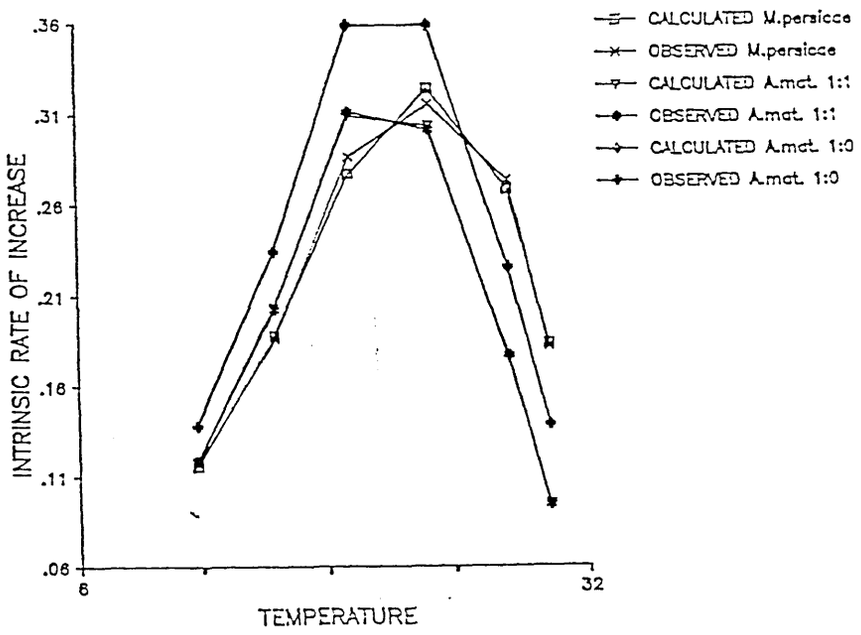


Figure 3.6 OBSERVED VALUES OF rm AND VALUES OF rm PREDICTED BY THE POLYNOMIAL REGRESSION

3.5 DISCUSSION

Determination of the intrinsic rate of increase gives a means of estimating the maximum attainable rate of increase under controlled conditions and helps to understand how environment affects the innate capacity for increase of species on which the rate of growth of population depends. The results therefore demonstrate the value of using rm in comparing the species of both A. matricariae and its host M. persicae or the effect of different temperatures on population growth. It has been shown that, the comparison of populations by means of their net reproductive rates may be quite misleading unless the mean lengths of generations are the same. Two or more population may have the same net reproduction but their rm may be quite different because of different lengths of their generations. For this reason the parameter, Ro, has a limited value as it must always be considered in relation to the length of generation T. The values of rm presented here provide a direct comparison between the performance of the aphid and its parasitoid at different temperatures. Differences between the finite rates of increase of the two species were evident. At any given temperature between (12-20°C), values of λ for A. matricariae were higher than those for M. persicae. A. matricariae had a slightly smaller rate of increase at 24°C than M. persicae, but M. persicae had a higher rate of increase at both 28 & 30°C. The maximum rate of increase of A. matricariae occured at 20°C while it was at 24°C for M. persicae. The results suggest that both species are suited to warm but not particularly hot conditions, which can be realized in glasshouse conditions in mild summers and warm winters. In A. matricariae (a bisexual species), the total number of births in any period has been divided by a factor representing the sex ratio of species, since the calculation of rm is based on females only. It should be noticed that the measurement of both sex ratio and total fecundity is not possible. The only way to measure total fecundity is by dissection of all host aphids to obtain egg counts which prevent rearing the parasitoid to

emergence where sex could be recognized. So the results were based on effective eggs per host and the supernumerary eggs were excluded. There was no need to divide the progeny by a sex ratio factor in case of parthenogenetic M. persicae where all the progeny are females. So for A. matricariae two values of rm were given. One with a sex ratio of 1:0 female:male which provided an idea of maximum capacity the species possess for increase. The other sex ratio of 1:1 female:male demonstrated the more relevant rm based on realistic sex ratio determined in an earlier experiment (Section 2). A sex ratio of 1:1 for the species, means that only half eggs laid by the parasitoid will produce females which means a 50% decline in fecundity. However the difference in rm when this is taken into consideration is not very marked, for example at 20°C rm declines only from 0.3585 to 0.3105 a reduction of 0.13%. Differences in sex ratio can cause proportional changes in real fecundity but do not cause similar proportional changes in rm. This is because rm varies only as the natural logarithms of changes in fecundity (Messenger, 1964b). Differences in time of development and reproductive period has a much greater influence on rm. This is due to the fact that rm varies in linear inverse proportion to generaton time T. This means that, taking twice as long to develop and oviposit causes rm to decline by 50% provided fecundity and survival rates remain unchanged. It has been shown that the intrinsic rate of increase is determined to a much greater extent by the rate of oviposition in the first few days of adult life than by the total number of eggs laid in the life time. Generally most of the contribution was made during the first few days of adult life, taking a much longer time to produce an equal proportion of the total young. For example, in A. matricariae, at 20°C, 92% of the contribution to the next generation had been during the first 3 days of adult life but 94% of the total young were not produced until the 5th day. For M. persicae, at 20°C, 91% of the contribution to the next generation has been made by the first 7 days of adult life but 92% of the total young were not produced until the

27th day.

Therefore, with each successive day in the life of the adult the number of eggs laid makes a smaller contribution to the value of rm. So, for a maximum value of rm the optimum age schedule of fecundity is the one which has an early maximum. For the calculation of rm the life table beyond the end of reproductive period has no significant importance. The biological significance of these facts in the population dynamics of these species is that the rate of reproduction during the first few days of adult life of both species were more important in deciding the value of rm of the population than the total number of young produced over the whole life span. A relative importance of age specific survival in deciding the value of rm is itself a function of rm. When rm is large it is mostly determined by the oviposition in early adult life. There is a wide variation in the nature of egg schedule fecundity of both species. A. matricariae lays most of its eggs in a very short time in comparison with its host M. persicae. The advantage of this mode of oviposition is obvious and is probably responsible for the great success of this species in laboratory conditions. The values of rm of the two species were very close at low temperature of 12°C and was greater for the parasitoid at 16-20°C. The rm for the parasitoid was slightly less than that for M. persicae at 24°C, and much less at higher temperatures of 28-30°C. This means, if the two species co-existed at mild temperature of 16-20°C and if other factors were equal, the parasitoid would be expected to become the dominant species. At very high temperatures, the aphid would eventually become the dominant species but would require a much longer time. Different species of host plants (Frazer, 1972) and biotypes of aphid species (Cartier, 1959) have been shown to produce different fecundity and survival rates. By using the same host plants, and biotypes of aphids, it has been shown that temperature has a profound effect on the growth of population of both M. persicae and A. matricariae. Both species exhibited capacities for increase in these experiments at all temperatures

between (12-30°C) as indicated by calculated values of finite rate of increase (λ) where (λ) values were greater than 1. At temperatures 28-30°C, survival and fecundity greatly reduced causing a decrease in (λ). At 32°C, not shown in tables, populations were unable to maintain themselves and died out within the first generation. In such a case (λ) would be less than 1 and rm would be negative, the death rate exceeds the birth rate and the population eventually dies out. A value of 1 for (λ) means rm = 0 which means a population could maintain itself but could not increase, and in this sense represents a threshold for increase of the population under specified conditions (Messenger, 1964b). The upper temperature threshold for growth of population of aphid as well as the parasitoid was somewhere between 30-32°C. Modifications of innate capacity for increase of these populations by temperature was exerted through its influence on survival, fecundity and development. The total fecundity of M. persicae decreased as temperature increased between (20-24°C) but rm increased because developmental time decreased and maximum fecundity was attained earlier. The values of rm for M. persicae obtained in the present study of 0.286 at 20°C on brassicae seedlings compare well with that found in the literature for M. persicae and other aphid species. Barlow (1962) found rm for M. persicae on tobacco leaves to be 0.447 at 20°C. Harrison, (1969) obtained an rm value of 0.26 for M. persicae on tobacco at 22°C. DeLoach, (1974) obtained a value of 0.270 for M. persicae on cabbage at 20°C. Wyatt & Brown, (1977) suggest it to be 0.314 for M. persicae on chrysanthemum at 24°C. Siddiqui et al., (1973) found it to be 0.364 for the pea aphid Acyrthosiphon pisum (Harris) on pea plant at 20°C. Messenger, (1964b) found an rm of 0.325 at 21°C for Therioaphis maculata (Buckton) on alfalfa seedlings. The case of A. matricariae is more complex, for not only does the occurence of superparasitization affect realized fecundity but the variations possible in the sex ratio of progeny produced must be considered as well. In addition, mating in this species is essential to produce female progeny while female

age at the time of oviposition also influences the sex of eggs laid. Published data is insufficient to make comparison of A. matricariae with the same species in term of their life table statistics. In our study the rm was found to equal 0.311 for a sex ratio of 1f:1m and 0.3589 for a sex ratio of 1f:0m at 20°C. The results are however comparable with other aphidiids. Messenger (1964b) working on Praon palitans Muesebeck parasitizing Theriophis maculata found rm = 0.247 for a sex ratio 1f:1m and rm = 0.288 for a sex ratio 1f:0m at 21°C measured as effective eggs. Mackauer, (1983) found an rm of 0.358 at 20.5°C for A. smithi with an assumed sex ratio of 50% females, parasitizing pea aphid Acyrthosiphon pisum. Cohen & Mackauer, (1987) reported an rm of 0.371 at 23°C for Ephedrus californicus Baker on pea aphid A. pisum for a sex ratio of 1f:1m. It is obvious that meaningful comparison of the parameters between studies is difficult as experiments are seldom carried out under identical conditions and small differences in development time affect life table parameters.

The predictive models study shows that a high correlation was found between developmental time and the reciprocal of rm between 12-24°C, for both species M. persicae and A. matricariae. At high temperatures of (28-30°C) this relation did not hold. A similar close relationship between rm and developmental time were found in the literature. Sidiqui et al., (1973) found a high correlation coefficient for the relationship between 1/rm and development (r = 0.996) for the pea aphid A. pisum. DeLoach, (1974) also found a high correlation between rm and age at first reproduction (r = 0.9956) for M. persicae. The model of Siddiqui et al., (1973) predicted the values of rm for M. persicae and A. matricariae under this study satisfactorily within 12-24°C, but tended to overestimate the true values at 28-30°C. At 28-30°C the relation does not hold because the exposures to deleterious high temperatures which affected development time, fecundity and longevity. So the increased mortality, reduced fecundity and longevity resulted in reduced values of rm at such high temperatures. The model did

not predict values of rm for A. matricariae as closely as for M. persicae because the correlation of rm with development time on which the model is based was not as high for A. matricariae. The results were in line with other authors. Siddiqui et al., (1973) used their model to predict Barlow's 1962 data on M. persicae. Their model predicted the values of rm closely for M. persicae with an average deviation of 12.7%. Sidiqui et al., (1973) used their model also to predict the values of rm satisfactorily for the pea aphid A. pisum with average deviation between observed and computed values of rm of 4.2%. DeLoach, (1974) used the Siddiqui et al., (1973) model to satisfactorily predict the values of rm for three species of aphids one of which was M. persicae with an average difference between empirical and computed values for rm of 6.7%.

Tanigoshi, Hoyt, Browne and Logan (1975) proposed a model to predict rm in which they pointed out that development period and 1/rm are closely related as are developmental period and temperature. The relationship between rm and temperature can be expressed indirectly as the regression of the reciprocal of rm on development period:

$$1/rm = a + px$$

Where p is the developmental period. Development period as a function of temperature can be found from polynomial relation between developmental time p and temperature

$$p = a + bx + cx^2 + dx^3$$

By substituting the development period values with values of development from the polynomial regression and combining constants they were able to give a model which is based on linear regression of the relationship between 1/rm and development time. They used the model to satisfactorily predict the values of rm for the McDaniel spider mite Tetranychus mcdanieli McGregor. Since their observed data occured within the linear portion, it

gave good results. But the extrapolation of their curve beyond the observed data is not expected to give good results. So, as long as their model is reliable only within linear limits, no significant improvement over Siddiqui et al., (1973) is achieved.

Therefore a polynomial model was proposed under this study in which it is pointed out that since the development period and 1/rm are closely related as are development period and temperature it follows that rm and temperature are correlated and can be expressed directly as the regression of rm on temperature. By using the polynomial model it was possible to obtain an excellent fit to the observed data. The regression formula gave a very good empirical technique to examine the influence of temperature on rm. Evaluation of various models used for predicting rm indicates that the more general method of polynomial regresson analysis provided the flexibility needed to determine the best curve over all temperatures. Polynomial regression analysis was found to be the most suitable method of determining and describing the temperature - rm relationship, as polynomial regression accurately predicted the values of rm over the whole range of temperature, while other methods could only predict the values of rm satisfactorily within a linear portion of the curve.

The statistic rm was primarily used to describe the effects of temperature on the population dynamics. The values of rm can be used in a number of ways:

1. As a growth rate index: rm is a true measure of the rate at which a population of species will increase in numbers at different temperatures. rm summarizes in one figure the degree of mortality and fertility in a population, at the same given time, when any effect of the existing age structure of the population (which for most insects in nature changes continuously) on this rate of increase is eliminated (Messenger, 1964b).

2. As a climatic index: Lower temperature causes a lower real rate of increase, high temperature the opposite. rm may provide a correlative measure or climatic index for the way in which an organism can be expected to respond to different temperatures (Graham, 1959; Barlow, 1962; Messenger, 1964b). Population of both species are expected to persist and increase in numbers only where rm has a value greater than zero. rm can be usd to determine the climatic limits to existence of an organism. Various sets of temperature conditions need to be tested to the point where the value of rm approaches zero (Birch, 1948; Andrewartha & Birch, 1954).

3. As a numerical rating index: rm can be used as a measure of effectiveness of the parasitoid in suppressing the growth of populations of its host under different physical conditions. Under the present results, in warm temperatures (16-24°C) the parasitoid has the potential of preventing the population of its host from increasing to economic damaging levels. In cooler weather (12°C) and at high temperatures (28-30°C) although the parasitoid would be able to persist (rm greater than zero) it is unlikely to be able to control the increase of its host.

It is shown from comparison of life tables that aphids develop to maturity faster, have a shorter generation time, reproduce sooner in the life cycle and survive longer than the parasitoid. However the parastoid has a greater total fecundity as well as greater initial fecundity rates. The calculation of intrinsic rate of increase, rm, demonstrated how the different influences of development, survival and fecundity is summarised in a single meaningful quantitative index reflecting the collective influences of temperature.

The present results indicated that under certain temperatures the rate of population increase of A. matricariae can be higher than that of its host M. persicae. While such information, may be useful in the study of aphid parasite systems it may not offer full knowledge of the potential of a

parasitoid as a biological control agent. As, the number of aphids to be parasitized in the field may be effectively limited by the searching efficiency of the parasite rather than by the number of eggs available (Mackauer & van den Bosch, 1973).

SECTION 4 THE EFFECT OF HOST DENSITY ON LONGEVITY, FECUNDITY, INTRINSIC RATE OF INCREASE, SUPERPARASITIZATION AND FUNCTIONAL RESPONSE OF *A. matricariae*

4.1 GENERAL INTRODUCTION

Various extrinsic and intrinsic factors influence fecundity and life span and consequently population growth rate. Temperature is thought to be one of the most important climatic factors and the role it plays has been investigated in an earlier chapter (Section 2). Apart from climatic factors, density is regarded as a key factor that affects population growth. To date, the assessment of the effectiveness of natural enemies has been based largely on knowledge of their ability to attack prey, their life history in relation to that of prey and environmental tolerance (Murdoch, 1973). Without neglecting the importance of these characteristics, however, it is widely recognized that searching capacity is also vitally important, because it determines the ability of predators to locate prey and to maintain their numbers at various prey densities.

The establishment of parasitization efficiency values for different parasitoids and host densities is a critical element in the study of their population interactions (Doutt, 1964b). The study of parasitoid-host population interactions also provides the numerical data for calculating the number of parasitoids needed to regulate the estimated pest population (Knipling & Gilmore, 1971).

Solomon (1949) defined the functional response as 'a change in the number of host attacked in a fixed period of time by a single parasitoid when the initial host density is changed'. A type 2 functional response curve was found for a number of other aphidiids (Dransfield, 1979; Mackauer, 1983; Liu Shu-sheng, 1985).

The question of superparasitization and egg distribution relative to host

density has been recently investigated. Host discrimination, the ability to distinguish parasitized from unparasitized hosts, is an aspect of parasitoid behaviour that is commonly involved in the host selection process (van Lenteren, 1981). The selection of suitable hosts by an insect parasitoid female is most critical for survival of its progeny (Salt, 1935; Vinson & Iwantsch, 1980a).

Vinson (1976) defined superparasitization as the presence of more than one individual of the same species within a host and multiple parasitism as parasitism by different parasitoid species. The final effect of superparasitism as a competitive relation among the parasite larvae of the same species and within a single host aphid is that only a single parasite larva survives and successfully completes its development. Host descrimination is defined by Salt (1934) as the ability of a parasite to distinguish unparasitized from parasitized hosts and to lay eggs in the former. This definition has been extended to include the ability of parasitoids to distinguish hosts containing different numbers of parasite eggs and to lay preferably only in those with the lowest numbers (van Lenteren, Bakker and Alphen, 1978). Parasitoids are able to discriminate through some sort of host marking. There are both external and internal host marking substances. Salt (1934) working on Trichogramma evanescens was the first to show that parasitoids could discriminate between unparasitized and parasitized hosts. He was also the first to report that a parasitoid left a factor that inhibited further attack. Inhibitory factors have been termed spoor factors, trail odours, search deterrent, deterrent pheromones and host marking pheromones. The searched areas are marked and this reduce the searching of such areas and leads to parasitoid dispersal (Richerson & Borden, 1972). Various accessory glands are responsible for marking substances.

Discrimination and marking of hosts has been controversial since

entomologists studying the same parasitoids came out with conflicting findings regarding host discrimination or presence of host marking.

Quantitative studies of insect superparasitization began when Fiske (1910) derived the relationship between the percentage parasitization of a group of hosts and the average number of eggs deposited in each host assuming the egg was laid singly. This relationship was later described by the Poisson formula:

$$P = 100\ (1 - e^{-m})$$

p = % parasitization m = average number of parasite eggs in each host

The argument is repeatedly made that parasitoids with the ability to discriminate and to avoid superparasitized hosts should have a selective advantage. Mathematical models have been developed that describe the behaviour of such parasitoids in terms of expected egg frequency distributions (Bakker, Eijsackers, van Lenteren & Meelis, 1972; Rogers, 1975; Pollard, 1977). First, poisson formula was applied to the frequency distribution of parasite egg among available hosts

$$P_x = m^x \cdot e^{-m}/x!$$

P_x = proportion of hosts containing x egg each x (0, 1, 2,...).

The poisson distribution is most easily used but it is inappropriate for use with small samples (Snedecor & Cochran, 1980). Recently, a number of bionomial distribution equations were introduced by Rogers (1975) and Pollard (1977). As this species A. matricariae is a solitary parasitoid, special attention is given to the question of superparasitization.

The literature mentions very little about the influence of host density on population growth rate of A. matricariae. Recent work by Messenger (1968) and Mackauer (1983) gave a more detailed account of these relationships for other aphidiid species, in which they found population growth rate is

strongly influenced by host density. The quantitative effect of the reactions of parasitoids to variations in the densities of their hosts still remain an affair of major concern among ecologists.

The aim of this study is to investigate the influence of M. persicae density on fecundity, life span, intrinsic rate of increase, superparasitization and functional response of A. matricariae.

4.2 GENERAL MATERIALS AND METHODS

Fecundity, life span, functional response, superparasitization and rate of population increase of A. matricariae to host density was determined in experimental arenas made of ventilated plastic boxes 173 x 115 x 63 mm containing 7-day old turnip seedlings. The seedlings were transplanted into small vials 50 x 25 mm. Each box held 6 vials. 3rd-4th nymphal instars were randomly placed on the turnip seedlings and allowed to settle for at least one hour before the parasitoid was added to the arena. The performance of A. matricariae was determined at 8 levels of aphid availability 5, 10, 15, 20, 30, 50, 100, 200 aphids/day. Each density was replicated 6 times. Time elapsed between replicates was 7-15 days. Each female tested was taken from a culture cage 0-12 hours after emergence. Parasitoids and hosts were exposed to each other for 24 hours after which parasitoids were transferred at the same time each day to another arena containing a fresh host supply at the same density. Transfers were continued until the death of the parasitoids. All aphids were left to feed on turnip seedlings till emergence except 4 out of 6 replicates for the 2nd parasitization, were allowed to feed for only 4 days until the parasitoid eggs hatch, and were then preserved in 80% ethanol for subsequent dissection to assess the degree of superparasitization. In the case of the 4 replicates of aphids dissected at each density for the 2nd fecundity, any dissected aphid with at least one larvae or more is included in the count of number of parasitized aphid for fecundity and functional response data.

The experiments were carried out at a constant temperature of 20°C inside an incubator with 60-80% r.h. and constant illumination provided by 6 8-watt fluorescent tubes giving intensity of 25-30 W/m^2.

4.2.1 FECUNDITY

The estimate of the number of eggs laid and of aphids parasitized reflect two different estimations of fecundity as only one larvae per aphid completes development to adult in aphidiids. Although the number of eggs laid represent the maximal potential fecundity, it is the number of aphids parasitized that represents the true fecundity. So, under this study fecundity was measured as the number of aphids parasitized. Therefore in the case of the 4 replicates of aphids dissected at each density for the 2nd day fecundity, any dissected aphid with at least one larva or more is included in the count of number of parasitized aphid for fecundity data.

4.2.2 LONGEVITY

Longevity data is analysed by using Lt_{50}, time for 50% mortality as well as using the Weibull frequency distribution as a model of survivorship (Pinder et al., 1978). The proportion surviving at time t is given by:

$$F(t) = 1 - \exp(-[(t/b)^c])$$

where b and c are the scale and shape parameters of the distribution.

4.2.3 FUNCTIONAL RESPONSE

Five functional response curves were obtained for the first five successive days of A. matricariae fecundity by plotting realized fecundity against aphid density. The functional response curves were analysed by two models:

1. By disc equation of Holling (1959b), its terms were transformed to accomodate a host-parasitoid model.

$$Na = a\,Tt\,N / (1 + a\,Th\,N)$$

Where Na = the number of hosts parasitized, a = the rate of successful searching, Tt = total time in which hosts and parasitoids are exposed to each other, Th = the oviposition time which would include time taken to discover and identify a host once encountered and strike it for purpose of egg laying, and N = the host density.

The constants a and Th were estimated using two methods. First by using Holling's graphic way of fitting the disc equation to a set of functional response data. By plotting Na/N against Na at each density level and straight line will be fitted to the data by least squares technique:

$$Na/N = - a\,Th\,Na + Tt\,a$$

the slope of the line is equal to - a Th. The intercept on the ordinate is equal to a Tt. Secondly, the constants a, Th were estimated by least squares regression to the linear transformation (Livdahl & Stiven, 1983):

$$N/Na = 1/Tt + Th\,N/Tt$$

the slope is the reciprocal of the attack rate and the intercept multiplied by the time of exposure gives the handling time.

2. By using the random parasite equation (Messenger, 1968; Royama, 1971; Rogers, 1972):

$$Na = N\,[1 - \exp(-\,a\,Tt\,/\,1 + a\,Th\,N)]$$

The values of a and Th were estimated by linear regression of:

1 / In proportion of host surviving against density.

A linear form of the equation is

$$\log e\ (1 - Na/N) = a\ Th\ Na - a\ Tt$$

The estimated values of a and Th were substituted in the above models to judge if the number of aphids parasitized during the fixed exposure period vary with host density according to the disc equation or not.

To satisfy the Holling model assumptions, the experiment design was made in a way to accomodate the primary biological hypothesis but also conform to requirements of statistical analysis. Total time of exposure of hosts to parasitoids, size and shape of test arena was held constant within and across all densities used. The experiment time was long enough (24 hours) to test fully the oviposition response of the parasites.

4.2.4 INTRINSIC RATE OF INCREASE

The Intrinsic rate of increase of A. matricariae was computed independently for each host density following the same procedure (Section 3) by iterative substitution of values of rm in the equation of Birch (1948).

$$\Sigma\ e^{-rm\ x}\ lx\ mx = 1$$

where Lx is the probability at birth of being alive at age x, Mx is age schedule of birth is the number of young born per day per female alive at mid-point of each day and x is the mid point of each age group.

The relative contribution of each age group to the value of rm is given by

$$lx\ mx\ e^{5-rm\ x} \quad \text{(Birch, 1948)}$$

The mean time to adult under these experimental conditions at 20°C was determined in an earlier experiment (Section 2.4) as 13.5 days and added to the pivotal age of each female cohort. The Mx values were based on

the number of hosts actually parasitized (true fecundity) counted as mummies or any host with one or more parasitoid larvae in case of dissected aphids. Two sex ratios were used. A sex ratio of 1f:0m is given to show the maximum theoretical capacity for increase under the experimental conditions. A more realistic capacity was estimated according to a sex ratio of 1:1 as determined in an earlier experiment (Section 2.4).

4.2.5 SUPERPARASITISM

Aphids of second day parasitization were left to feed on turnip seedlings for only an additional 4 days till parasitoid eggs hatched and developed to first instar stage and were easily recognized before they were preserved in 80% ethanol for subsequent dissection. For each parasitoid the number of eggs laid and the number of hosts parasitized per exposure was estimated by dissecting several aphids selected at random from the 8 densities. The proportion dissected at each density was 5/5, 10/10, 15/15, 20/20, 25/30, 35/50, 70/100 & 140/200. The data were tabulated in the form of frequency distribution of the number of hosts attacked and the number of eggs laid per host attacked per 24 hour exposure. Egg distributions were obtained by pooling the data for individual parasite female for 4 replicates for each density. Egg distribution was analysed under the assumption that egg mortality is negligible and based on larvae count found at dissection. Thus, the frequency distribution of the larvae represent that of the eggs. To test the hypothesis that parasitoids search and parasitize hosts at random and the ability of the parasitoid to discriminate between parasitized and non-parasitized hosts was carried out by fitting a binomial distribution model to the data from individual females using the equation of Rogers (1975).

$$Nx = N\ C^{n}\ (1/N)^{x}\ (1 - 1/N)^{n-x}$$

where Nx = the number of hosts containing x egg, n = the total number of eggs laid by the parasitoids and N = the total number of hosts present during the experiment.

The estimated Nx's were summed for all individuals tested at each host density to obtain the predicted overall distribution to be compared with the observed overall distribution using the chi-square test of goodness of fit.

4.3 FECUNDITY RESULTS

Fecundity is shown as age specific fecundity (Mx) in Figure (4.1) The mean number of aphids parasitized per female increased rapidly and reached a peak on day 2 of adult life, the peak was followed by a gradual decline. This basic pattern of aphid parasitization was consistent for all but the lowest host density. When only 5 aphid/day were provided to the parasite, the parasitization rate varied little, although a minor peak was evident on day 2. A majority of all aphids were parasitized during the first 4 days for the two lowest densities and over the first 3 days for higher densities. The total number of aphids parasitized during the parasitoid's life time varied greatly ($P<0.05$) with the density of aphids (Table 4.1).

4.4 LONGEVITY RESULTS

Longevity is shown as age specific survival (Lx) in Figure (4.2) The average life span was 7 days. Table (4.2) shows the value of the two Weibull parameters and the calculated Lt_{50} for A. matricariae at the 8 different densities. No significant difference ($P>0.05$) between the values of scale b at different densities were found. All values of shape parameter c, were bigger than 1. The time for 50% survival was almost similar. The

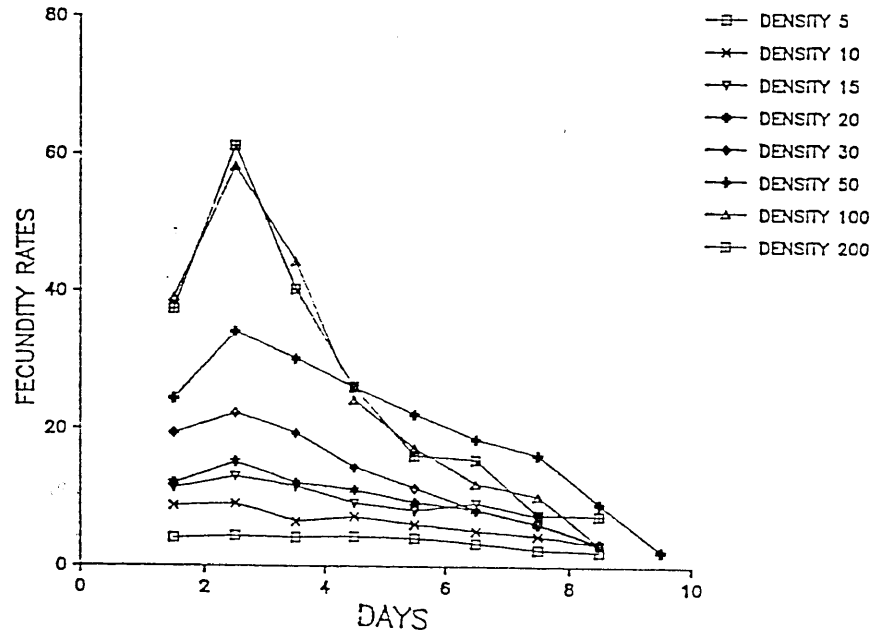


Figure 4.1 AGE SPECIFIC FECUNDITY OF A. matricariae AT DIFFERENT M. persicae DENSITIES

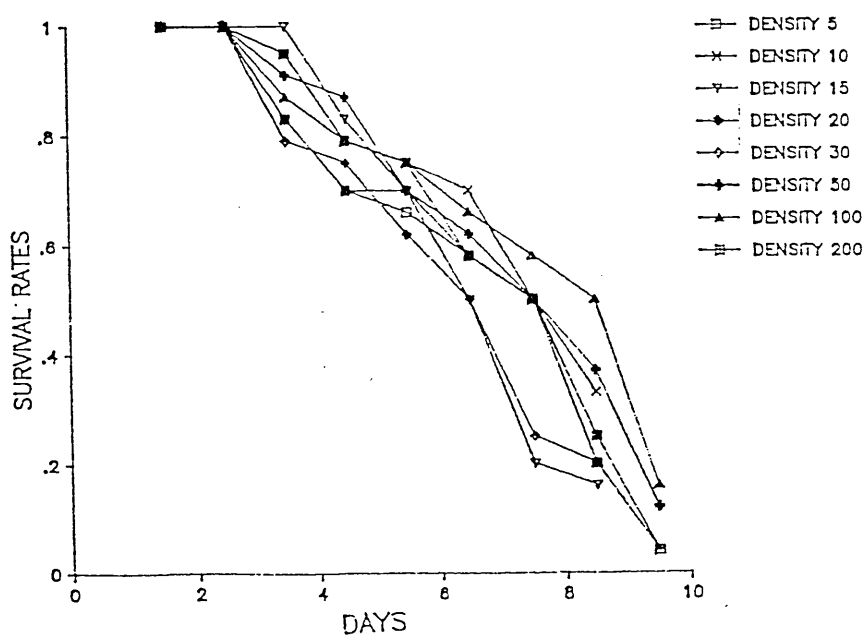


Figure 4.2 AGE SPECIFIC SURVIVAL OF A. matricariae AT DIFFERENT M. persicae DENSITIES

Table 4.1 EFFECT OF DENSITY ON FECUNDITY OF A. matricariae.

Density	Mean fecundity	s.e	l.s.d. 5% = 22.341
5	28.17	2.65	f
10	49.83	5.07	ef
15	69.33	7.84	de
20	76.83	7.59	d
30	102.16	3.74	c
50	181.66	14.54	b
100	207.00	7.6	a
200	210.33	7.3	a

Means with the same letters are not significantly different.

Table 4.2 ADULT LONGEVITY OF FEMALE A. matricariae: WEIBULL PARAMETERS FOR SURVIVAL CURVES AT VARIOUS APHID DENSITIES.

Density of M. persicae per box	b	c	Lt_{50}
5	6.92 a	2.66	6.03
10	8.48 a	2.49	7.32
15	7.34 a	2.96	6.49
20	7.36 a	2.53	6.37
30	6.58 a	2.73	5.75
50	7.89 a	2.58	6.85
100	7.87 a	2.52	6.81
200	7.32 a	2.77	6.42

Numbers followed by the same letter not significantly different at the 5% level (tables of Thoman & Bain, 1969).

survival rates and adult life span of the female parasitoid seemed to be independent of host density.

4.5 INTRINSIC RATE OF INCREASE RESULTS

The age specific survival (lx) and fecundity rates (mx) for each age interval (x) are given (Appendices 4.1-4.8). The demographic statistics of A. matricariae are given for each host density in Table (4.3) for a sex ratio of 1:1 and in Table (4.4) for a sex ratio of 1f:0m. The net reproductive rate (Ro) decreased almost 9 times as the host density decreased from 200 to 5. The intrinsic rate of increase, increases with host density reaching a value of 0.3495 female/female/day at density 200 aphids/day when 100% of progeny were assumed females. Or 0.3022 female/female/day when 50% of progeny were regarded females at the same density 200 aphids/day. The time required for the population to double in numbers was almost twice as long at the lowest than at the highest host density. The increase in rm is manifested in the finite rate of increase (Figure 4.3). The mean generation time was not influenced by host density.

The amount of contribution of each age group to the value of rm for A. matricariae at different densities of its host aphid and two sex ratios are presented (Appendices 4.9 - 4.16). The results demonstrate that the value of rm was largely determined, over 80% contribution, by the first 4 days of adult life. At density 50, a contribution of 88-89% to the value of rm was accounted for in the first 4 days of adult life, even though only 62.7% of the total number of young was produced during this time. This phenomenon became more pronounced at high densities.

When rm values are plotted against natural logarithms of host density, the regression lines for the two sex ratios were found to be parallel to each other (Figure 4.4).

Table 4.3 DEMOGRAPHIC STATISTICS OF A. matricariae WITH A SEX RATIO OF 1:1 REARED AT DIFFERENT DENSITIES OF M. persicae APHIDS.

Host density	Reproductive rate G.R.R.	Ro	Rate of increase rm	λ	Generation time T	Doubling time D.T.
5	14.45	10.671	0.1513	1.16	15.65	4.58
10	25.15	20.748	0.1953	1.22	15.53	3.55
15	34.95	27.733	0.2174	1.24	15.28	3.19
20	38.75	30.153	0.2218	1.25	15.36	3.13
30	52.15	40.5695	0.2461	1.28	15.05	2.82
50	91.40	73.637	0.2782	1.32	15.45	2.49
100	104.15	91.6225	0.3018	1.35	14.97	2.30
200	105.8	91.938	0.3022	1.35	14.96	2.29

G.R.R. = gross reproductive rate, Ro = net reproductive rate, r_m = intrinsic rate of increase, λ = finite rate of increase.

Table 4.4 DEMOGRAPHIC STATISTICS OF A. matricariae WITH A SEX RATIO OF 1F:0M REARED AT DIFFERENT DENSITIES OF M. persicae APHIDS.

Host density	Reproductive Rate G.R.R.	Ro	Rate of increase rm	λ	Generation time T	Doubling time D.T.
5	28.9	21.341	0.1963	1.22	15.59	3.53
10	50.3	41.131	0.2415	1.27	15.39	2.87
15	69.9	55.466	0.264	1.30	15.21	2.63
20	77.5	60.304	0.2679	1.31	15.30	2.59
30	104.3	81.139	0.2934	1.34	14.98	2.36
50	182.8	147.273	0.3244	1.38	15.39	2.14
100	208.3	183.245	0.3489	1.42	14.96	1.99
200	211.6	183.874	0.3495	1.42	14.92	1.98

G.R.R. = gross reproductive rate, Ro = net reproductive rate, r_m = intrinsic rate of increase, λ = finite rate of increase.

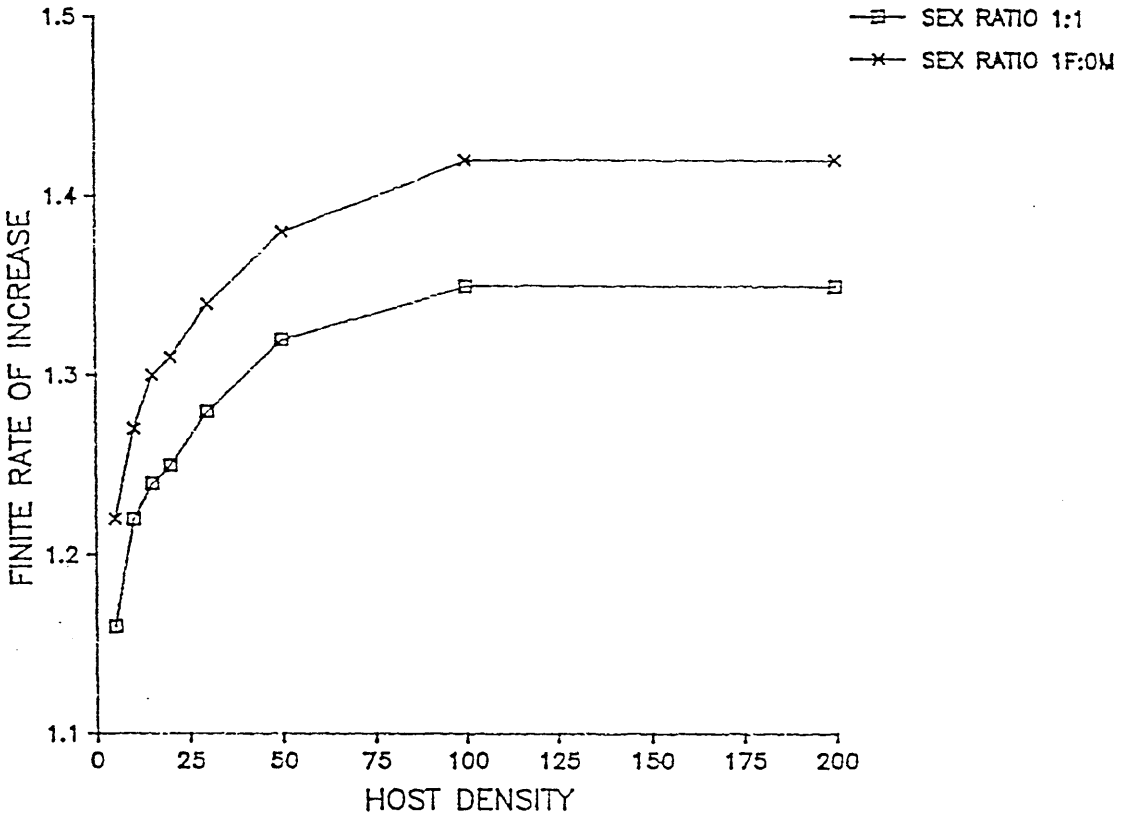


Figure 4.3 THE RELATIONSHIP BETWEEN THE FINITE RATE OF INCREASE OF A. matricariae AND M. persicae HOST DENSITY

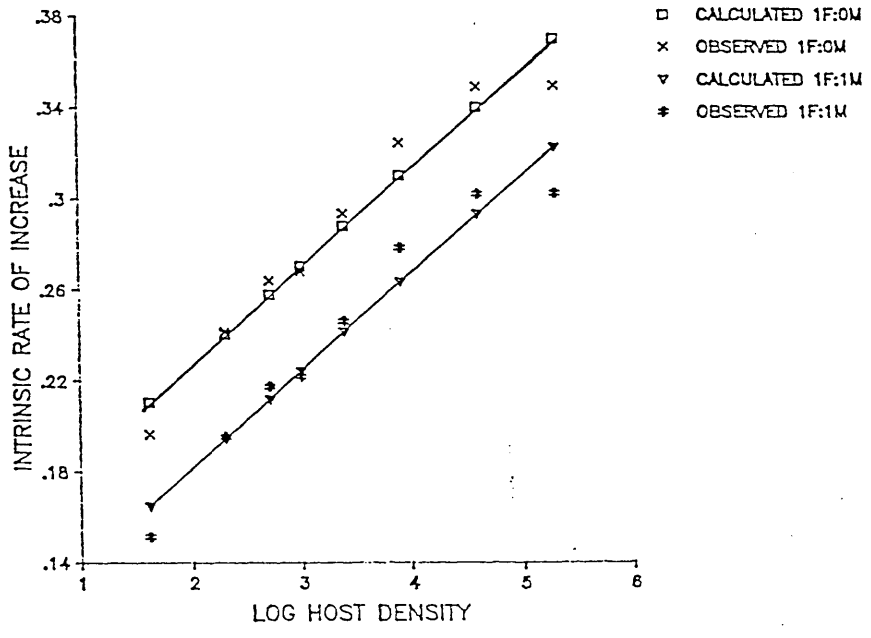


Figure 4.4 THE RELATIONSHIP BETWEEN THE INTRINSIC RATE OF INCREASE OF A. matricariae AND M. persicae HOST DENSITY

4.6 FUNCTIONAL RESPONSE RESULTS

The relationship between life time total fecundity of A. matricariae and host density is shown in Figure (4.5). The number of hosts parasitized increases as host density increases but the rate of increase declines eventually to stabilise at the asymptotic maximum value. This means the rate of increase declines towards a limit imposed probably by the parasitoid's egg supply. Since the mean number of parasitized aphids ceased to increase with host density when the latter passes 100 aphid/day, it is evident that A. matricariae shows a Holling type 2 functional response in which the rate of attack declined with increasing host density. Detailed functional response data are obtained by plotting the mean number of aphids parasitized per female per 24 hours exposure of the 2nd day of parasitoid life time, on which daily fecundity reaches its maximum, against host density. Again a type 2 functional response was obtained (Figure 4.6). That is the response rises at a constantly diminishing rate towards a plateau leading to a reduction in the percentage parasitization with increase in host density (Figure 4.7).

The functional response of A. matricariae under the latest experiment set-up was analysed using the Holling (1959) disc equation. The estimated values of search rate (a) and handling time (Th) were as follows

1. By linear regression of Holling (1959) which was significant $F_{1,6}$ = 36.295 ($P<0.01$) giving the value of handling time as 0.008972 days and the search rate as 0.9458 per box per day.

2. By using least square regression to the linear transformation of Livdahl & Stiven (1983) which was significant $F_{1,6}$= 2133.5 ($P<0.01$) giving the value of handling time as 0.00796 days and the search rate as 1.082 per

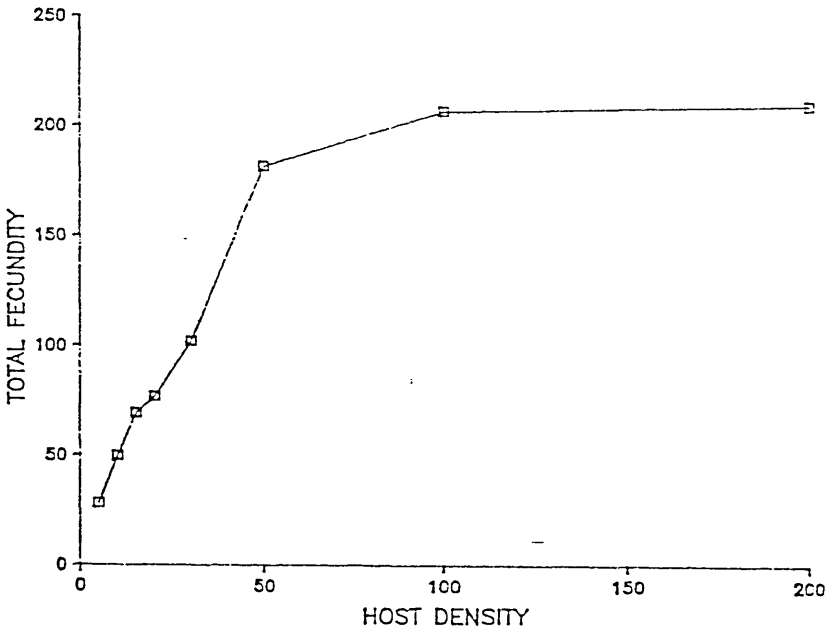


Figure 4.5 THE RELATIONSHIP BETWEEN LIFE TIME TOTAL FECUNDITY AND HOST DENSITY

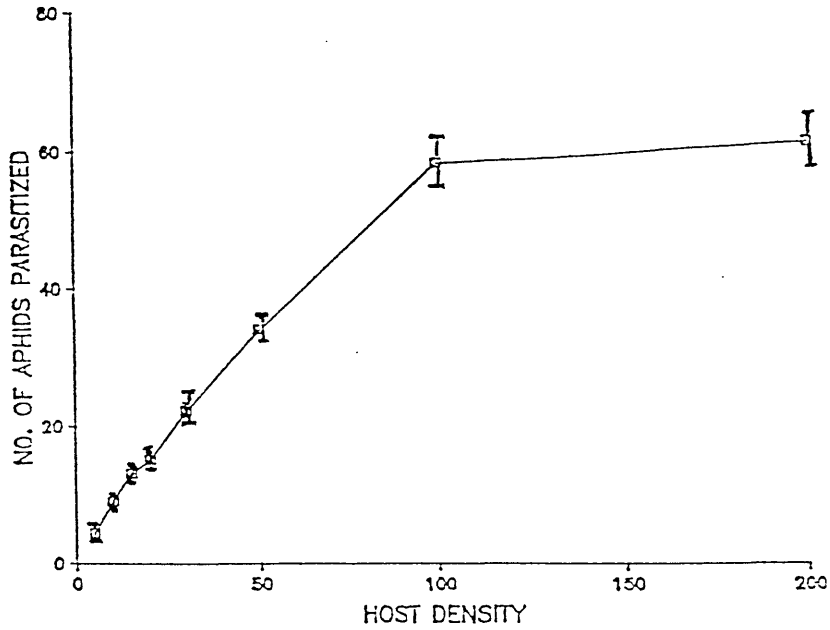


Figure 4.6 FUNCTIONAL RESPONSE CURVE OF A. matricariae FOR THE SECOND DAY PARASITIZATION.

Bars = standard errors

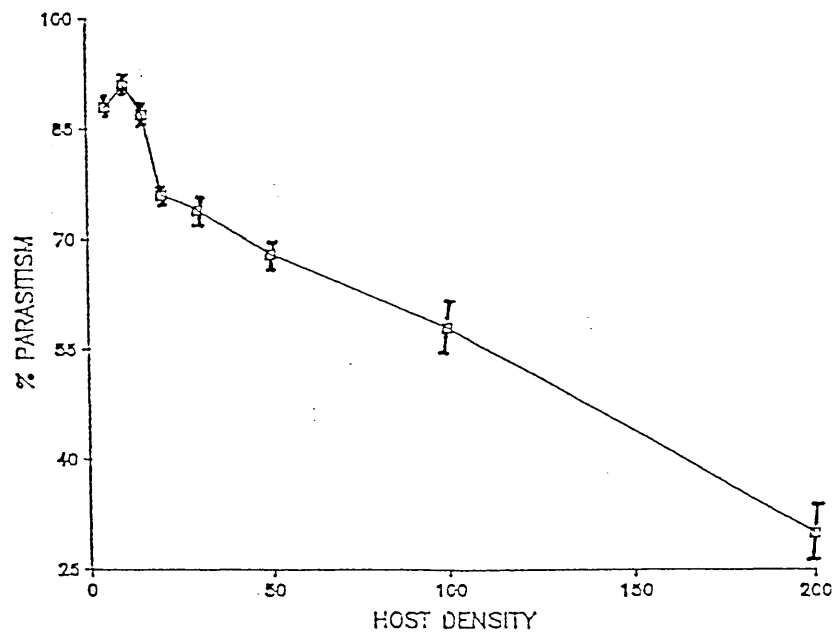


Figure 4.7 THE RELATIONSHIP BETWEEN PERCENTAGE PARASITISM AND HOST DENSITY DURING THE SECOND DAY PARASITIZATION

Bars = standard errors

box per day.

3. By using the linearized form of random parasitoid equation (Messenger, 1968; Royama, 1971; Rogers, 1972) which gave significant relationship $F_{1,6}$= 153.107 ($P<0.01$) from the regression equation (Figure 4.8) the value of A = -0.340884 stands for elevation and B = -0.011247 intercept. The handling time (Th) is computed as Th = -B = 0.011247 days, the searching rate (a) is calculated as a = -1/A = -1/-0.340884 = 2.9335 per box per day.

There was no need to correct the values of search rate and handling time for the diel period as the experiment was carried out in continuous illumination. The curves in Figures (4.9, 4.10, 4.11) were calculated from Holling, Livdahl and random estimations respectively. The chi-square goodness of fit test shows that the curves calculated using the 3 methods of estimates fit the observed date well. χ^2 = 2.239 ($P>0.05$), χ^2 = 5.91008 ($P>0.05$) and χ^2 = 1.837 ($P>0.05$) for Holling linearization, Livdahl linearization and random parasitoid linearization respectively. This indicates that the departure of data from the curve is in no case significant ($P>0.05$). The predicted number of aphids parasitized were very close with the observed ones in every case (Tables 4.5, 4.6 & 4.7), especially with random equation linearization.

To determine whether the functional response of the parasitoid changed through adult life, a detailed analysis was carried out for the first five days of adult life time (Figure 4.12). In general the number of aphids parasitized decreased over time. The trend of decrease in the numbers of aphids parasitized was apparent at host density 200. In comparison with 2nd day, the parasitized aphids were less than half on the 4th day and only a quarter on the 5th day. The random parasitoid equation (Royama, 1971; Rogers, 1972) fits the data well for the five days of adult life, the predicted and observed values are given (Tables 4.8, 4.9, 4.10 & 4.11). A

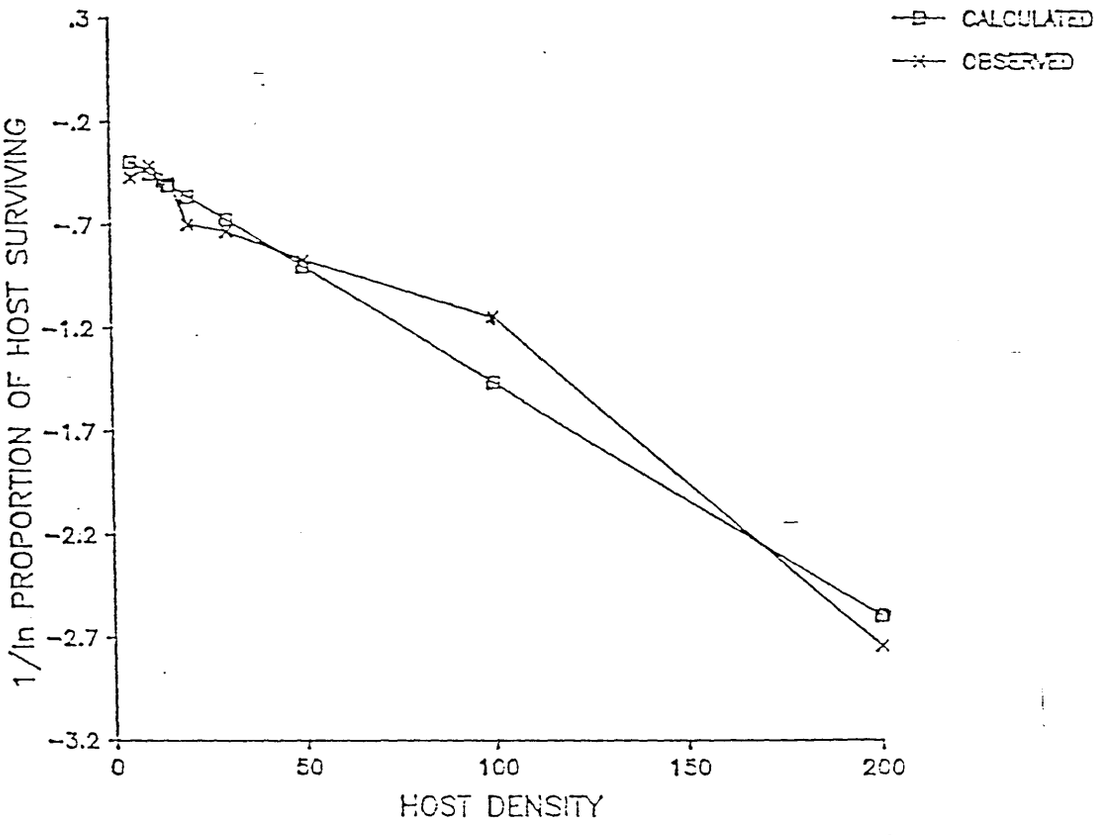


Figure 4.8 THE LINEAR REGRESSION OF 1/In (PROPORTION OF APHIDS SURVIVING) AGAINST HOST DENSITY

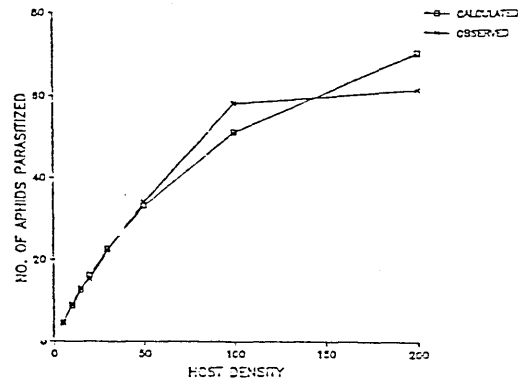


Figure 4.9 FUNCTIONAL RESPONSE CURVE FOR A. matricariae FOR THE SECOND DAY PARASITIZATION CALCULATED FROM THE HOLLING EQUATION USING THE HOLLING LINEARIZATION

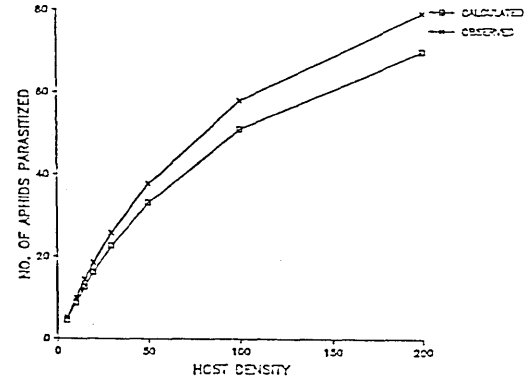


Figure 4.10 FUNCTIONAL RESPONSE CURVE FOR A. matricariae FOR THE SECOND DAY PARASITIZATION CALCULATED FROM THE HOLLING EQUATION USING THE LIVDAHL LINEAR TRANSFORMATION

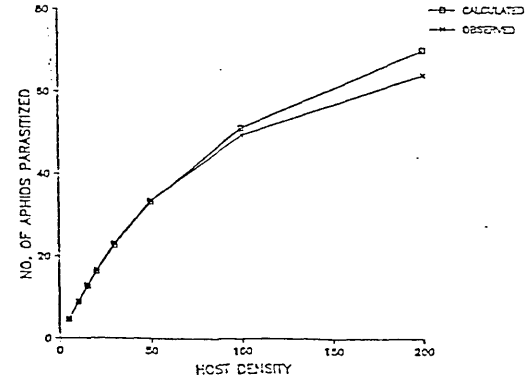


Figure 4.11 FUNCTIONAL RESPONSE CURVE FOR A. matricariae FOR THE SECOND DAY PARASITIZATION CALCULATED FROM THE RANDOM PARASITOID EQUATION

Table 4.5 EXPECTED NUMBER OF ATTACKS AS PREDICTED FROM HOLLING EQUATION USING HOLLING LINEARIZATION FOR THE SECOND DAY PARASITIZATION BY A. matricariae.

Density	Observed no. attacked	Expected no. attacked	χ^2 goodness of fit
5	4.4	4.54	0.004
10	9.1	8.72	0.02
15	13.1	12.59	0.02
20	15.2	16.17	0.06
30	22.3	22.62	0.05
50	34.1	33.20	0.02
100	58.2	51.16	0.97
200	61.2	70.13	1.14
			2.239 NS

NS = nonsignificant at the 5% level, χ^2 d.f. = 7.

Table 4.6 EXPECTED NUMBER OF ATTACKS AS PREDICTED FROM HOLLING EQUATION USING LIVDAHL LINEARIZATION FOR THE SECOND DAY PARASITIZATION BY A. matricariae.

Density	Observed no. attacked	Expected no. attacked	χ^2 goodness of fit
5	4.4	5.19	0.12
10	9.1	9.96	0.07
15	13.1	14.38	0.11
20	15.2	18.46	0.58
30	22.3	25.77	0.47
50	34.1	37.81	0.36
100	58.2	58.13	0.00008
200	61.2	79.47	4.20
			5.91008 NS

NS = nonsignificant at the 5% level, χ^2 d.f. = 7.

Table 4.7 EXPECTED NUMBER OF ATTACK AS PREDICTED FROM THE RANDOM PARASITOID EQUATION FOR THE SECOND DAY PARASITIZATION BY A. matricariae.

Density	Observed no. attacked	Expected no. attacked	χ^2 goodness of fit
5	4.4	4.60	0.009
10	9.1	8.90	0.004
15	13.1	12.89	0.003
20	15.2	16.58	0.11
30	22.3	23.13	0.03
50	34.1	33.48	0.011
100	58.2	49.46	1.54
200	61.2	64.06	0.13
			1.837 NS

NS = nonsignificant at the 5% level, χ^2 d.f. = 7.

Table 4.8 EXPECTED NUMBER OF ATTACKS AS PREDICTED BY THE RANDOM PARASITOID EQUATION FOR THE FIRST DAY PARASITIZATION BY A. matricariae.

Density	Observed no. attacked	Expected no. attacked	χ^2 goodness of fit
5	4.1	4.4	0.02
10	8.8	8.2	0.04
15	11.4	11.4	0.00
20	12.1	14.3	0.34
30	19.4	18.8	0.019
50	25.1	25.1	0.00
100	39.1	33.0	1.13
200	37.4	39.0	0.066
			1.615 NS

NS = nonsignificant at the 5% level, χ^2 d.f. = 7.

Table 4.9 EXPECTED NUMBER OF ATTACKS AS PREDICTED BY THE RANDOM PARASITOID EQUATION FOR THE THIRD DAY PARASITIZATION BY *A. matricariae*.

Density	Observed no. attacked	Expected no. attacked	χ^2 goodness of fit
5	4.2	4.23	0.0002
10	6.5	7.98	0.27
15	11.6	11.28	0.009
20	12.1	14.19	0.31
30	19.4	19.04	0.0068
50	30.2	26.02	0.67
100	44.3	35.50	2.18
200	40.3	43.10	0.18
			3.626 NS

NS = nonsignificant at the 5% level, χ^2 d.f. = 7.

Table 4.10 EXPECTED NUMBER OF ATTACKS AS PREDICTED BY THE RANDOM PARASITOID EQUATION FOR THE FOURTH DAY PARASITIZATION BY *A. matricariae*.

Density	Observed no. attacked	Expected no. attacked	χ^2 goodness of fit
5	4.3	4.2	0.0024
10	7.2	7.6	0.02
15	9.2	10.3	0.117
20	11.1	12.4	0.136
30	14.4	15.6	0.09
50	26.0	19.5	2.17
100	24.2	23.7	0.011
200	26.1	26.6	0.0094
			2.556 NS

NS = nonsignificant at the 5% level, χ^2 d.f. = 7.

Table 4.11 EXPECTED NUMBER OF ATTACKS AS PREDICTED BY THE RANDOM PARASITOID EQUATION FOR THE FIFTH DAY PARASITIZATION BY A. matricariae.

Density	Observed no. attacked	Expected no. attacked	χ^2 goodness of fit
5	4.1	4.5	0.036
10	6.1	7.5	0.26
15	8.1	9.4	0.18
20	9.3	10.8	0.21
30	11.4	12.5	0.10
50	14.3	14.3	0.00
100	17.2	15.9	0.11
200	16.2	16.8	0.02
			0.916 NS

NS = nonsignificant at the 5% level, χ^2 d.f. = 7.

Table 4.12 COMPARISON OF FUNCTIONAL RESPONSE PARAMETERS OF A. matricariae FOR THE FIRST FIVE DAYS OF ADULT LIFE CALCULATED BY THE RANDOM PARASITOID EQUATION

Days	Searching rate	Handling time	χ^2
first day	2.658	0.02122	1.615 NS
Second day	2.934	0.011247	1.837 NS
Third day	2.267	0.018407	3.626 NS
Fourth day	2.696	0.033175	2.556 NS
Fifth day	5.942	0.056113	0.916 NS

NS = nonsignificant at the 5% level, χ^2 d.f. = 7.

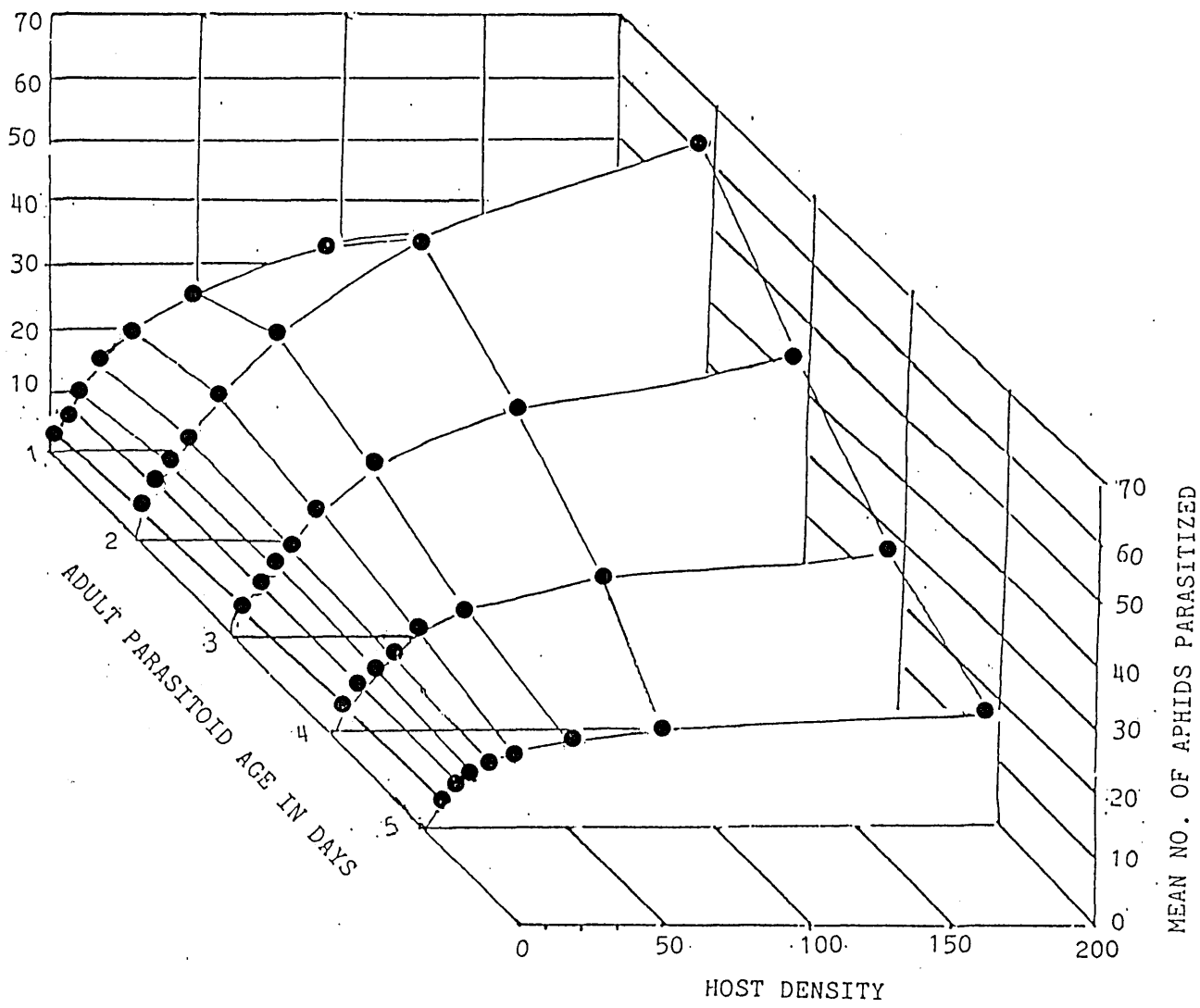


Figure 4.12 MEAN NUMBERS OF APHIDS PARASITIZED DAILY BY A. matricariae DURING THE 5 FIRST DAYS OF ADULT LIFE AT DIFFERENT HOST DENSITIES

comparison of functional response parameters, handling time and rate of search of A. matricariae during the first five days is shown in table (4.12). The estimates of (a) and (Th) increased insignificantly from the first to fourth day but differed greatly on the 5th day for searching rate.

4.7 SUPERPARASITIZATION RESULTS

Table (4.13) illustrates the degree of superparasitization as the percentage of aphids superparasitized and the number of parasitoid larvae per parasitized aphid. The percentage of hosts parasitized was high when fewer than 15 hosts were available (87-91%), but it decreased with host density to 30.6% at the highest density of 200. Superparasitization also was most pronounced at aphid density 5 (80%) and decreased with increase in density to reach 2.5% at density 200. The high degree of superparasitization at density 5 is also linked with high number of parasitoid larvae per parasitized aphid at this density.

The frequency distribution of parasitoid larvae in their host aphids for the 8 host densities, where the observed and calculated binomial random distributions are compared are presented in Table (4.14) and Figure (4.13). The results show that, at low host densities where the percentage parasitization was so high, the difference between observed and random distributions was not significant. The chi-square goodness of fit test indicates that the departure of observed distribution from the calculated one is in no case significant ($P>0.05$) at 5, 10, 15 and 30 densities. A significant difference ($P<0.05$) from random distribution was found at 20 and 50 densities. A highly significant difference from random was found at 100 density ($P<0.001$) and at 200 density ($P<0.01$). This difference from random is due to the observed high frequency of aphids with one parasitoid larvae than expected from random. As density increases more hosts were attacked than expected according to random hypothesis which suggests A. matricariae avoids the already parasitized hosts at high densities.

Table 4.13 EFFECT OF M. persicae APHID DENSITIES ON PARASITIZATION BY A. matricariae.

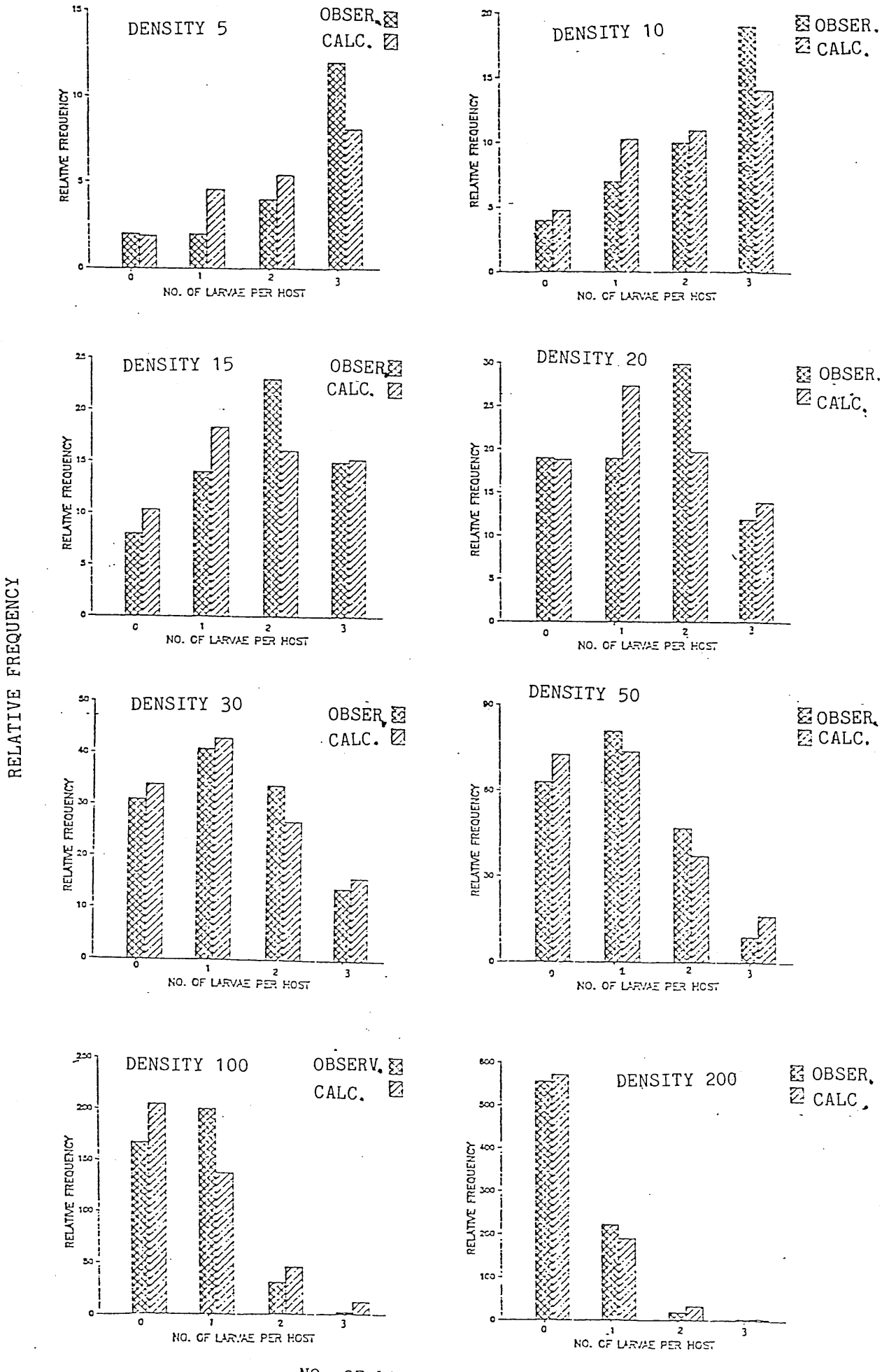
Density of aphids	Average no. of of larvae laid per female		Average no. of larvae per aphid		Average no. of larvae per parasitized aphid		% of aphids parasitized	% of aphids super-parasitized
	x	s.e.	x	s.e.	x	s.e.		
5	16.8	1.5	3.4	0.3	3.8	0.3	88.0	80.0
10	22.3	2.9	2.2	0.2	2.5	0.4	91.0	72.5
15	25.5	4.4	1.7	0.3	1.9	0.3	87.3	63.5
20	29.5	2.7	1.5	0.2	1.9	0.2	76.0	52.5
30	34.5	3.6	1.2	0.1	1.5	0.1	74.3	40.0
50	48.8	4.4	0.98	0.09	1.4	0.09	68.2	28.0
100	66.8	7.8	0.67	0.08	1.1	0.08	58.2	08.0
200	65.0	9.6	0.33	0.05	1.1	0.09	30.6	02.5

Table 4.14 DISTRIBUTION OF LARVAE OF A. matricariae AT EIGHT DENSITIES OF ITS HOST M. persicae TESTED AGAINST RANDOM BINOMIAL MODEL.

Density of aphids	Observed no. of larvae				Predicted no. of larvae by binomial model				χ^2 goodness of fit	
	0	1	2	>2	0	1	2	>2		
5	2	2	4	12	1.89	4.57	5.42	8.12	3.677	NS
10	4	7	10	19	4.77	10.27	10.93	14.03	3.005	NS
15	8	14	23	15	10.35	18.34	16.07	15.25	4.557	NS
20	19	19	30	12	18.83	27.41	19.75	14.01	8.555	*
30	31	41	34	14	33.93	43.04	26.96	16.07	2.656	NS
50	63	81	47	9	72.66	73.75	37.25	16.34	7.849	*
100	167	200	31	2	204.5	137.37	45.96	12.16	48.797	***
200	555	224	18	3	571.44	192.39	32.21	3.97	12.174	**

χ^2 d.f. = 3, NS = nonsignificant at the 5% level, * = ($P<0.05$), ** = ($P<0.01$), *** = ($P<0.001$).

Figure 4.13 OBSERVED AND CALCULATED RANDOM BINOMIAL LARVAL DISTRIBUTION OF A. matricariae AT 8 DENSITIES OF THE HOST M. persicae


DENSITY 5
OBSER.
CALC.
DENSITY 10
OBSER.
CALC.
DENSITY 15
OBSER.
CALC.
DENSITY 20
OBSER.
CALC.
DENSITY 30
OBSER.
CALC.
DENSITY 50
OBSER.
CALC.
DENSITY 100
OBSERV.
CALC.
DENSITY 200
OBSER.
CALC.
RELATIVE FREQUENCY
NO. OF LARVAE PER HOST
RELATIVE FREQUENCY
NO. OF LARVAE PER HOST

4.8 DISCUSSION

4.8.1 LIFE SPAN, FECUNDITY AND INTRINSIC RATE OF INCREASE

The results and analysis indicate that the change in density of host aphid M. persicae seems to have no effect on longevity of A. matricariae, as no significant difference ($P>0.05$) between the values of scale b parameter was found. The values of shape parameter c were almost similar and bigger than 1 for all densities indicating type 1 survivorship curve in which the age specific mortality rate increases with increase in time, in other words, the survivorship curves are an increasing function of age (Pinder et al., 1978). Fecundity of the parasitoid is strongly influenced by changes in host density. Although the basic pattern of parasitization was consistent for all except for 5 aphid/day density but the total number of aphids parasitized during parasitoid's life time differed greatly ($P<0.05$) with change in host density.

As survival rates were similar, differences in intrinsic rate values at different host aphid densities were caused mainly by variations in the number of young produced per female per density. Because the fecundity pattern and age specific survival were similar at different densities, host density showed no effect on generation time (Tables 4.3 & 4.4). The number of hosts parasitized differ directly with host density, hence rm vary accordingly. Temperature was used (Section 3) to show the way in which rm may be changed by climatic factors. The present results illustrate the way in which rm may be altered by changes in a biofactor, density. However, any biotic factor that influences any one or more of the components of rm that is fecundity, longevity and development time will cause rm to vary accordingly. The results also suggest the sex ratio to be an important biofactor, e.g. at host density 100, a 50% decrease in females led to 13.5% decrease in value of rm. Because the Mx values were corrected for sex ratio by multiplying with a constant value, the regression lines for the two sex

ratios were parallel to each other when rm is plotted against log density (Figure 4.4).

The values of rm obtained provided a direct comparison of intrinsic rate of increase of A. matricariae under different host densities. Thus rm as a single quantitative figure is useful as indicator of actual population growth under different densities. As the parameter rm was used as an ecological index (climatic index) by Messenger (1964b), it can be also used as a bio-index as a quantitative measure of the response of the species to a particular biotic factor. Data about the effect of host density on intrinsic rate of increase of A. matricariae was not found in the literature to make comparison possible. The results are comparable with that found for other aphidiid species. Mackauer (1983) reported for A. smithi parasitizing different densities of the pea aphid A. pisum that rm = 0.358 at density 100 assuming an overall sex ratio of 50% females among the progeny of A. smithi and rm = 0.168 at 5 aphid/day assuming the same sex ratio. The present results are 0.3018 and 0.1513 for densities 100 and 5 aphid/day respectively when 50% of progeny are assumed females. Liu Shu-sheng (1985) found rm to equal 0.1730 at host density 10 which increased to 0.3720 at host density 200 for A. sonchi on sowthistle aphid H. lactucae with an assumed overall sex ratio of 70% females among the progeny. The present results show rm to increase from 0.2415 at density 10 to 0.3495 at density 200 of aphids but with an overall sex ratio of 100% females.

4.8.2 FUNCTIONAL RESPONSE

The functional response of a predator is an important concept for the understanding of the dynamics of predator-prey systems (Lundberg, 1988). Analysis of functional responses have also been applied to host-parasitoid system (Messenger, 1968; Hassell et al., 1977). Mathematical models which describe the outcome of searches for hosts by insect parasitoids need a component which defines the ability of parasitoid to attack a host

population. The two parameters which make up this component are the instantaneous attack rate (a) and the handling time (Th) of the parasitoid. Hassell & May (1973) suggest that estimation of these parameters is of value in comparing potential parasitoids for bio-control programmes. The absence of an alternative model necessitates the use of Holling's (1959b) disc equation and random parasitoid equation of Messenger (1968), Royamma (1971) and Rogers (1972).

Holling's equation assumes that the parasitoid searches at random and that all hosts have the same probability of being encountered regardless of host distribution. Although this assumption does not fit very well for aphids which tend to be patchily distributed especially under natural conditions. The models are still appropriate for situations where aphids of uniform age 3-4th instar, have been introduced into a box and have settled at random on the host seedlings. The Holling's model has been subject to criticism by Messenger (1968) for not allowing the depletion of available prey during the course of predation. Therefore the random parasitoid equation of Royama (1971) and Rogers (1972) which permit the exploitation of the host was used as well. The validity of the random equation has been questioned. The linear transformation for fitting the disc equation or random parasitoid equation breaks assumptions required by regression analysis, the independent variables are not independent (Livdahl & Stiven, 1983; Houck & Strauss, 1985). Livdahl & Stiven suggested the use of an alternative linear transformation as a solution to this problem, which is also used in the analysis.

Parasitization rate increased in a non-linear manner as host density increased indicating a type 2 functional response of Holling (1959a) (Figure 4.6). But the curve was almost straight in the 3 lower densities. This kind of response which is almost linear at first then levelling off more rapidly than the model predicts has been witnessed by a number of workers

(Messenger, 1968; Dransfield, 1979). It is explained by the oviposition pattern of aphidiids. The oviposition pattern of A. matricariae (Section 2) occurs in cycles of activity during which successive attacks take place alternated by periods of rest. As time goes on rest periods become more frequent and prolonged. The actual handling time for A. matricariae is not more than 1-2 seconds. The resting period is included in handling time. If at low host densities these resting periods are not longer after more aphids have been parasitized the proportion of time spent searching will not significantly decrease with increasing density and thus the relationship of number attacked to density will be linear. Above certain host densities when oviposition is frequent the resting periods are likely to be much longer to allow maturation of ova, resulting in a rapid levelling off of the curve (Dransfield, 1979). The type of functional response found is similar to that reported for many aphidiids. Hart, De Jonge, Colle, Dicke, van Lenteren and Ramarks (1978) reported for A. matricariae with a maximum density of 32 aphids on a paprika leaf, using a very small arena of 23.76 cm^2 that there is an increase in the number of parasitizations with increasing host density and the percentage parasitized decreased. They reached this conclusion with only visual fitting of the curve without an attempt to fit a model. Messenger (1968) found a type 2 functional response for Praon exsoletum (Nees) on spotted alfalfa aphid Therioaphis maculata (Buckton). Dransfield (1979) obtained a curvilinear type 2 response for Aphidius urticae (Haliday) parasitizing cocksfoot aphid Hyalopteroides humilis (Walker). Mackauer (1983) found a convex Holling type 2 response for A. smithi on the pea aphid A. pisum. A type 2 functional response was also found for A. sonchi on H. lactucae (Liu Shu-sheng, 1985). Hofsvang & Hagvar (1983a) suggested a type 2 functional response for Ephedrus cerasicola Stary parasitizing M. persicae during 1 hour exposure.

Hassell et al., (1977) argued against the notion that type 2 functional response are typical of invertebrate predators and suggested that sigmoid

type 3 responses may be much more common than previously thought. There are increasing reports of type 3 functional responses in invertebrates (Murdoch & Oaten, 1975; Dransfield, 1979; Shirota et al., 1983). However, Livdahl & Stiven (1983) claim that no studies in which this departure from type 2 functional response has actually been tested statistically. Examples of sigmoid functional responses (Murdoch & Oaten, 1975; Hassell et al., 1977) have relied heavily on visual inspection (Livdahl & Stiven, 1983). The type 3 response is of interest because it is the only response that causes the percentage of hosts parasitized to increase with the initial increase in host density and hence theoretically the only one that can contribute to host regulation over this lower range of host densities. It is expected when an increase in host density results in a decrease in handling time and/or increase in search rate and /or increased total time in the patch (Hofsvang & Hagvar, 1983a). Type 2 functional response can not contribute to the stability of predator-prey interactions (Hassell & May, 1974; Murdoch & Oaten, 1975). It therefore follows that if the predator has a type 2 functional response, stability results from other components affecting the predator or prey (Hassell et al., 1977). Sigmoid functional responses are density dependent up to some threshold prey density and may contribute to stability if average prey densities fall below this. For this reason many studies have been concerned merely with determining the shape of functional response curve by the parasitoid with the hope of estimating its ability or inability to regulate populations.

The linear regressions of Holling (1959b) and Livdahl & Stiven (1983) for the disc equation and the linear regression of Royama (1971) and Rogers (1972) for the random parasitoid equation were subject to criticism for yielding biased estimates (Williams & Juliano, 1985). Although, linear regressions were found appropriate and desirable when relative estimates of attack rate and handling time are sought. However, the predicted values of parasitized aphids found under the present study using linear regressions

estimates were generally in agreement with the observed mean numbers of aphids parasitized at each host density ($P>0.05$, χ^2 goodness of fit). The parameters of handling time (Th) and rate of search (a) for the 2nd day parasitization for A. matricariae were estimated from Holling equation (1959b) using Holling linearization and Livdahl & Stiven (1983) linearization and from the random parasitoid equation (Royama, 1971; Rogers, 1972). The predictions from the random parasitoid equation were found more accurate (χ^2 goodness of fit = 1.837 N.S.). Therefore the random parasitoid equation was used to estimate the handling time and searching rate parameters for the other 4 days of life time fecundity of A. matricariae. It was found that the random parasitoid equation fits the observed data well for all the 5 days tested and the departure of data from the calculated curve is in no case significant ($P>0.05$). The handling time and rate of search for the second day parasitization of A. matricariae were found to be 0.011247 days (16.20 minutes) and 2.9335 per box per day respectively using random parasitoid equation (Rogers, 1972).

Different times of exposure , cage volumes, host plant, host aphid species and parasitoid species make comparisons with previous results difficult. However, no data for these parameters were found in the literature for A. matricariae. The results are favourably compared with other aphidiid species using the random parasitoid equation (Royama, 1971; Rogers, 1972). Dransfield (1979) on his study on A. urticae on H. humilis obtained 0.0104 days for handling time and 1.11 per container per day for rate of search. Mackauer (1983) reported the handling time to equal 0.0033 days and rate of search to equal 6.62 per arena per day for A. smithi on A. pisum. Liu Shu-sheng (1985) found it to be 16.10 minutes for the handling time and 11.60 for rate of search for A. sonchi parasitizing H. lactucae. It should be noticed that the true handling time observed for A. matricariae is not more than 2 seconds. But the handling time estimated from the equation includes a resting period, so it lies within the handling time range reported in

literature. Handling time theoretically is the factor limiting parasitization rate. Therefore the maximum potential parasitization rate can be estimated from the handling time. The parasitization rate must eventually be limited by either handling time or egg complement (Holling, 1959b). The estimated handling time of 16.20 minutes suggests that A. matricariae can potentially parasitize 90 aphids/day. This implies that the total egg complement and not the handling time is the limiting factor for maximum parasitization. The search rate of the parasitoid and area searched in unit time, is useful in determining the bility of parasitoid to locate suitable hosts even at low host densities. The effectiveness of a parasitoid is measured in part by its ability to locate hosts efficiently at low host densities and to parasitize large number of hosts at high densities (Huffaker & Messenger, 1976). According to Holling (1959b, 1966) the proportion of total time spent in handling hosts must increase as host density increases and more hosts are found. The consequent reduction in time spent searching must reduce the searching efficiency at high host densities. A. matricariae parasitized average host densities of 88, 91 and 87% of hosts at the 3 lowest densities of 5, 10 and 15 aphids/day respectively suggesting that it was an effective parasitoid at low densities. Small and simplified arenas were used in this study as they have been in many functional response studies in the literature. Although, search rates estimated in such arenas are of restricted value in describing search rates under glasshouse conditions, they indicate that A. matricariae is a potentially effective parasitoid.

Short term functional response experiments in many cases present an oversimplified picture. Therefore examination of the ability of a parasitoid to respond to changes in host densities over their entire life history was conducted. Figure (4.6) shows that A. matricariae exhibits a functional response to increasing host density by parasitizing more hosts but the parasitization rises at a decelerating rate as host density

increases indicating a type 2 functional response. A similar curvilinear type 2 functional response was found separately for each day for the first 5 days of adult life (Figure 4.12). The results show that handling time and searching rate change as a female parasitoid increases in age. Time is an important factor, a consequence of it is that the parasitoid age increases and this may result in changes in their physiological condition and hence modify their attack rate. This should be expected from the pattern of age specific fecundity of A. matricariae in which egg-laying increases rapidly to reach maximum on 2nd day and then declines rapidly. The type of response may change if the time of exposure at different densities is not fixed (van Lenteren & Bakker, 1976). Despite the fact that handling time and searching rate were not constant throughout time, the random parasitoid equation (Rogers, 1972) gave a good fit to the functional response data for the 1st, 2nd, 3rd, 4th and 5th day of adult parasitoid life.

A fit to the disc equation does not mean that the parasitoid behaves in the manner assumed in deriving the equation. Fox and Murdoch (1978) observed a reasonable conformity of their data with the disc equation although they were able to judge through direct observation that handling time and attack rate were not constant through time. Although the biological assumptions of the disc equation appear rigid, the disc equation described laboratory data fairly well. Livdahl & Stiven (1983) stated that conformity of experimental results with the disc equation indicates either that the assumptions are not frequently violated, that their violation does little to alter the basic form of the relationship or that the estimated parameters serve in an adequate predictive capacity even if they do not in fact estimate precisely the qualities that they claim to stand for. The variation in functional response parameters through time has also been observed by Mackauer (1983) for A. smithi and by Liu Shu-sheng (1985) for A. sonchi. The functional response of E. cerasicola parasitizing M. persicae on paprika plant was curvilinear when the exposure time was only 1 hour and

changed to linear when exposure time increased to 6 hours (Hofsvang & Hagvar, 1983a). The rate of attack and handling time were also found to change with other factors. Dransfield (1979) demonstrated that Aphidius uzbekistanicus Luzhetski has a convex Holling type 2 functional response when parasitizing the preferred cereal aphid Metopolophium dirhodum Walker but a sigmoid Holling type 3 response when parasitizing the less preferred H. humilis. Cook & Hubbard (1980) showed that both handling time and rate of search declined as host density increased for Nemeritis canescens (Grav.) on the flour moth Plodia interpunctella Hubner. Several other factors, both internal and external, have been shown to influence response curves, e.g prey size (Thompson, 1975), prey defence (Morris, 1963) and hunger (Holling, 1959b).

These factors suggest that it is unreasonable to expect a single curve to be representative of the full range of responses by a parasitoid to host density. In laboratory many of the above factors are controlled. The response is usually measured in a simple environment and in the absence of many factors that could potentially alter the form of response. A single parasitoid species may exhibit several different types of functional responses each with a different implication to the interaction and to the biological control potential of the parasitoid (Murdoch & Oaten, 1975; Hassell et al., 1977). Therefore a single functional response may provide an inadequate or incomplete description of the whole parasitization process. This indicates that caution should be taken when extrapolating a given functional response to a later point in time and space. Thus functional response curves as generally obtained may provide insufficient information on the real behaviour and capabilities of parasitoids irrespective of the type of response exhibited. Results of the functional response tests in simplified experimental situations should of course be treated with caution when applied to real world systems (Abrams, 1982).

4.8.3 SUPERPARASITIZATION

Superparasitization is reported in a number of aphidiids (Vevai, 1942; Hafez, 1961; Schlinger & Hall, 1960; Wiackowski, 1962; Force & Messenger, 1964; Stary, 1964; van Lenteren, 1981; Mackauer, 1983; Cloutier, 1984). The larval stage is the parasitoid stage in which the severe competitive relations is found. This kind of competetion is a direct result of superparasitization. The final end of this intraspecific competition is only a single parasitoid larva succeeds to complete development. The supernumerary larvae are eliminated mainly by physical attack or physiological suppression (Salt, 1961; Vinson & Iwantsch, 1980a). No marks have been observed in first instar larvae inside dissected aphids indicating that no physical attack through the use of strong mandibles took place. It is most likely that the supernumerary parasitoid larvae are eliminated by physiological suppression through secretions of toxins, enzymes or lack of oxygen.

The results and analysis show that superparasitization does occur at all densities. Occurence of superparasitization does not mean that the parasitoid is unable to discriminate between the parasitized and nonparasitized hosts. The nonrandom larval distribution at high host densities with high frequency of aphids containing only one larvae and fewer are unparasitized than expected from binomial distribution suggest that A. matricariae is capable of discriminating between parasitized and nonparasitized hosts. The female may be able to discriminate but will eventually oviposit in parasitized hosts if only such hosts are met during long periods. Superparasitization most probably occurs when the female urge to oviposit becomes intense in time after numerous encounters with parasitized hosts. This means that A. matricariae may prefer to oviposit in already parasitized hosts rather than limiting her egg production. It is quite common for oviposition restraint to break down when the parasitoid-

host ratio is high particularly in laboratory experiments (Singh & Sinha, 1982). This might explain the high degree of superparasitization found at low host densities. The restricted availability of unparasitized hosts for prolonged periods and the need to oviposit has been considered as a possible factor for superparasitization in a number of hymenopterous parasitoids (Salt, 1934; Singh & Sinha, 1981; Mackauer, 1983; Cloutier, 1984). Mackauer (1983) pointed that superparasitization may result from 3 sources:

1. Multiple egg deposition during a single attack.

2. Multiple attack and oviposition during the same encounter.

3. Multiple encounter and repeated parasitization.

Multiple egg deposition in a single thrust is not reported in aphidiids (Liu Shu-sheng, 1983). Multiple encounters and repeated parasitization is most probably the case with low host densities when parasitoids confront only parasitized hosts for a prolonged period. This is confirmed by direct observation. With increase in host density, multiple encounters will be less common especially if all hosts have an equal chance to be encountered. This is most likely when the present simplified experiment set-up in which aphids of uniform size, age and morph were placed at random on uniform seedlings of minimum foliage surface inside small boxes. Superparasitization at high densities then may result either from nonrandom search or multiple attack within one encounter. Nonrandom search results if some hosts were less obtainable than others because they are located in places less accessible or some aphids are more acceptable, but the simplified experimental set-up mentioned above reject such a possibility. So, multiple attack and oviposition during the same encounter is most likely the main reason for superparasitization at high host densities. Therefore, A. matricariae females are capable of distinguishing between parasitized and nonparasitized hosts. This is more pronounced at high host density but this

tendency is not perfect as they are not persistent in their avoidance of superparasitization especially at low host density. Messenger (1968) found that superparasitization is common in Praon exsoletum (Nees) which results probably from the apparent inability of the female to detect the aspects of host suitability. However, the results are comparable with those of Hofsvang & Hagvar (1983b) for E. cerasicola, Mackauer (1983) for A. smithi and Cloutier (1984) for A. nigripes. They all demonstrated that their respective aphidiid parasitoids discriminate between parasitized and nonparasitized hosts when the available number of hosts is not small. The ability of insect parasitoids to distinguish between parasitized and nonparasitized hosts and presearched and searched areas allows for optimum survival of progeny and utilization of hosts and is considered to be a common behavioural element among parasitoids (Doutt, 1959). As all but one parasitoid larva are eliminated by competition in A. matricariae as with other aphidiids, the deposition of more than one egg per host may appear to be wasteful. Salt (1961) stated that superparasitization is generally considered wasteful because of reduced probability of survival of offspring due to intraspecific competition. Nevertheless superparasitization is perhaps the best strategy at low density (Mackauer, 1983).

SECTION 5 SEARCHING BEHAVIOUR

5.1 INTRODUCTION

The entomophagous insects perceive their environment at several heirarchial levels and forage in a stepwise process (Flanders, 1953; Hassell and Southwood, 1978). At each level in the sequence two sorts of stimuli operate. 'Attractant' stimuli elicit orientation to areas containing hosts and 'arrestant' stimuli elicit a reduction in the distance or area covered per unit time by parasitoids moving within those host areas. An attractant is defined as a chemical that causes animals to make oriented movements towards its source. The definition implies a direct chemo-orthokinetic component in the behaviour namely the causing of movement as well as the orienting of that movement (Shorey, 1977). Kennedy (1978) defined attractants as chemicals that congregate insects as a result of undirected kinetic reactions either slowing down or stopping locomotion (orthokinesis) or changing the rate of turning (klinokinesis). What arresting effect any chemical has, however, depends entirely on how these two mechanisms are combined.

Examples of orthokinesis and klinokinesis responses were found for the braconid Cardiochiles nigriceps Vier. to host salivary gland extract on filter paper (Vinson & Lewis, 1965). Trichogramma evanescens Westw. responds to host female scale extract on cloth surfaces (Lewis, Sparks & Redlinger, 1971).

The chemicals used by parasitoids as cues for host selection are known as kairomones (Brown et al., 1970; Nordlund, 1981). Parasitoids often use different kairomones at various stages of the host selection sequence (Nordlund, Strand, Lewis & Vinson, 1987). These kairomones may be: Volatile chemicals that attract parasitoids from a long distance (Nordlund, Lewis & Gueldner, 1983); or contact chemicals that elicit intense searching in the vicinity of the contaminated substrate (Vinson, 1975); or stimulate host recognition and host acceptance (Nordlund et al., 1987). Contact kairomones

present in aphid honey-dew elicit intense local searching by Aphidius nigripes (Bouchard & Cloutier, 1984).

Olfaction is an important mechanism involved in host habitat location and host location by insect parasitoids (Vinson , 1981). Many parasitic Hymenoptera use olfactory cues and responses to orient first towards a potential host habitat and secondly towards their host (Vinson, 1981; Vet, van Lenteren, Heymans & Meelis, 1983).

After parasitoids have reached the host plant their search may be affected by plant topography. The aerial surfaces of plant display extraordinary diversity. They may be smooth or hairy with simple or complex hairs. Trichomes may be single celled or multicellular and both types may be glandular or non-glandular (Southwood, 1986). Dense trichomes probably impose physical barriers on insect parasitoids. Plant structure and leaf topography have been shown to affect walking speeds and number of turns for a number of parasitoids (Hulspas-Jordaan & van Lenteren, 1978; Obrycki & Tauber, 1984; Keller, 1987).

Almost no information is available on the role of allelochemics in mediating host finding in A. matricariae. In order to evaluate more fully the potential of A. matricariae, laboratory studies on the searching behaviour of this species were initiated with the objective of determining factors influencing this searching behaviour before and after it has arrived on the host plant.

5.2. SEARCHING BEHAVIOUR ON LEAVES

5.2.1 MATERIALS AND METHODS

Experiments were designed to test the effect of:

1. The lower and upper leaf surfaces of the same plant on searching behaviour
2 The leaf topography on searching behaviour.
3. The presence or absence of honey-dew and aphids on searching behaviour.

In these experiments walking speed, rate of turning and time spent searching were calculated for comparison. In the first experiment, the lower and upper surface of the same plant were compared. The plants used were potato Solanum tuberosum L. and turnip Brassica campestris rapa. In the second experiment lower leaf surfaces of six different plant species were used comprising potato, S. tuberosum; turnip, B. campestris rapa; faba bean, Vicia faba; lemon, Citrus lemon; cauliflower, Brassica oleracea var. botrydis and peach, Prunus persicae.

In the 3rd experiment, searching components were compared on the lower surface of leaves of 4 plants, namely potato, turnip, faba bean and lemon citrus. Three treatments were used: fresh clean leaves, leaves contaminated with honey-dew and leaves infested with aphids. Honey-dew was originally collected in petri dishes placed under dense colonies of a M. persicae culture, then dissolved in water 50% solution. An equal amount of 10 drops of the solution were painted on leaves, required to be contaminated. On infested leaves, a fixed density of twenty 3rd - 4th instar of M. persicae were randomly placed on required leaves.

The present study was made easier by a computer program called MicroMeasure. MicroMeasure was developed at Wye College, by Jon Varley (1989). Using a device called a genlock, an external video signal can be mixed with computer graphics produced by MicroMeasure allowing one to draw directly on top of the video picture and measure what is drawn. MicroMeasure requires a Commodore Amiga computer, colour monitor, genlock

device and video camera to be connected. MicroMeasure has several modes. The wiggly line mode was found to be the most appropriate for the present study, as it measures a convoluted line between two points. The movements of the insect is followed using a mouse. As movement starts, a stop watch is started on the screen which enables an insect to be followed for specific length of time. At the end of observation, the line length in addition to the speed and number of turns, is displayed.

PROCEDURE

Standardized female parasitoids 2-3 days old with previous oviposition experience were isolated for about 12 hours prior to testing, in clean plastic boxes containing only drops of drinking water. The experimental arena consisted of a petri dish 88 mm inside diameter and 14 mm high. Selected leaves were positioned inside the petri-dishes and placed individually under the video camera. Light was augmented by a Schott cold light source KL 1500-T, with two flexible arms mounted 10 cm over the upper surface of petri dish giving an illumination of about 45 W/m^2. Each observation started with the release of a single female parasitoid into the experimental arena containing a leaf. The duration of each observation was 5 minutes. The number of replicates were 15 for each treatment, in all experiments. For the 3rd experiment, for each group of 15 observations per treatment, one of the tracks taken by the parasitoid drawn directly on the monitor was selected at random. This track was traced on to a piece of acetate sheet placed over the monitor using a fine felt pen and later retraced on a paper to represent a pattern of search for specific treatments.

All experiments were conducted in the laboratory at 20 ± 4C. Walking speeds, turning angles and time spent searching were analysed using one way analysis of variance and any two treatments compared using a t-test.

5.2.2 RESULTS

Upper and lower leaf surfaces: Time spent searching, speed and rate of turns for upper and lower sides of leaf for turnip and potato plants is given in Tables (5.1 & 5.2). There was no significant difference ($P>0.05$) between upper and lower leaf surfaces with respect to speed, number of turns and time spent searching on either potato or turnip plants.

Leaf topography: Walking speeds, rates of turning and time spent searching on lower leaf surfaces of potato, turnip, cauliflower, peach, faba bean and citrus lemon are summarised in Table (5.3). The results demonstrate that leaf topography affects walking speed, rates of turning and time spent searching. The walking speed being fastest on faba bean. The rates of turning were least on lemon and faba bean. No consistent trend was found for variations on time spent searching, except that least time was spent searching on lemon.

The influence of honey-dew and aphids: The data in Tables (5.4, 5.5, 5.6 & 5.7) demonstrates the effect of honey-dew contaminated leaf and aphid infested leaf on searching components on potato, turnip, faba bean and lemon respectively. The results strongly suggest that the presence of honey-dew and host aphid influences speed, rate of turns and time spent searching. The speed was highest on clean leaves, generally lower on honey-dew contaminated leaves and lowest on aphid infested leaves for the four plant species. The number of turns on honey-dew contaminated leaves were more frequent than on clean leaves ($P<0.05$). For aphid infested leaves it was higher than that of clean leaves ($P<0.01$). This trend is seen in the four plant species. The searching time was increased on honey-dew contaminated leaves compared with clean leaves ($P<0.05$) for all species. A large increase ($P<0.01$) in searching time was found in aphid infested leaves for all plants.

Typical search patterns at each treatment are shown in Figure (5.1). Clean leaves are characterized by straight paths nearly linear with few

Table 5.1 SEARCHING BEHAVIOUR COMPONENT OF A. matricariae ON UPPER AND LOWER SURFACES OF TURNIP (n=15)

Treatment	Time spent searching (s) t test = NS		Speed mm/s t test = NS		No of turns > 75°C in 5 minutes t test = NS	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Lower surface	21.25	4.9	3.75	0.37	5.06	0.79
Upper surface	16.76	4.8	4.36	0.29	4.4	0.58

NS = nonsignificant at the 5% level.

Table 5.2 SEARCHING BEHAVIOUR COMPONENT OF A. matricariae ON UPPER AND LOWER SURFACES OF POTATO (n=15)

Treatment	Time spent searching (s) t test = NS		Speed mm/s t test = NS		No of turns > 75°C in 5 minutes t test = NS	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Lower surface	23.19	5.2	2.74	0.34	6.06	1.09
Upper surface	22.25	4.3	2.23	0.35	5.86	0.85

NS = nonsignificant at the 5% level.

Table 5.3 SEARCHING BEHAVIOUR COMPONENT OF A. matricariae ON LOWER SURFACES OF DIFFERENT LEAVES (n=15)

Treatment	Time spent searching (s) $F_{5,84}$ = 1.715 NS		Speed mm/s l.s.d. 5% = 1.149		No of turns >75° in 5 min l.s.d. 5% = 2.39	
	Mean	s.e.	Mean	s.e.	Mean	s.e.
Potato	23.19	5.2	2.75	0.3 c	6.06	1.9 A
Turnip	21.25	4.9	3.75	0.4 bc	5.07	0.8 AB
Peach	22.52	5.6	3.54	0.3 c	4.8	1.1 AB
Cauliflower	20.05	4.1	3.65	0.2 bc	5.13	0.9 AB
Lemon	07.58	1.6	4.75	0.6 ab	2.2	0.3 C
Faba bean	15.3	4.6	5.31	0.5 a	3.4	0.4 BC

Means within columns sharing the same letters are not significantly different at the 5% level, NS = nonsignificant at the 5% level.

Table 5.4 SEARCHING BEHAVIOUR BY A. matricariae ON CLEAN, HONEY-DEW COTAMINATED AND APHID INFESTED LEAF OF POTATO (n=15)

Treatment	Time spent searching (s) l.s.d. 5% = 37.495 Mean	s.e.	Speed mm/s l.s.d. 5% = 0.7749 Mean	s.e.	No of turns >75° in 5 min l.s.d. 0.1% = 10.478 Mean	s.e.
Clean leaf	023.18	05.2 c	2.75	0.3 A	06.06	1.09 x
Leaf + Honey-dew	088.67	15.6 b	2.35	0.3 A	17.0	2.04 y
Leaf + aphids	134.3	15.7 a	1.27	0.1 B	31.5	2.76 z

Means within columns sharing the same letters are not significantly different at the 5% level.

Table 5.5 SEARCHING BEHAVIOUR BY A. matricariae ON CLEAN, HONEY-DEW CONTAMINATED AND APHID INFESTED LEAF OF TURNIP (n=15)

Treatment	Time spent searching (s) l.s.d. 5% = 37.9735 Mean	s.e.	Speed mm/s l.s.d. 5% = 0.79117 Mean	s.e.	No of turns >75° in 5 min l.s.d. 5% = 6.0438 Mean	s.e.
Clean leaf	021.24	04.9 c	3.75	0.4 A	05.06	0.8 z
Leaf + Honey-dew	118.2	13.3 b	2.33	0.3 B	14.8	2.3 y
Leaf + aphids	163.1	18.1 a	1.64	0.2 B	26.9	2.8 x

Means within columns sharing the same letters are not significantly different at the 5% level.

Table 5.6 SEARCHING BEHAVIOUR BY A. matricariae ON CLEAN, HONEY-DEW CONTAMINATED AND APHID INFESTED LEAF OF FABA BEAN (n=15)

Treatment	Time spent searching (s) l.s.d. 5% = 33.926 Mean	s.e.	Speed mm/s l.s.d. 5% = 1.121 Mean	s.e.	No of turns >75° in 5 min l.s.d. 1% = 5.827 Mean	s.e.
Clean leaf	15.3	04.6 b	5.3	0.5 A	03.4	0.4 z
Leaf + Honey-dew	32.9	09.4 ab	3.3	0.3 B	09.4	1.3 y
Leaf + aphids	64.9	17.6 a	2.1	0.3 C	19.5	2.2 x

Means within columns sharing the same letters are not significantly different at the 5% level.

Table 5.7 SEARCHING BEHAVIOUR BY A. matricariae ON CLEAN, HONEY-DEW CONTAMINATED AND APHID INFESTED LEAF OF LEMON (n=15)

Treatment	Time Spent searching (s) l.s.d. 5% = 23.657 Mean	s.e.	Speed mm/s l.s.d. 5% = 1.2045 Mean	s.e.	No of turns >75° in 5 min l.s.d. = 5% = 1.378 Mean	s.e.
Clean leaf	07.58	01.6 b	4.75	0.6 A	2.2	0.3 y
Leaf + honey-dew	18.55	02.3 b	3.18	0.33 B	5.8	0.6 x
Leaf + aphid	60.5	14.1 a	2.0	0.3 B	5.13	0.5 x

Means within columns sharing the same letters are not significantly different at the 5% level.

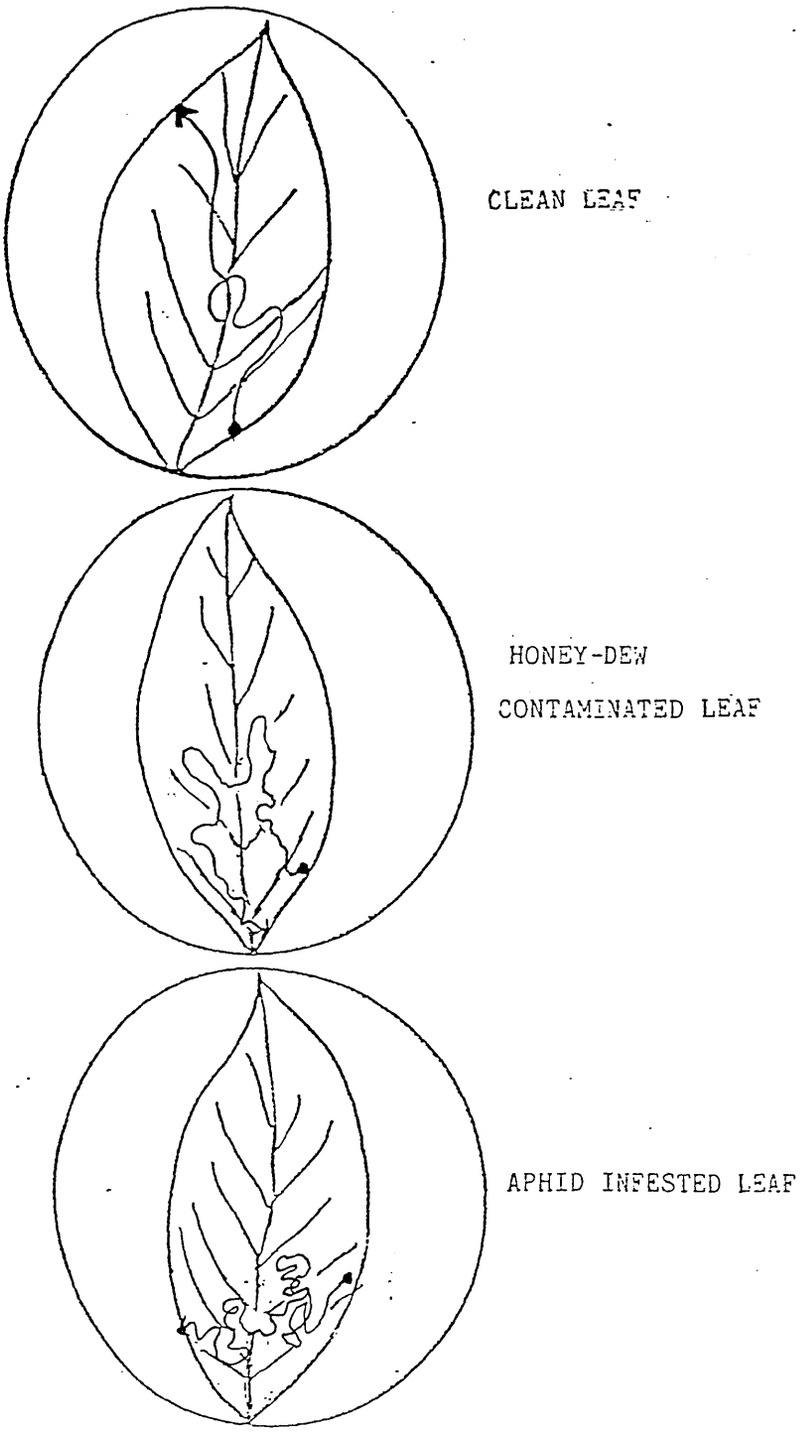


Figure 5.1 SEARCH PATTERN OF A. matricariae ON CLEAN, HONEY-DEW CONTAMINATED AND APHID INFESTED TURNIP LEAVES

gentle turns whilst contaminated leaves and aphid infested ones show convoluted paths with frequent sharp turns. The convoluted paths are more apparent on infested leaves.

5.2.3 DISCUSION

The effect of leaf side of the same plant on searching behaviour showed that there was no significant difference between either side of the leaf for potato and brassica plants with respect to speed of walking, number of turns and time spent searching ($P>0.05$). These results suggest that leaf side of the same plant seems to have no influence on searching behaviour components of A. matricariae. This finding in addition to the fact that M. persicae preferentially settle on lower surface of leaves made it feasible to study the effect of leaf topography only on the lower leaf surface of different plant species.

The results of the present study to elucidate the role of leaf morphology on searching behaviour, indicates that walking behaviour differs on plant species due to morphological differences in leaf structure particularly trichome form and density (Appendices 5.1 - 5.3). The walking speed was found to be inversely proportional to the hairiness, whilst the rates of turning was positively correlated. This is in line with the literature for other parasitoids. Hulspas-Jordaan & van Lenteren (1978) in their investigation of the relationship between host-plant leaf structure and parasitization efficiency of the parasitic wasp Encarsia formosa Gahan a parasitoid of the glasshouse whitefly Trialeurodes vaporariorum (Westwood) found that there is a large variation in walking speed on the various host plants. On the hairiest leaves (cucumber) the walking speed was low, on the smooth ones (paprika) it was high and it was moderate on the moderately hairy leaves (tomato). Keller (1987) found that the walking speed of female Trichogramma exiguum Pinto & Planter were fastest on maize and soybean, intermediate on tomato and slowest on wooly mullien which is the hairiest. Similarly there was a difference in rates of turning along the paths of

walking. The rate of turning was smallest on maize, intermediate on soybean and greatest on wooly mullien. Obrycki & Tauber (1984) found that under glasshouse conditions there is a direct relationship between the density of glandular trichomes on aphid resistant potato clones Solanum tuberosum x S. berthaultii and S. berthaultii and the adverse effects on 11 aphidophagous species. The negative effects include a reduction in searching time and in distance moved. Such results may imply that differential responses to leaf surfaces may affect searching rates on different plant species. Since, walking speed is important to parasitization efficiency, so variation in walking speeds on different plants under this study may lead to different parasitization rates. If walking speeds translate directly into host locating rates, the parasitization on faba bean or citrus lemon will be greater than on potato assuming equal leaf surfaces and similar densities of parasitoids and aphids. Hulspas-Jordaan & van Lenteren (1978) found that the wasp E. formosa are much more hindered by the stiff hairs on cucumber leaves which reduces their walking speed and this diminishes their parasitization efficiency. They concluded that differences in control results were partly due to differences in leaf topography and particularly in the hairiness of the leaves. An example of drastic reduction in parasitization due to leaf morphology is given by Rabb & Bradley (1968) for Trichogramma minutum Riley which failed to parasitize eggs of the tobacco hornworm Manduca sexta Johannson on fresh tobacco foliage but readily attacked eggs on other substrates. The tiny parasitoids became stuck to the tobacco leaf in the gummy exudate of the trichomes. The same authors (1968) found that the parasitoid Telenomus sphingis Ashmead being larger than T. minutum was able to cope with the sticky substrate to some extent but its movements on tobacco were inhibited and it parasitized significantly fewer eggs on tobacco than on any other substrate. The difference in leaf surface structure can potentially cause large variations in parasitization rates. It follows, the direct relationship between the structure of leaves of the

host plant and the parasitization efficiency of the parasitoid is important for success of biological control. Such results may have practical implication for biological control of M. persicae in the glasshouse. It is likely that biological control efficiency may be increased by using host plant varieties having few trichomes. But such hairless varieties may be more susceptible to attack by aphids. The higher the population of aphids the more difficult to obtain satisfactorily control. On the other hand, M. persicae were found unable to effectively colonize some potato varieties (Xia & Tingey, 1986). This resistance results from leaf trichomes as well. In Solanaceae specialized glandular trichomes, the type V1 in particular (a short multicellular stalk with 2-4 celled glandular head and monocellular base) play a critical role in resistance against insects. The defensive action dependent upon the plant/insect system arises from a diversity of causes and effects : A highly trichomatous state presenting a physical barrier which reduces the ability of the insect to gain access to the plant surface and thus to feed or oviposit, or because of the ability of trichomes containing chemicals to poison the insect, or because of the ability of insect fractured trichomes to exude sticky chemicals that severely impede the insect ability to move, feed and survive (Duffey, 1986).

It is not always correct that the results of laboratory studies may predict the magnitude of effects of plant surface characteristics on parasitoid behaviour in the field. Obrycki, Tauber & Tingey (1983) showed that under field conditions the negative effects of glandular pubescence on beneficial insects were reduced and that natural enemies are present and can cause aphid mortality on pubescent clones. This reduction in detrimental effects of glandular trichomes on biological control agents in the field is explained partly as a result of the effects of dust, wind and rain on glandular trichome adhesiveness. However, the locomotion of females of different strains of Trichogramma maidis Pint. & Voeg. was measured under standardized conditions and compared to their efficiency in field parasitism

of eggs of Ostrinia nubilalis for several years by Bigler, Bieri, Fritschy & Seidel (1988). The travel speed of the females of different T. maidis strains was found to be positively related to the potential for parasitism in the field. They concluded that, the travel speed can therefore be used as a parameter to estimate the capacity for host location and the efficiency of a T. maidis strain for inundative biological control programmes.

The results clearly indicate that the parasitoid A. matricariae female changes its searching behaviour components following encountering honey-dew contaminated leaf or aphid infested leaves. This is manifested in a significant reduction in walking speeds, associated with significant increases in number of turns and time spent searching as well. Honey-dew most probably acts as an arrestant stimulus analogous to contact chemicals produced by hosts of many parasitoids. Waage (1978) illustrated that the ichneumonid Nemeritis canescens Grav., responded to the mandibular gland secretion of its host Plodia interpunctella Hubn. by exhibiting a complex orthokinetic response involving stopping, walking at reduced speed, and probing with ovipositor. In response to removal of the chemical following presentation, as would occur when the insect left the edge of the chemical patch, the wasp exhibits a klinotactic response which directs it back to the patch. This turning back response at the patch edge greatly increases the time spent on a patch of contact chemical. The weakening of this response determines when a host patch is abandoned. The weakening is slowed by increasing the concentration of contact chemical on the patch and by oviposition while on the patch. Bouchard & Cloutier (1984) showed that when Aphidius nigripes Ashmead encountered a potato aphid Macrosiphum euphorbiae (Thomas) honey-dew treated area on filter paper, female parasitoids exhibited arrestment, antennal examination, abdominal protraction, reduced walking speed and increased turning. Upon losing contact with the honey-dew contaminated substrate, parasitoids often exhibited a klinotactic response which drove them back to the treated area. McGregor & Mackauer (1989)

found that the time spent searching during a single visit by A. smithi females was significantly shorter on clean broad bean leaves than on leaves covered with droplets of pea aphid Acyrthosiphon pisum (Harris) honey-dew. The presence of carbaryl residues on leaves did not impair this response. The results also agree with what Langenbach & van Alphen (1986) found on their investigation of searching behaviour of Epidinocarsis lopezi (de Santis) in which females of E. lopezi were offered cassava leaves with and without wax produced by their host cassava mealy bug Phenacoccus manihoti Matille-Ferrero. They found that walking speed of the females was lower, the duration of visits was longer, and females spent more time preening on wax contaminated leaves than on clean leaves.

The reduction in searching speed after an encounter with honey-dew may also increase the efficiency with which wasps respond to the next host as the slow moving parasitoids were much more successful. Arrestment in response to the presence of honey-dew would increase the probability of locating a clump of aphids. The host M. persicae usually lives in clusters, therefore it would be quite possible that another aphid can be found near the site where the first host was encountered. The parasitoid tends to stay in the vicinity of the host encountered and to search for another aphid in this restricted area. This behaviour is called area concentrated search by Smith (1974). The longer time spent searching in the presence of honey-dew is due to wasp intensive search. Therefore the area concentrated search of the wasp after host encounter is considered to raise the wasp's probability of encountering the next host. So a switchover from linear to concentrated searching as shown in searching patterns Fig (5.1) induced by the presence of honey-dew or aphids would be advantageous for the parasitoid.

A comparison of search patterns in Figure (5.1) indicates that two kinds of search can be distinguished, random and nonrandom search. Random search

is an extended traverse in which turns when they occur are gradual and sweeping. The few number of turns was reflected in high speeds (Tables 5.4, 5.5, 5.6 & 5.7). Nonrandom search is characterized by many sharp turns and a smaller area of leaf examined. It characterizes a more concentrated search pattern in which the parasite may retraverse considerable areas. This non-random search with tighter turning pattern implies that more efficient search is made on contaminated and infested leaves. This is always confirmed by more time spent searching in contaminated and infested leaves (Tables 5.4, 5.5, 5.6 & 5.7). A similar switchover in behaviour was observed by Evans (1976) for Anthocoris confusus (Reuter) and by Nakamuta (1982) for the lady beetle Coccinella septempunctata L. with their prey M. persicae. Richerson & Borden (1972) in their investigation of search patterns of the braconid Coeloides brunneri Viereck of Douglas-fir beetle larvae confirmed the present results and concluded that the female parasitoid located its host through 4 distinct phases of host finding: Random search, non-random search, oviposition and non-search (cleaning & resting). Ovipositional probes are the culmination of successful host finding.

5.3 SEARCHING BEHAVIOUR ON WHOLE PLANTS

5.3.1 MATERIALS AND METHODS

The investigation was made in experimental arenas composed of a clear acetate cage 22 cm tall, 14 cm wide at the top and 14.5 cm wide at the bottom. Turnip plants Brassica campestris rapa potted singly in 98 mm diameter pots grown in peat based compost, were used. Plants were 12 - 14 cm high, had two leaves of 7 - 8 cm in length and two smaller ones of 5 - 6 cm in length, with stem of about 3 cm high and petioles 3 - 7 cm in length. Potted plants were placed in the centre of the cage. Standard parasitoids described above were used.

Two experiments were carried out. The first experiment was designed to study the effects of:

1. The presence or absence of honey-dew on time spent searching.

2. The presence or absence of aphid exuviae on time spent searching.

3. The presence or absence of aphids on time spent searching.

So, four treatments were used:

a. Control: plants without honey-dew, exuviae or aphids.

b. Plants contaminated with honey-dew. An equal amount of 40 drops of honey-dew solution (50%) was spread on leaves, petioles, heart and stem over each plant.

c. Plants contaminated with aphid exuviae. About 100 aphid exuviae collected from dense colonies of M. persicae were distributed randomly over each plant needed to be contaminated.

d. Plants infested with aphids. About 100 3rd - 4th instar of M. persicae were distributed randomly on each plant needed to be infested.

Four plant sections were distinguished for recording and analysing the parasitoid behaviour: The lower surface of leaves (4 leaves), the upper surface of leaves (4 leaves), the stem and petioles and the heart (the plant terminal bud).

At the beginning of each test, a single female parasitoid was released at the base of each plant and observed continuously for 30 minutes. Each female was tested only once. The number of replicates was six, time elapsed between replicates 1-3 days and 3 observations made per replicate. The main activity recorded was the time spent searching on each of the four sections of the plant. A parasitoid was considered to be searching when it walked on the plant, frequently making brief stops to probe the plant surface with antennae or mouth parts. All experiments were conducted at laboratory room temperature of 20 ± 4°C.

The second experiment was designed to study the effect of leaf side on the time spent searching and parasitization success of A. matricariae in terms of number of aphids parasitized per exposure time. Standard females as mentioned above were used. About 60 3rd-4th instars of M. persicae were distributed on the upper surfaces of the four leaves, 20 aphids on each of the two larger leaves and 10 aphids on the two smaller ones. The same density of 60 3rd-4th instar of aphids were distributed on lower surfaces of leaves.

At the beginning of each experiment, a female parasitoid was released into the arena. A fresh female was used for each experiment. The searching behaviour was recorded for one hour. The time spent searching only on leaves was recorded. Searching was recognized as walking on the plant while palpating its surface. The number of replicates was 15. After each experiment, aphids from each leaf surface were transferred to turnip seedlings and kept separately inside plastic boxes until mummification. All experiments were performed in the laboratory at 20 ± 4°C.

5.3.2 RESULTS

The results for time spent searching for A. matricariae female tested on clean, honey-dew contaminated, aphid exuviae contaminated and aphid infested whole plant is presented in Table (5.8). The results clearly show that plant structure did affect time spent searching. No significant difference between times spent on both sides of leaves were found ($P>0.05$) for clean and honey-contaminated leaves. But more time was spent on the upper ($P<0.05$) than on the lower surface for aphid exuviae contaminated and aphid infested leaves. Less time ($P<0.05$) was spent on stem + petioles and heart in comparison with either side of the leaf for all treatments.

When the upper side of the leaf was compared for different treatments, less time was spent searching ($P<0.05$) on clean leaves in comparison with either honey-dew contaminated or aphid exuviae contaminated or aphid infested leaves. Less time was spent searching ($P<0.05$) on clean leaves compared with the rest of treatments for the lower side of leaves. Similarly less time ($P<0.05$) was spent searching on clean stem + petioles and heart.

The data given in Table (5.9) shows the time spent searching on leaves of the whole plant and the number of mummies found on either side of the leaves. The results indicate that, the parasitoid female spends approximately the same time on each side of leaves ($P>0.05$). The proportion of encounters resulting in successful attacks in terms of mummified aphids was significantly higher on upper surfaces ($P<0.01$) than on lower ones resulting in a higher percentage parasitism per female on upper surface.

5.3.3 DISCUSSION

The results of searching behaviour of A. matricariae using whole plants strongly suggest that searching behaviour is directed during the final stage of the foraging process after alighting on the turnip plant. The parasitoid

Table 5.8 TIME SPENT SEARCHING BY A. matricariae ON CLEAN, HONEY-DEW CONTAMINATED, EXUVIAE CONTAMINATED AND APHID INFESTED WHOLE TURNIP PLANT (n=18)

Treatment	Time spent searching (minutes) Lower leaf l.s.d. 5% = 1.785	Upper leaf l.s.d. 5% = 2.751	Stem + petioles l.s.d. 5% = 0.9206	Heart l.s.d. 5% = 0.76778	row l.s.d. 5%
Clean plant	2.75 A c	02.8 A b	1.25 AB b	0.8 B b	1.158
Honey-dew Contaminated	4.6 A b	04.5 A b	1.45 B ab	1.4 B ab	1.308
Aphid exuviae Contaminated	8.7 B a	11.3 A a	2.25 C a	1.9 C a	1.868
Aphid infested	8.4 B a	13.1 A a	2.3 C a	1.9 C a	2.382

Means within columns sharing the same small letters (a-d) are not significantly different, means within rows sharing the same capital letters (A-D) are not significantly different.

Table 5.9 TIME SPENT SEARCHING AND PARASITIZATION SUCCESS OF A. matricariae ON LOWER AND UPPER LEAF SURFACES OF WHOLE TURNIP PLANTS (n=15)

Treatment	Time spent searching t test = NS Minutes	s.e.	No of mummies t test = * Mean	s.e.
Lower surface	12.47	1.13	10.07	2.12
Upper surface	14.07	1.38	19.6	2.18

NS = nonsignificant at the 5% level, * = significant at the 5% level.

used the topography of the plant to direct its search to those areas of plant preferred by aphids as feeding sites. On clean plants, the parasitoid has been shown to forage and spend more time on leaves rather than heart or branches and stem (Table 5.8). This pattern of spending significantly more time on leaves than either stem or heart is not only shown for clean plants but also on contaminated and infested plants as well. So plant structure influenced the time spent searching. The parasitoid also direct its search towards areas where cues to their host are present. This is demonstrated by significantly more time spent on contaminated or infested leaves or stem or heart than on clean ones. The preference for leaves over heart and stem is accelerated in the presence of honey-dew or aphid exuviae or aphids (Table 5.8). This suggests that the plant is scanned in a predetermined schedule as still they spend more time on leaves. Such behaviour will increase the probability of parasitoids encountering their hosts which settle on leaves. Thus, the parasitoid uses the topography of plants and the expected distribution of its host and its secretions and excretions to maximize the profitability of search. Arrestment of the parasitoid on particular areas of plant due to slowing down of locomotion (orthokinesis) or changing the rates of turns (klinokinesis) when encountering honey-dew or aphid exuviae or host aphid led to the significant increase in time spent searching on contaminated and infested parts in comparison to clean ones.

This arrestment process leads to concentrated search which implies a switch-over from linear to concentrated searching which would be advantageous for the parasitoid. If a host is not found in the vicinity of the honey-dew or aphid exuviae, it might be better for the wasp to give up searching and to go to other areas as soon as possible. So, the switch-over from concentrated to linear search triggered by not finding a host in a short period would also be advantageous (Hassell & Southwood, 1978; Waage, 1978). This may explain the shorter period spent searching on honey-dew contaminated in comparison to host aphid infested areas. A comparable

arrestment behaviour is witnessed by Carter & Dixon (1984) for C. septempunctata larvae on cereal aphid Sitobion avenae (Fab.). In the presence of honey-dew, larvae spent longer, searching the ears resulting in greater exploitation of prey than in the absence of honey-dew.

Plant structure was found to affect the time spent searching by A. matricariae females with significantly less time spent on petioles, stem and heart. This led to another experiment which was conducted to assess the effect of plant structure using only upper and lower surfaces of leaves on time spent searching and parasitization success for an extended period of exposure of 1 hour (Table 5.9). No significant difference ($P>0.05$) was found for time spent searching on either side of leaves. Such a result was not expected since the lower surface is the preferred feeding site for M. persicae. A possible explanation is that phototactic responses of parasitoids overruled the effect of leaf surface assuming equal densities of aphids on both sides. Consequently, a significantly higher ($P<0.05$) percentage of parasitization on upper surfaces than on the lower ones found under this study would not be surprising. Phototactic responses of the parasitoid which overrule the effect of leaf surface and resulting in parasitoids spending an almost equal time on both sides of leaves, may render lower surface aphids less accessible and upper surfaces ones more exposed assuming equal densities on both sides. Another possible explanation is that the A. matricariae female is more active in ovipositional behaviour under the direct light of upper surfaces than under the dim light of lower surfaces resulting in a lower percentage of parasitization on lower surfaces assuming equal densities of aphids on both sides.

The present results are comparable with those of Gardner & Dixon (1985) despite the fact that they did not compare the two sides of leaves of the same plant with respect to percentage parasitism. These authors (1985)

found that on their study of foraging behaviour of Aphidius rhopalosiphi (De Stefani-Perez) in relation to wheat plant structure that A. rhopalosiphi will encounter and parasitize Metopolophium dirhodum (Walker) feeding on leaves more frequently than Sitobion avenae (Fabricius) which feeds on the ear. This would limit the parasitoid ability to regulate populations of the cereal aphid S. avenae. Thus, differences in plant structure and chemistry (presence of honey-dew, exuviae, etc.,) can potentially cause great variations in parasitization rates.

5.4 ROLE OF OLFACTION IN HOST FINDING

5.4.1 MATERIALS AND METHODS

Standard female parasitoids used in this experiment were less than 3 days old, had been confined with males and had previously been exposed to aphids. They were kept isolated in plastic boxes for 12 hours prior to the experiment with only drops of water.

The olfactometer used was basically similar to the one developed by Vet, van Lenteren, Heymans and Meelis (1983) as an air-flow olfactometer for measuring olfaction responses of hymenopterous parasitoids and other small insects.

The apparatus (Plate 5.1) consists of a 4-arm star-shaped exposure chamber, which is made in two parts of transparent perspex. Each point of the star runs without obstruction into a 5 mm inside diameter stainless steel tube. This arrangement is held firmly on the perpex floor sheet by 4 metal fasteners. Air leaks are prevented by silicone grease. Each arm of the chamber was connected to a set of four 90 x 22 mm plastic vials. That closest to the chamber serves as a trap to catch insects reaching there. The odour source material was placed in the second. The third contained distilled water to obtain uniform humidity in incoming air. The outer vial is equipped with a fine flowmeter used to measure air flow. The air flow was obtained with a vacuum compressor by pumping air out of the chamber through a 1-cm diameter hole in the centre of the floor which creates a distinct moving air field in the chamber. With the extractor tube separated this hole is also used to introduce insects into the chamber. The air flow through the 4 arms is balanced by regulating each arm separately with the flowmeter by squeezing the extractor tube with a screw fastener.

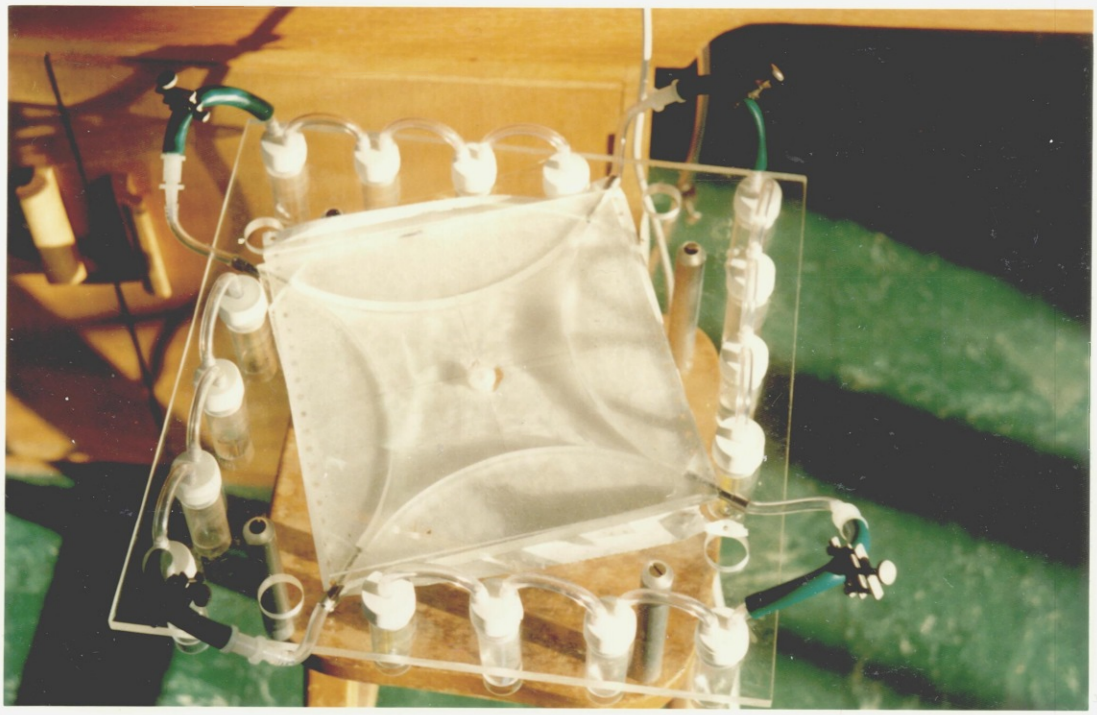


Plate 5.1 THE OLFACTOMETER (THE VACUUM PUMP IS NOT SHOWN)

PROCEDURE OF EXPERIMENT

Initially the experimental odour fields were set-up in the chamber with an equal flow rate for each arm. The extractor tube was disconnected to allow the test insect to enter the chamber through the 1-cm hole using 50 x 20 mm vials. Parasitoids to be tested were introduced individually. Parasitoids walked up into the chamber within minutes due to their positive phototactic reaction. Then the extractor tube was reconnected and the air flow restarted. The parasitoids were allowed a maximum of 15 minutes to make a final choice between the four air fields. A final choice was recorded when the parasitoid left the chamber through one of the arms, but not necessarily to reach the catching vial. The approximate boundaries of the 4 air fields were drawn on clear acetate placed on top of the chamber. Before a final choice was made, the time spent by a parasitoid walking in each of the 4 fields was recorded using a stop watch. A. matricariae did not seem to be disturbed by the presence of the observer. All experiments were designed as binary choice tests. Parasitoids were given a simple choice between test material odour and control blank odour. The test materials were placed in two opposite arms, the two other arms being the control ones. Each experiment was replicated 5 times with 6 parasitoids tested per replicate. After the first replicate, the vials containing the test materials were washed with running water. For the second replicate, the material tested as the source of odour was placed in the two arms which served as controls for the first replicate to remove any bias in the set up. All experiments were carried out in the laboratory at 20 ± 4°C, with a light source provided by fluorescent tubes fixed in the ceiling about 2.5 meters above the chamber giving about 40 W/m^2 light intensity. The test materials used as a source of odour were:

1. Six fresh clean mature leaves of turnip, B. campestris rapa of 3 cm length for each test tube.

2. Six fresh clean mature leaves of potato, S. tuberosum of 3 cm in length for each tube.

3. Honey-dew collected in petri dishes placed under dense colonies of M. persicae. The honey-dew was dissolved in water 50%, then 60 drops of solution were spread on filter paper tapes for each test tube.

4. A density of 60 exuviae collected from dense colonies of M. persicae for each test tube.

5. A density of 60 aphid individuals of M. persicae at different stages of development for each test tube.

6. Six mature leaves of turnip of 3 cm in length contaminated with 60 drops of honey-dew and 60 exuviae and infested with 60 individuals of M. persicae at different stages of development for each test tube.

If the parasitoid left the chamber for more than one minute, the observation would be stopped and the remaining experimental time is assigned to the odour field finally chosen.

5.4.2 RESULTS

Table (5.10) summarizes the female A. matricariae responses, in terms of percentage choosing test fields and the mean time spent in each field. A. matricariae did not show a positive response to either clean fresh potato or fresh clean turnip leaves ($P>0.05$). This is confirmed by the mean time spent per field which did not differ significantly between the test and control fields ($P>0.05$). The attraction was the highest for turnip leaves contaminated with honey-dew and aphid exuviae and infested with aphids ($P<0.001$). The attraction was as high as well for living aphid populations ($P<0.001$). The females also positively responded to honey-dew ($P<0.05$) as well as to aphid exuviae ($P<0.05$).

Table 5.10 RESPONSE OF A. matricariae FEMALE TO DIFFERENT ODOURS IN A 4-FIELD AIRFLOW OLFACTOMETER (n=30)

Material tested	% Choosing test field (number) χ^2 test	Time spent in test field Minutes	s.e.	Time spent in control field Minutes	s.e.
		Paired t test			
Turnip leaves	53.3 (16) NS	4.4	0.23	4.76	0.32 NS
Potato leaves	56.7 (17) NS	4.5	0.25	4.48	0.22 NS
Aphid exuviae	70.0 (21) *	5.3	0.2	2.96	0.35 ***
Honey-dew	73.3 (22) *	5.48	0.3	2.64	0.26 ***
M. persicae	83.3 (25) ***	7.5	0.32	1.72	0.2 ***
Turnip leaves + honey-dew + aphids	90.0 (27) ***	8.4	0.2	1.16	0.19 ***

NS = nonsignificant at the 5% level, * = significant at the 5% level, *** = significant at the 0.1% level.

A highly positive attraction in terms of a greater percentage of parasitoids choosing the test field over control ones was always reinforced by a highly significant longer time spent walking in such fields ($P<0.001$).

No repellent action among the offered materials was found, since no preference for control ones was observed.

5.4.3 DISCUSSION

In the present study a superior four-field air flow olfactometer is used instead of the old Y and T tubes. In the four-field air flow olfactometer four distinct fields of odours are created in the chamber which enables parasitoids to move and scan freely the odour fields given in adjacent areas. There is usually a turbulance at the junction of Y and T tubes which results in mixing of odours offered, small parasitoids therefore have difficulty in making chemotactic responses in this situation (Vet et al., 1983).

The present results reveal that the sense of smell can exert an influence on the choice of the searching female A. matricariae. Female parasitoids were strongly attracted by odours from living aphids as well as from leaves infested by aphids. A. matricariae females most probably use olfactory cues to locate their hosts. In contrast, Read et al., (1970) using a Y-tube olfactometer found that a colony of 250 Brevicoryne brassicae tested 24 hours after removal from collard was not attractive to Diaeretiella rapa McIntosh. However, positive responses to aphid host odour have been reported by a number of authors. Schuster & Starks (1974) observed the attraction of the parasitoid Lysiphlebus testaceipes (Cresson) to its host the green bug Schizaphis graminum (Rondani) in a Y tube olfactometer. Powell & Zhi-li (1983) using a horizontal glass Y-tube olfactometer, found that Aphidius uzbekistanicus Luzhetski responded to cereal aphids Sitobion avenae (F.) and Metopolophium dirhodum (Walker) whilst A. ervi Haliday,

which has a broad host range, responded to M. dirhodum and the pea aphid Acyrthosiphon pisum (Harris). Bouchard & Cloutier (1985) using a four-field air flow olfactometer, found that Aphidius nigripes Ashmead were strongly attracted by odours from a preferred host Macrosiphum euphorbiae Thomas and also from a less preferred hosts M. persicae and Aphis nasturtii Katt. Moreover, A. nigripes females responded positively to odours from a non-host aphid Rhopalosiphum maidis Fitch. They suggest that females react nonspecifically to volatiles emanating from various aphid species. Assuming that such general attraction by aphid odour is used to locate hosts over relatively short distances by A. nigripes then host species selection could still be achieved either through proper host habitat selection and/or contact recognition of potential hosts. Then a broad response to nonspecific aphid odours may still be highly adaptive in enabling searching parasitoids to quickly find aphid colonies dispersed among plants.

The findings of the present study showed that A. matricariae females are attracted by honey-dew and aphid exuviae odours of their host M. persicae carried by the airstream. Honey-dew and aphid exuviae are good indicators of the presence of aphids on plants, not only as a contact effect resulting in intensified searching by A. matricariae (Section 5.2) but by attracting females from a distance by means of olfaction. Such results strongly suggest that A. matricariae females uses volatile chemicals emanating from honey-dew and exuviae of their host aphid as a distance kairomone to find and locate host aphids. A positive attraction to honey-dew is reported in the literature. Bouchard & Cloutier (1985) found that the honey-dew produced not only by the preferred M. euphorbiae but also the much less preferred M. persicae and A. nasturtii and even from nonhost R. maidis was very attractive to female A. nigripes. Different honey-dew ingredients are probably responsible for its contact and olfactory actions. The arrestant effect of honey-dew on the aphid predator Chrysopa carnea Stephens is due to sucrose, whereas volatile breakdown products of tryptophane act as

attractants (van Emden & Hagen, 1976).

Although the present results strongly suggest that the female A. matricariae uses olfactory cues for host finding, care should be taken in extending laboratory results to field conditions. As positive responses in an olfactometer do not imply long range attraction. The present results may not prove long range attraction by the parasitoid to host aphid or honey-dew or aphid exuviae. But the results imply that once in the habitat of the potential host, most probably by other means than olfaction, the searching females has the capacity to select through olfactory cues, places where hosts are most likely to be available.

The results illustrate that A. matricariae females failed to respond to either turnip or potato plants. A comparison of these results with that of previous workers reveal that there is no systematic response to host plants by various hymenopterous parasitoids. A similar negative response was reported by Bouchard & Cloutier (1985) for A. nigripes which did not respond to potato plants, the food plant of their host. But Read et al., (1970) found that in D. rapae both sexes showed a marked attraction to fresh collard leaves Brassica oleracea. The females were considerably more responsive than males. They identified allylisothiocyanate, a mustard oil present in Cruciferae, as the major substance involved in the attraction of the parasitoid to species of Cruciferae. Similar results were found by Schuster & Starks (1974) for L. testaceipes females which gave positive responses to sorghum, their aphid food plant. Powell & Zhi-Li (1983) showed A. uzbekistanicus females responded to wheat leaves only and both males and females of A. ervi responded to wheat and bean leaves, the food plants of their host aphids. Read et al., (1970) concluded that D. rapae locate the habitat of potential host aphids by an olfactory response to volatile chemicals emanating from the aphid host plants. Once in the selected habitat discovery of the hosts occurs only by random searching.

A complete lack of response was shown by A. matricariae females under the present study for potato and turnip, preferred food plants of their host aphid. A possible explanation for this is that their host insect M. persicae is extremely polyphagous attacking a wide range of host plants belonging to different families. This wide range of host plants makes it very difficult for A. matricariae to use plant volatiles as a means of host plant selection, as it will have to comprehend a wide range of plant odours. This is certainly not the case for parasitoids attacking insect hosts exhibiting greater host specificity. Such as D. rapae (Read et al., 1970) and A. uzbekistanicus (Powell & Zhi-Li, 1983) with few plant volatiles which can easily be recognized and used as a means of host habitat finding.

Doutt (1959, 1964b) states that the first phase of host finding is host habitat location. The absence of selective olfactory responses to the host food plants exhibited by A. matricariae females is not contradicting this statement. It is only that A. matricariae females may use other than olfactory cues to locate the habitat.

Read et al., (1970) states 'It seems likely that the methods of habitat selection by D. rapae evolved after that of B brassicae, most populations of which feed on Cruciferae and are therefore subject to parasitization by this species. The nature of parasite response to the plant rather than to the aphid itself, has subsequently rendered those populations of polyphagous aphids such as M. persicae which happen to be feeding on cruciferous plants more vulnerable to parasitization by D. rapae than populations feeding on plants of other plant families'.

Here, it can be speculated that the methods of habitat selection by A. matricariae evolved after that of M. persicae, the populations of which feed on a wide range of plants. The nature of the parasitoid response specifically to the aphid rather than the plant has subsequently made these populations of M. persicae more vulnerable than other species.

5.5 VISUAL RESPONSES TO TRANSMITTED LIGHT

5.5.1 INTRODUCTION

Light may be defined as any radiation capable of causing a visual sensation directly. Light waves occupy only a very small fraction of the spectrum of electromagnetic waves (Section 1.9). The lower limit is generally taken as being between 330-440 nm and the upper limit between 760-780 nm (1 nm (nanometer) = 10^{-9} m). The visible spectrum can be divided into a number of approximate wave length ranges each of which makes a certain colour impression on the human eye:

380-436 nm violet, 436-495 nm blue, 495-556 nm green, 556-589 nm yellow, 589- 627 nm orange and 627-780 nm red.

Electromagnetic radiation with wave lengths just beyond the violet and red ends of the visible spectrum are known as ultraviolet and infrared radiation respectively. The limits of ultraviolet are considered lying between 100 - 400 nm, subdivided to 3 regions. The limits of infrared radiation are usually considered between 780 nm and 1 mm subdivided into 3 bands.

A photometer measures visible light (0.4-0.7 μm) in terms of intensity. A spectrophotometer measures light as a function of wavelength.

Wave length specific behaviour occurs when different behavioural patterns of an animal have markedly different spectral sensitivities (Menzel, 1979). Recent electrophysiological and structural studies imply that the number of different colour receptors differs across the eye and that these receptors are embodied within a single ommatidia in different combinations. Whether or not an insect is using the different spectral sensitivities of their receptors for colour vision can be determined only by studying the behaviour of the insect. In such experiments, the insect must be shown to be able to discriminate colours seen either simultaneously or successively solely on

the basis of wave length differences of the test colour and not by virtue of different brightness.

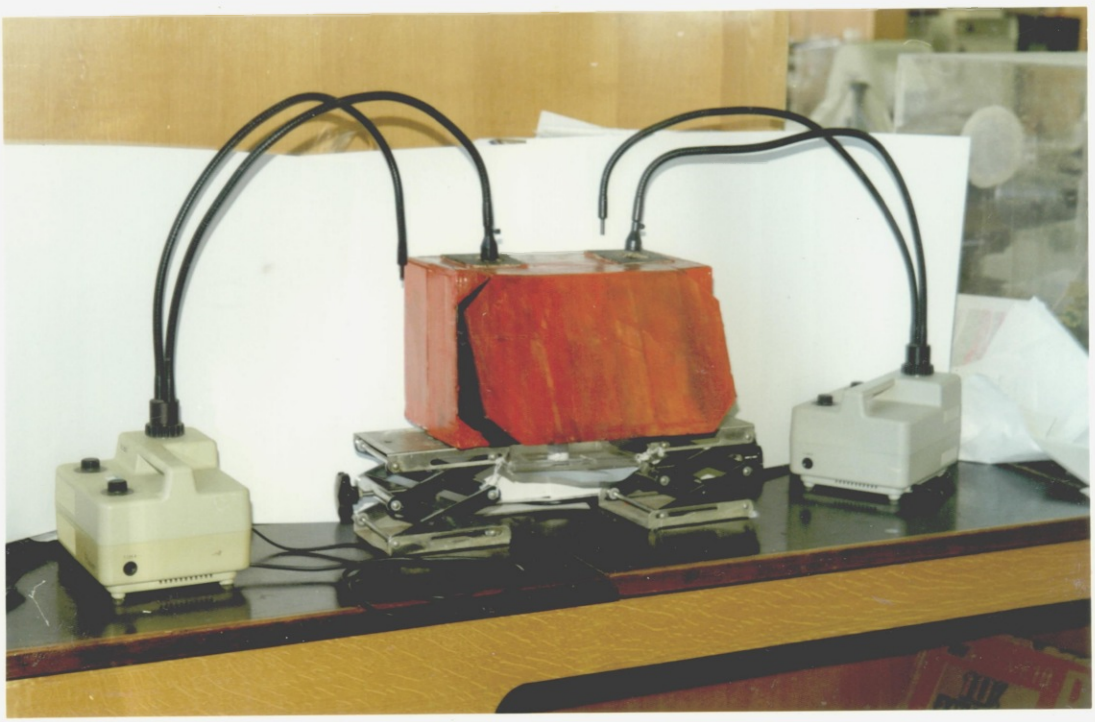
Colour responses of A. matricariae became of more interest when they failed to respond to odour of some of their host plant leaves (Section 5.4).

The objective of this study is to judge whether A. matricariae uses visual cues to orient towards its host plants.

5.5.2 MATERIALS AND METHODS

Female parasitoids used were of about 3 days old, kept isolated in plastic boxes for at least 24 hours without plants and aphids but provided with drops of 50% honey solution.

The parasitoid response to transmitted light was tested in a specially designed light response chamber (Plate 5.2). The chamber was composed of a small cardboard box 17 x 19 x 32 cm which served as a flight arena. A horizontally hinged door was cut in one wall of the chamber to allow access to the interior. The interior of the arena was painted matt black to give sharp contrast. It was not interrupted by supports, so that insects released through a 2.5 cm hole made in the centre of the ceiling (to fit a 2.5 x 5 cm release tube) had an unobstructed view of the light directly below. The lights were directed through two 4 cm^2 windows cut 15 cm apart in the floor. Windows were fitted with movable 6 cm^2 transparent glass mounted between holders in the box and fixed with plastic tape along the edges. The inside surface of transparent glass was smeared with oil to trap insects landing on it. A Schott cold light source KL 1500-T, provided with a Wotan xenophot HLX, 15 V 150 W bulbs, with flexible light guides (swan-neck) was used as a source of light for each window. Heat was kept constant in both sides by using heat filters Schott KG1, 3 mm thick (42 x 42 x3 mm) ref. no 158300 which were fixed in filter holders just in front of the bulb. Brightness was controlled by a brightness control which offers brightness in



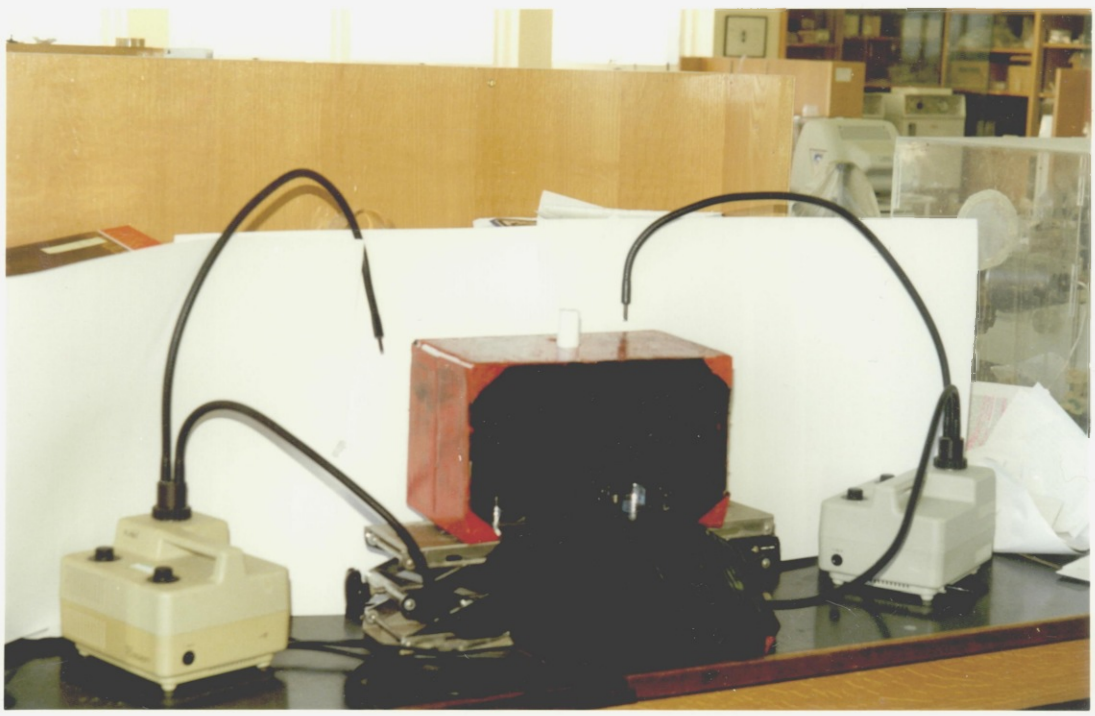


Plate 5.2 FLIGHT CHAMBER FOR TESTING A. matricariae RESPONSE TO MONOCHROMATIC LIGHT

stages. The lower brightness limit could be extended by increasing the distance from the lamp and by using neutral grey filters or Kodak wratten neutral density filters, in the filter holder. The intensity of the test light was measured 5 mm from the ground glass inside the flight chamber using a photometer. An intensity of about 10-15 W/m^2 was used throughout the experiments. Filters with screw or push fittings were used in combination with the focusing attachment with spherical lens at the end of swan-neck. Four screw fit filters ref. no. 158210 in blue, red, green and yellow were used. The four filters used, their respective manufacturer number and dominant transmission wave length are given below:

B.W 19E 023 3x yellow 560 nm

B.W 19E 091 8x red 670 nm

B.W 19E 480 5x blue 430 nm

B.W 19E 461 4x green 514 nm

Colours were compared in two way comparisons. During each test, 10 female parasitoids were released at the ceiling through the 2.5 cm hole made in the ceiling. Each test lasted 30 minutes. Different parasitoids were used for each test. After testing the hinged door was raised and the number of parasitoids captured on the sticky glass was counted and removed. A washed glass with fresh oil was used for each replicate. Five replicates were made for each test. The time between replicates varied with a maximum of 24 hours. The parasitoid attraction to each of the transmitted colour light was expressed as the mean number of insects captured on each. The attractiveness of any two colours was statistically compared using a paired t-test. All trials were carried out at a laboratory temperature of 20 ± 4°C inside a large cardboard box (45 x 30 x 22 cm) painted matt black with zero intensity reflection to prevent distraction.

5.5.3 RESULTS

Table (5.11) shows that in tests using two colours, A. matricariae female's response to transmitted coloured light differed with the colour group tested. A preference for green was dominant. The parasitoid showed a significant preference for green colour over the other 3 colours ($P<0.001$). The least preferred colour was the red one. When compared with all other colours, a highly significant ($P<0.001$) preference was shown for the non-red in all series tested. The parasitoid heirarchy of preference was green, then yellow, then blue.

5.5.4 DISCUSSION

The results of the sensitivity of A. matricariae to different wave lengths of monochromatic light clearly indicates that green and yellow were particularly favoured with green being the most attractive. This attraction to colours such as green and yellow, which is independent of odour, suggests that the female parasitoid is attracted to plant leaves through visual cues. Since yellow comes second in the heirarchy of preference, it seems that in the field or glasshouse, green, green yellow and yellow or different shades of green are attractive. This is because positive attraction is not absolute. There is still some attraction to the less preferred colour yellow. But the avoidance of red was almost absolute when comparisons were made with the rest of colours.

The colour of most leaves of different plants does not differ much in hue. The hue is always at yellow - green of about 550 nm. But leaves in general differ in intensity and tint. The colour of potato and turnip leaves are characterized by low intensity of about 20% (Southwood, 1986). It is therefore most likely that if insects adapt at all they are adapted to specific tint or intensity, although such responses seen unlikely. It is possible that some species have evolved a degree of preference for the

Table 5.11 MEAN NUMBER OF A. matricariae ATTRACTED TO TRANSMITTED MONOCHROMATIC LIGHT IN PAIRED CHOICE TESTS (n=10)

Choice test	Green		Red		Yellow		Blue		
	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.	
1	8.6	0.24	0.0	0.0					***
2	6.8	0.37			3.2	0.34			**
3	8.2	0.3					0.8	0.19	***
4			0.0	0.0	5.6	0.24			***
5			0.0	0.0			3.6	0.25	***
6					4.8	0.58	2.2	0.2	**

Paired t test ** (P<0.01) *** (P<0.001)

colour of their host plants especially those species whose host plants have colours different from normal green. However, it is most likely that the response of A. matricariae is not specific to green. The attraction is possible to all shades of green plant foliage. If this happens it excludes the possibility that the response is a specific attraction to certain food plants of its host M. persicae. Since M. persicae is extremely polyphagous attacking a wide range of host plants. Such nonspecific response seems to be advantageous for parasitoids which do not limit themselves to specific hosts. It was difficult to obtain all hues in exactly the same brightness, so, such preference for green and yellow may not be translated as a true colour vision for A. matricariae. Evidence that parasitoid compound eyes show major peak sensitivities at 514 nm and 560 nm would need electrophysiological studies. But Agee, Boller, Remund, Davis & Chambers (1982) claim that specific colours to which a species is most responsive need not correspond with the wave lengths to which the photoreceptors of that species are most sensitive, i.e., response may be controlled by a higher order of neural input than the first order receptor level.

In the present study the parasitoid was captured after arriving at a colour source by a sticky substance on glass so no account was made of the length of time it might remain in an area lacking plant and aphids. The results are comparable with that found in the literature. The pea aphid parasitoid Aphidius ervi Haliday was tested for its response for transmitted light. In dual choice tests, green (wave length 514 nm) was six times more attractive than blue green (424 nm), or two times more attractive than yellow green (523 nm). Yellow green was two times more attractive than blue green (Goff & Nault, 1984). A preference for green was also reported by Hollingsworth, Hartsack & Lingren (1970) for spectral response of the adult ichneumonid wasp Campoletis perdistinctus Viereck. But Arthur (1966) found that the ichneumonid Itoplectis conquisitor (Say) demonstrated a response for blue. This is most probably a short wave response characteristic of

dispersal flight and can not be considered as a host habitat location mechanism. Under the present study, such possibiliy is excluded or at least made minimum by the especially designed flight chamber in which monochromatic light shone through windows on the floor. Such design facilitates landing flight studies which could be considered in a host habitat location mechanism. It seems that response to green serves as a mechanism by which flying parasitoids generally orient to vegetation. Their aphid hosts do so in response to yellow (Kennedy, Booth & Kershaw, 1961). Thus, long distance orientation for A. matricariae appears to be dominated by nonspecific signals such as vegetation colour. Such an orientation might be an early step in the parasite location of its host habitat. Nevertheless, such behaviour of A. matricariae corresponds with general common sense which allows the parasitoid the variability which may be necessary to gain the greatest dispersion to cope with a wide range of host plants of its host aphid.

SECTION 6 GLASSHOUSE EXPERIMENTS

6.1 THE AGGREGATION RESPONSE OF A. matricariae

6.1.1 INTRODUCTION

One mechanism that has received much attention recently is aggregation by parasitoids to patches with relatively many hosts (Hassell & May, 1974; Waage, 1978, 1979; Hassell, 1984; Lessels, 1985; Hagvar & Hofsvang, 1987). Up to now, the behaviour and foraging strategies of only a few parasitoids have been examined and even these have only been studied within a limited environmental concept (Vinson, 1984). The aggregation response is defined by Hassell (1982) as the relationship between the number of searching parasitoids or some comparable measure such as the time spent searching and host density per patch. Waage (1978) defined the patch as an area containing the contact chemical produced by the host, the limit of chemical describes the limit of host movement and the chemical elicits a distinct arrestment response in moving parasitoids. Parasitoids discover their environment at several hierarchical levels and forage in stages. The forager in response to physical and chemical cues is first attracted to one level and then arrested within it while seeking out lower level cues in pursuit of their prey (Waage, 1978). The search is thus gradually confined to successively smaller sections of the habitat until the host is located. Hafez (1961) presumed that movement between these sections are random. The allocation of foraging time between patches of hosts involves the two decisions of which patches to visit and how long to spend in each patch. Cook & Hubbard (1977) states that 'in consideration of the strategies adopted by insect parasitoids when searching for their hosts it is realistic to assume that an underlying objective of their behaviour is to have as many offspring as possible which survive to reproduce in the next generation'. Natural selection will favour those strategies which result in reproductively efficient distribution of the parasitoid's egg complement

among the available host population. Ayal (1987) found a high directional nonrandom search for D. rapae suggesting a highly developed foraging strategy. It is now well established that direct density dependent relationships from patch to patch can be a powerful stabilizing influence on interactions (Hassell, 1984).

The study of foraging behaviour and measurement of parasitism in the glasshouse is important in evaluating the potentials of A. matricariae. The aim of this study is to examine the aggregative response of A. matricariae under glasshouse conditions.

6.1.2 MATERIALS AND METHODS

Host plants Brassica campestris rapa were sown about the same time for each replicate. They were potted singly in pots of 12 cm diameter containing peat based compost. They were grown under ordinary glasshouse conditions until about 2 weeks before the start of the experiment. The plants were about 15-22 cm in height with 5-7 leaves throughout the experiment. The plants were infested in the glasshouse with different number of aphids from a stock culture 1-3 days before the experiment. The final aphid number was counted and adjusted on the same morning as the experiment started. The infestation was carried out in such away that different categories of plants with about the same density per plant were obtained. Each experiment had 6 categories of densities selected as 0, 20, 50, 100, 300 and 600 aphids, 4 plants for each category. In all 24 plants were arranged in 6 rows. The position of different plants with different densities was at random to eliminate any bias in the set up. The plants were placed 15 cm apart in every direction. The same arrangement was repeated for all replicates. The number of replicates were 3. The time elapsed between any two replicates was about 2 weeks. In each experiment 50 females of A. matricariae were released over the plants. The parasitoids were less than 3 days old. All experiments started early in the morning.

The number of parasitoids on each plant was recorded, by carefully examining all leaves on each plant, at intervals of 1, 2, 3, 6, 9 and 24 hours after the release of parasitoids. The parasitoids did not seem to be disturbed by such examination. After the last inspection, the parasitoids were collected with the use of an aspirator from the plant, those on walls and ceilings were left to die before the beginning of a new replicate. Mummies on the plants were counted within 7-8 days from the time of release of parasitoids and removed. Percentage parasitization was calculated for each plant by dividing the number of mummies on the plant by its initial aphid density. The study was carried out during May-September, 1989 in small glasshouse cubicles. Temperature varied between 20 - 30°C during day time and between 20 - 18°C during the night. Photoperiod varied from 16 - 11 hours according to the month.

6.1.3 RESULTS

Table (6.1) shows the average number of females observed per plant, at different host densities and different intervals from the release. After one hour from release, there was no significant difference ($P>0.05$) in the number of females accumulated at different host densities. From 2 hour on, there were significantly higher numbers of females accumulating at high densities of 100, 300 and 600 ($P<0.05$). This trend of accumulating at high densities especially of 100, 300 and 600 increased significantly ($P<0.05$) with time after release as well. The colonization pattern is illustrated in Figure (6.1). The percentage parasitism decreased with an increase in density (Figure 6.2). The relationship between percentage parasitism, estimated from the number of mummies on the plants that resulted from the visitation pattern during 24 hours, and host aphid density was tested for linearity by constructing a 2 x 5 contingency table (Table 6.2) (Steel & Torrie, 1981). The regression coefficient of proportion of mummies p_i on the score (Z_i) is tested. On the null hypothesis, no relation between p_i

Table 6.1 AVERAGE NUMBER OF A. matricariae FOUND ON TURNIP INFESTED WITH DIFFERENT DENSITIES OF M. persicae RECORDED AT VARIOUS TIME PERIODS AFTER THE PARASITOID RELEASE (n=50)

Host density	hours after release						
	1 hr	2 hr	3 hr	6 hr	9 hr	24 hr	Row
	l.s.d.	l.s.d.	l.s.d.	l.s.d.	l.s.d.	l.s.d.	l.s.d.
	1.524	0.8303	1.145	0.7834	0.8685	0.5885	
0	1.5 A a	0.2 B f	0.4 B c	0.1 B b	0.1 B b	0.2 B d	0.822
20	1.4 A a	0.8 B c	0.5 B c	0.4 B b	0.6 B b	0.3 B d	0.736
50	1.0 B a	1.3 B bc	1.5 B cb	0.8 B b	2.8 A a	1.7 B c	1.125
100	1.1 C a	1.8 BC bc	2.1 AB ab	2.7 A a	2.7 A a	2.5 AB b	0.791
300	2.1 C a	2.2 BC a	3.2 A a	2.9 AB a	3.2 A a	3.4 A a	0.768
600	1.6 C a	2.1 BC a	3.0 ABC a	3.1 ABC a	3.4 AB a	3.7 A a	1.529

All l.s.d. values are at the 5% level, means within columns sharing the same small letters (a-d) are not significantly different at the 5% level, means within rows sharing the same capital letters (A-D) are not significantly different at the 5% level.

Table 6.2 TESTING A LINEAR REGRESSION OF PROPORTION OF APHIDS PARASITIZED (p_i) ON THE SCORE (Z_i) WHEN RELEASING 50 A. matricariae AT DIFFERENT DENSITIES OF M. persicae

Aphid density	Score Z_i	Parasitized aphids n_{i1}	Nonparasitized aphids n_{i2}	Total n_i	P%	$n_i Z_i$
20	0.2	18	42	60	70	12
50	0.5	54	96	150	64	75
100	1.0	129	171	300	57	300
300	3.0	471	429	900	48	2700
600	6.0	993	807	1800	45	10800
		1665	1545	3210	5669	13887
		n_1	n_2	n	P	

P% = proportion of aphids parasitized as a percentage. Data taken from total of 3 replicates.

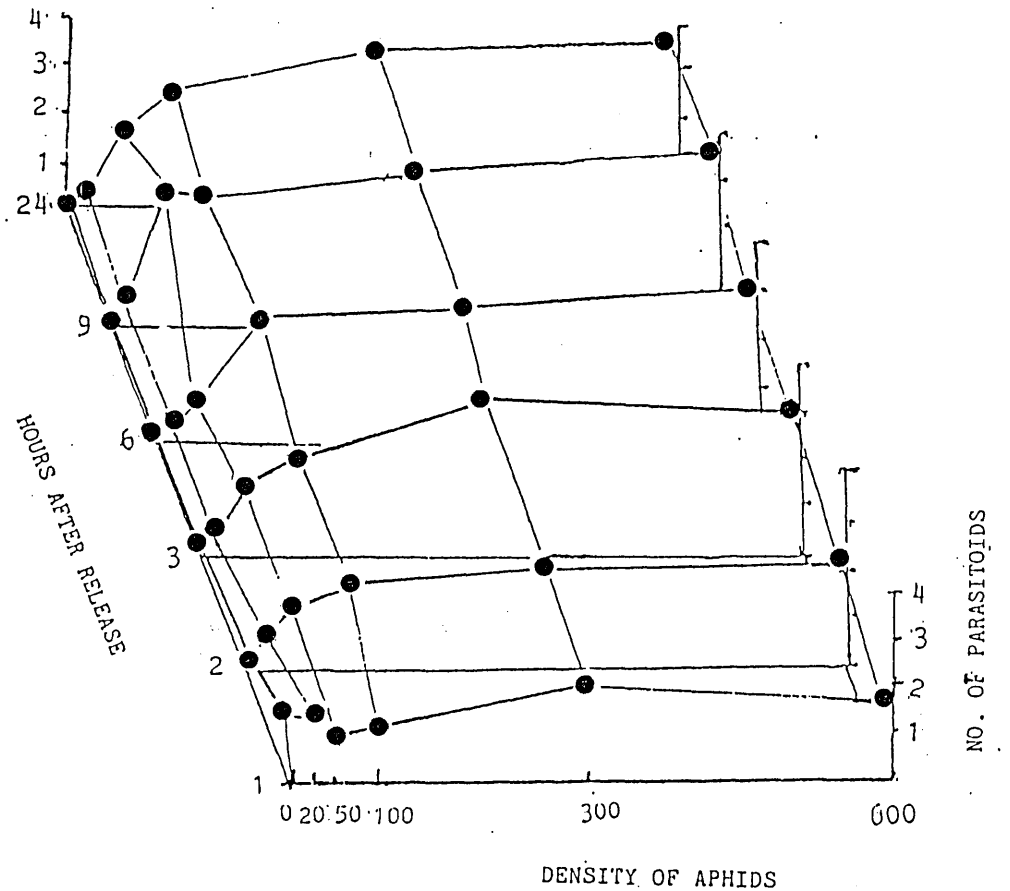


Figure 6.1 MEAN NUMBER OF A. matricariae ON TURNIP INFESTED WITH DIFFERENT NUMBERS OF M. persicae, RECORDED AT VARIOUS TIME PERIODS AFTER THE PARASITOID RELEASE.

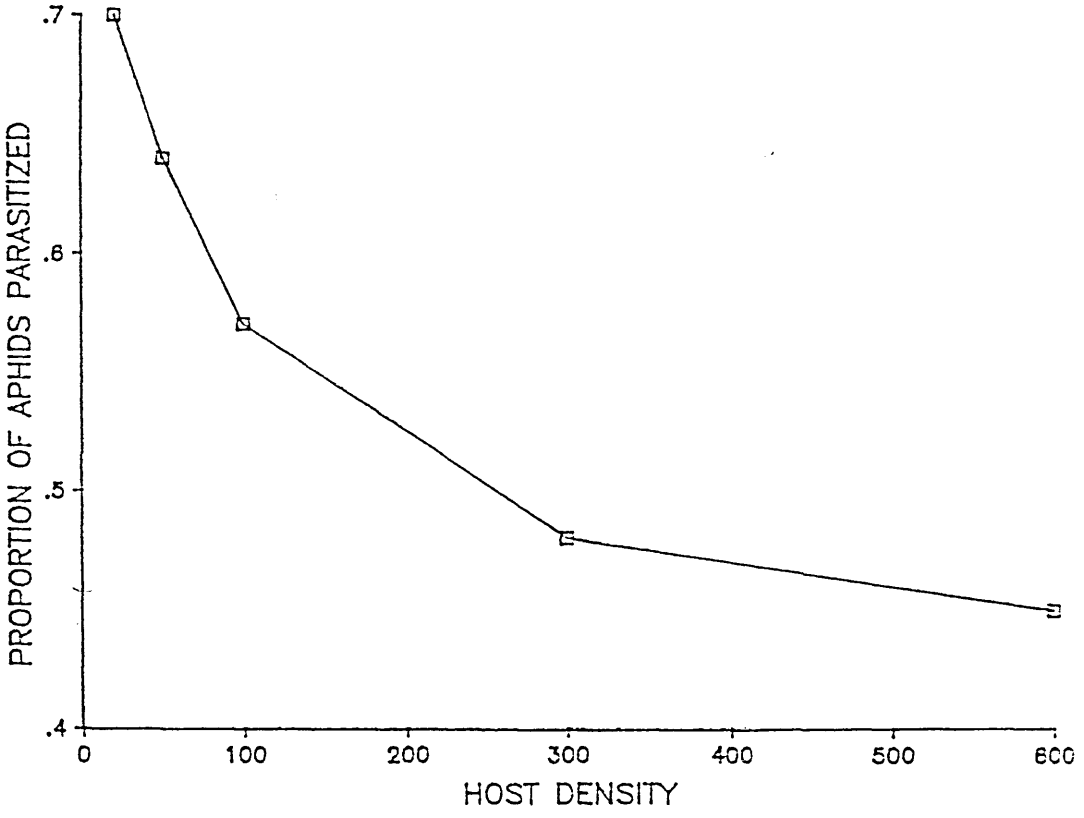


Figure 6.2 THE RELATIONSHIP BETWEEN PERCENTAGE PARASITISM BASED ON A MUMMIES COUNT AND M. persicae DENSITY

and Z_i is assumed. Each p_i is distributed about the same mean, estimated by P with variance Pq/n_i. The regression coefficient b is calculated as usual except that each p_i must be weighted by the sample size n_i on which it is based (Snedecor & Cochran, 1980). The criterion for testing b is given by the following equation:

$$\chi^2 = \frac{\left[\sum_i n_{i2} Z_i - n_{\cdot 2}(\sum n_i . Z_i / n_{\cdot\cdot})\right]^2}{\left[\sum_i n_i . Z_i^2 - \left(\sum_i n_i . Z_i\right)^2 / n_{\cdot\cdot}\right](\bar{p})(1-p)}$$

which distributed approximately as χ^2, and has one degree of freedom

$$\chi^2 = \frac{[(42x0.2+96x0.5+171x1+429x3+807x6) - (1545)(13887)/3210]^2}{[12x0.2+75x0.5+300x1+ 2700x3+10800x6 - (1387)^2/3210](.5669)(.43308)}$$

$$\chi^2 = 107275.84/3231.655 = 33.20 \text{ ***}$$

This indicates a highly significant inverse linear relationship between the host aphid density and the percentage of aphid parasitized.

6.1.4 DISCUSSION

The results clearly indicate that the parasitoids A. matricariae tend to aggregate on plants with high host densities. This phenomenon became more prominent with time. In the real world the time spent by searching parasitoids in a patch and hence the aggregative response will depend primarily upon the probability of the plants being discovered and the time they spent there (Morrison & Strong, 1980). Aggregation in this experiment is most probably due to differences in the duration of visits to different density patches. The duration of visits to different density patches is influenced by arrestment responses to host secretion e.g. honey-dew or to rate of oviposition, both of which lead to arrestment on high host densities. Such a kind of arrestment is shown in (Section 5.2). Increasing the concentration of contact chemical on a patch which is effected by

increasing host density was found to increase the duration of patch visit (Waage,1978). The aggregation in high host density patches can probably arise through innate responses to host associated stimuli. A. matricariae has been shown to positively respond to aphid host and aphid secretion honey-dew in an olfactometer (Section 5.4). It is more probable that A. matricariae uses odour cues from M. persicae colonies to find aphid infested plants, once in the habitat. Odours from aphid colonies are certainly easier to discover from a plant with a high host density than from one with a low aphid density. A parasitoid might aggregate in higher density host patches simply because odour plumes from these patches will be more concentrated and therefore more likely to be intercepted and successfully followed (Waage, 1978). Cook & Hubbard (1977) and Waage (1978) have developed optimality models to describe and interpret host finding behaviour in parasitic wasps. Optimal foraging theory proposes that parasitoids can maximize their oviposition rates by aggregating in high density patches of hosts. Hagvar & Hofsvang (1987) found that the aphid parasitoid Ephedrus cerasicola Stary when released into a small glasshouse containing paprika plants infested with different numbers of M. persicae, soon gathered on the most heavily infested plants. This non-random distribution is found also for Diaretiella rapae (McIntosh) whose hosts are distributed in clumps (Hafez, 1961). So, the classical modelling of parasitoid foraging as random (Nicholson & Bailey, 1935; Holling, 1959b) may therefore be appropriate to foraging within a level of environmental patchiness, as occurs in artificial set ups in the laboratory where a particular level of foraging is isolated from the natural sequence.

The corresponding pattern of percent parasitism per density (Fig 6.2) shows that despite the marked tendency for parasitoids to aggregate in the patches of high host density, parasitism per density is inversely density dependent. Despite the fact that direct density dependent relationships from patch to patch can be a powerful stabilizing influence on interactions

(Hassell, 1984). However, many have failed to detect density dependence. For example Morrison & Strong (1980) reported inverse density dependent relationships where percent parasitism is greatest in the lowest density patches. Such an inverse density dependence has been frequently reported recently (Hassell, 1982; Lessells, 1985). An inverse density dependence is also obtained (Section 4.3), in which a decelerating type 2 functional response was found for A. matricariae. Inverse density dependent parasitism, despite aggregation on high density hosts, may well be due to the increasing costs of energy and increasing time of finding each additional host. The costs of achieving a given proportion of parasitized hosts is therefore greater on high than on low density hosts. Morrison & Strong (1980) and Hassell (1982) present three reasons for that:

1. The parasitoid females may suffer egg depletion at high host density.

2. There may be higher rates of encounter with already parasitized hosts on high host density.

3. The handling time limits the exploitation of high host density.

The high fecundity rate for A. matricariae (Section 2.3), make depletion of eggs a poor explanation. Hagvar & Hofsvang (1987) put forward another explanation, of aphid escape behaviour. Aphid alarm pheromones may be more effectively spread in dense aphid colonies resulting in more frequent use of escape mechanisms as kicking or walking away. Interference has been shown to increase the rate of dispersal for D. rapae (Akinlosotu, 1978) and also has been reported to reduce searching efficiency (Beddington, 1975; Hassell, 1971). Therefore physical interference may be added as a possible reason for why percentage parasitism did not increase with host density.

The results obtained for visual and olfactory responses (Sections 5.5 & 5.4) respectively, suggest that host habitat selection by A. matricariae involves long range visual attraction to the green colour of plants which

most likely operate at high foraging levels, followed by chemical attraction to odours emanating from hosts or secretions associated with hosts which appear to operate at a lower level. Such results in addition to the effect of plant topography (Section 5.3) added to the present findings of aggregating at plants with high host densities indicates a highly developed foraging strategy employed by A. matricariae to maximize profitability mirrored in repeatable patterns of predetermined and advanced directional search.

6.2 EFFECT OF PARASITISM BY A. matricariae ON AGE SPECIFIC FECUNDITY AND POPULATION GROWTH OF M. persicae

6.2.1 INTRODUCTION

To assess the effect of parasitism, in the dynamics of host-parasitoid populations of M. persicae and A. matricariae, host aphid development and reproduction after parasitization should be investigated. Among the consequences of parasitism by entomophagous species are biochemical and physiological effects that frequently cause reduction in the growth, longevity and reproductive achievement of the host (Campbell & Mackauer, 1975b). For aphidiids these changes appear gradually as they do not inject a venom into the host during attack or oviposition. So, the host aphid continues to feed, grow and may even produce some progeny until the developing parasitoid larvae reaches a crucial destructive stage after completing about 30% of total development period, in the 3rd or 4th instar (Vevai, 1942; Stary, 1970). Various authors, Fox et al., (1967); Campbell & Mackauer (1975b); Liu Shu-sheng & Hughes (1984b) and Sequeira & Mackauer (1988) reported that aphids that became parasitized at an early nymphal stage will die before reaching the adult stage. However, when older instars became parasitized they reached maturity and produced a limited number of offspring before collapsing from the effects of parasitism. Campbell & Mackauer (1975b) demonstrated a quantitative effects of parasitism by Aphidius smithi Sharma & Subba Rao on the pea aphid Acyrthosiphon pisum (Harris) reproductive performance. Liu Shu-sheng & Hughes (1984b) and Sequeira & Mackauer (1988) follow the same procedure in assessing the impact of parasitism on the aphid reproductive achievement. The aim of this study is to assess the impact of parasitism by A. matricariae on reproductive performance of M. persicae in the glasshouse.

6.2.2 MATERIALS AND METHODS

Parasitoids used were females collected within 2-3 days after emergence from laboratory culture. M. persicae of known age were obtained in the laboratory by placing apterous viviparous aphids on clean potted turnip plants for a 4 hour period. Any nymphs produced during this period were transferred to new clean potted brassica plants inside culture cages (820 x 610 x 535 mm) and left to develop until they had reached the required age. In this manner, 7 cohorts of apterous nymphs and adults were obtained as follows:

1st instar	0 - 24 hours old
2nd instar	24 - 36 hours old
2nd instar	48 - 72 hours old
3rd instar	3 - 4 days old
4th instar	5 - 6 days old
adult	7 - 8 days old
adult	8 - 9 days old

A cohort of 20 aphids of identical age were placed on the underside leaves of potted turnip plants B. campestris rapa inside experimental arenas 22 cm tall, 14.5 cm in diameter made of transparent acetate with circular opening of 5.5 cm on top covered with gauze 40 mesh/cm for aeriation. Aphids were exposed to parasitization attack by introducing one female parasitoid into the arena for a period of 3 hours. After removal of the parasitoid, the 20 aphids were divided into 4 groups of 5 aphids each. Each group of 5 aphids was confined by a clip cage of 4.5 cm fastened to the leaves of potted brassica. This procedure was followed for the 7 cohorts of aphids mentioned above. In addition an eighth cohort consisted of 1st instar nymphs but were

not exposed to parasitization and used as a control. Plants were replaced with fresh ones if required. The number of replicates were 4 for each age class and for the control. The experiment was carried out inside a glasshouse cubicle at Wye during April-July, 1989. The temperature reached a maximum of 30°C during day and a minimum of 18°C during night. With 60-80% relative humidity. Aphids in all cohorts, including the control, were examined at 24 hours intervals at the same time. Development, mortality and fecundity were recorded. Dead aphids and any offspring produced were counted and removed. The age at which parasitized aphids died and became mummified was recorded. Aphids that did not show any symptoms of parasitism within 9 days following the attack were discarded and were not considered in the analysis. The effect of parasitism on M. persicae reproduction and population growth was assessed by constructing life tables, age specific fecundity (Mx) and age specific survival (Lx) for each age interval (x) of one day. From these data the intrinsic rate of increase (rm) was calculated from the equation:

$$\Sigma\, e^{-rmx}\, lx\, mx = 1 \qquad \text{(Birch, 1948)}$$

But by using the approximate method of Birch (1948) in which the generation time (T) was obtained by the formula

$$T = \Sigma\, x\, lx\, mx \;/\; \Sigma\, lx\, mx$$

And the intrinsic rate of increase by the formula

$$rm = \log e\, Ro/T \qquad \text{where } Ro = \Sigma\, lx\, mx$$

6.2.3 RESULTS

The data on mean development time from birth to adult, number of individuals mummified, length of reproductive period, mean number of young produced and average life span are presented in Tables (6.3 & 6.4). The age at which an aphid became parasitized influenced its subsequent development

Table 6.3 CONSEQUENCES OF PARASITIZATION BY A. matricariae ON DIFFERENT INSTARS OF M. persicae.

Stage attacked	Development time from birth-adult $F_{6,21}$ = 0.07 NS Mean	s.e.	Number of individuals mummified as 4th instar	as adult	Length of reproductive period l.s.d. 5% = 1.847 Mean	s.e.
1st instar 0-24 h	--		36	00	--	-
2nd instar 24-36 h	7.6	0.23	9	28	--	-
2nd instar 36-72 h	7.5	0.34	4	42	--	--
3rd instar 72-96 h	7.6	0.20	00	56	1.7	0.24 d
4th instar 4-5 day	7.4	0.15	00	49	2.9	0.23 d
Adult (7-8 day)	7.5	0.23	00	52	5.6	0.40 c
Adult (8-9 day)	7.6	0.21	00	48	7.8	0.64 b
Nonparasitized	7.6	0.29	00	00	16.2	1.2 a

NS = nonsignificant at the 5% level. Means sharing the same letters are not significantly different.

Table 6.4 CONSEQUENCES OF PARASITIZATION BY A. matricariae ON DIFFERENT INSTARS OF M. persicae.

Stage attacked	Number of progeny produced l.s.d. 5% = 4.593 Mean	s.e.	Duration of life span l.s.d. 5% = 2.220 Mean	s.e.
1st instar	---	---	6.1	0.18 F
2nd instar 24-36 h	--	---	7.5	0.34 EF
2nd instar 36-72 h	--	- -	8.4	0.29 E
3rd instar	06.3	0.274 e	9.1	0.26 DE
4th instar	11.5	0.535 d	11.0	0.39 CD
Adult (7-8 days)	19.3	1.16 c	12.1	0.76 BC
Adult (8-9 days)	29.2	1.27 b	14.1	1.1 B
Nonparasitized	69.2	2.88 a	27.8	1.6 A

Means within columns sharing the same letters are not significantly different.

and in particular the stage at which mummification occured. Nymphs that were parasitized during 24 hours of birth died as 4th instar. Aphids parasitized as 2nd instar (24-72 hours) or later completed development to mummify as adults. On average the aphids moulted to adults after about 7.5 days. Aphids parasitized on the first instar lived for about 6 days. So, longevity increased as the time of initial parasitization increased. Only aphids parasitized from the 3rd instar on produced offspring. The length of reproductive period was a function of aphid age at parasitization. The mean number of progeny produced per aphid increased with the age of aphid at the time of parasitoid attack.

The duration from initial parasitization to the termination of reproduction and to death (mummification) is given in Table (6.5) Each of the durations was relatively constant.

For a population of aphids all parasitized at the same age, rm can be calculated from the observed age specific fecundity, Mx and survival rates, Lx (Appendices 6.1 - 6.6). The age specific fecundity and survival rates are illustrated in Figures (6.3 - 6.4). The effects of parasitism on M. persicae population growth was reflected in changes in the intrinsic rate of increase, rm, (Table 6.6). Aphids that were parasitized during 72 hours, within the 1st and 2nd instars, contributed insignificantly to population growth. Only aphids that became parasitized during the 3rd instar, or later on, contributed to population growth. Under these conditions the value of rm increased with the age of aphid at the beginning of parasitization. The value of rm for aphids parasitized as adults of 7-8 days old was slightly more than double of those aphids parasitized in the 3rd instar. The curve (Figure 6.5) approached asymptotically the value of the intrinsic rate of increase of unparasitized aphids maintained under similar conditions. This is mirrored in the doubling time which gives the time in days that is required by a population to double in numbers (Table 6.6).

Table 6.5 EFFECT OF PARASITIZATION OF DIFFERENT INSTARS OF M. persicae BY A. matricariae SHOWING TIME TO DEATH AND TERMINATION OF REPRODUCTION (days)

Stage attacked	Duration from time of oviposition			
	To termination of reproduction $F_{3,12}$ = 1.032 NS		To death (mummification) l.s.d. 5% = 0.606	
	Mean	s.e	Mean	s.e.
1st instar 0-24 h	---	--	5.6	0.23 b
2nd instar 24-36 h	---	--	6.33	0.25 a
2nd instar 36-72 h	----	--	5.88	0.21 ab
3rd instar 72-96 h	4.55	0.12	5.83	0.21 ab
4th instar 4-5 days	4.6	0.13	6.4	0.12 a
Adult 7-8 days	4.35	0.09	6.28	0.21 a
Adult 8-9 days	4.58	0.10	6.1	0.18 ab

NS = notsignificantly different at the 5% level. Means sharing the same letters are not significantly different.

Table 6.6 THE EFFECT OF PARASITISM BY A. matricariae ON THE DEMOGRAPHIC AND BIOLOGICAL CHARACTERISTICS OF DIFFERENT AGE CLASSES OF M. persicae

Stage parasitized	G.R.R.	Ro	T	rm	λ	DT
3rd instar	6.2	3.22	7.865	0.149	1.16	4.65
4th instar	11.4	7.718	8.098	0.252	1.29	2.75
Adult 7-8 days	20.1	15.6466	8.978	0.306	1.357	2.27
Adult 8-9 days	30.0	23.084	9.8	0.32	1.377	2.17
Non parasitized	69.1	60.764	13.418	0.306	1.357	2.27

G.R.R. = gross reproductive rate (f/f), Ro = net reproductive rate (f/f), T = generation time (days), rm = intrinsic rate of increase, λ = finite rate of increase, DT = doubling time (days).

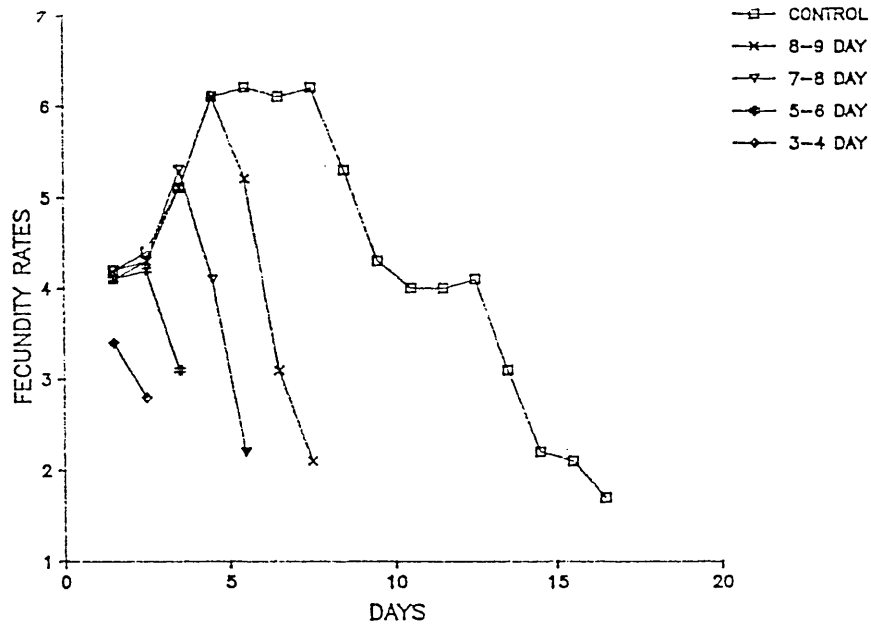


Figure 6.3 AGE SPECIFIC FECUNDITY OF UNPARASITIZED M. persicae AND OF APHIDS PARASITIZED BY A. matricariae AT VARIOUS AGES

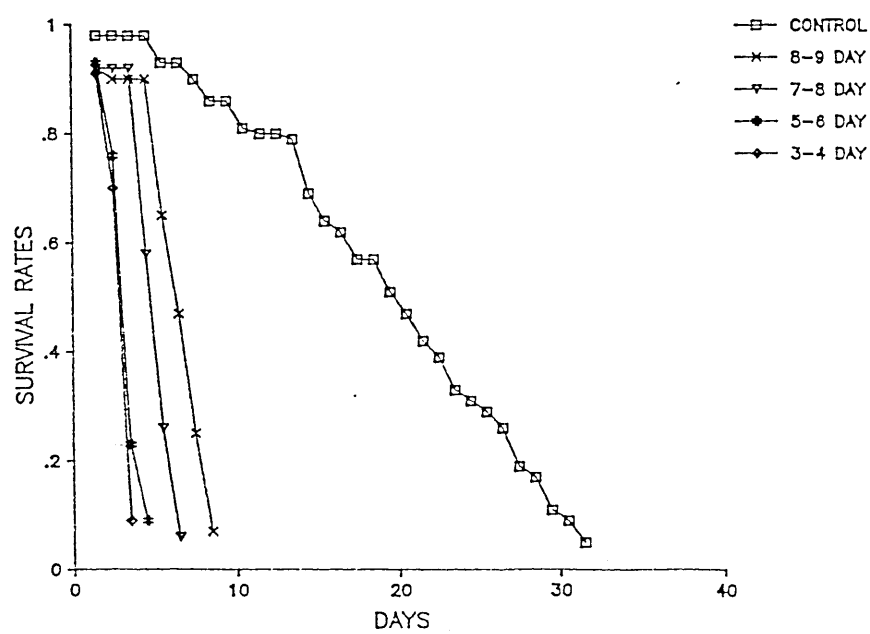


Figure 6.4 AGE SPECIFIC SURVIVAL OF UNPARASITIZED M. persicae AND OF APHIDS PARASITIZED BY A. matricariae AT VARIOUS AGES

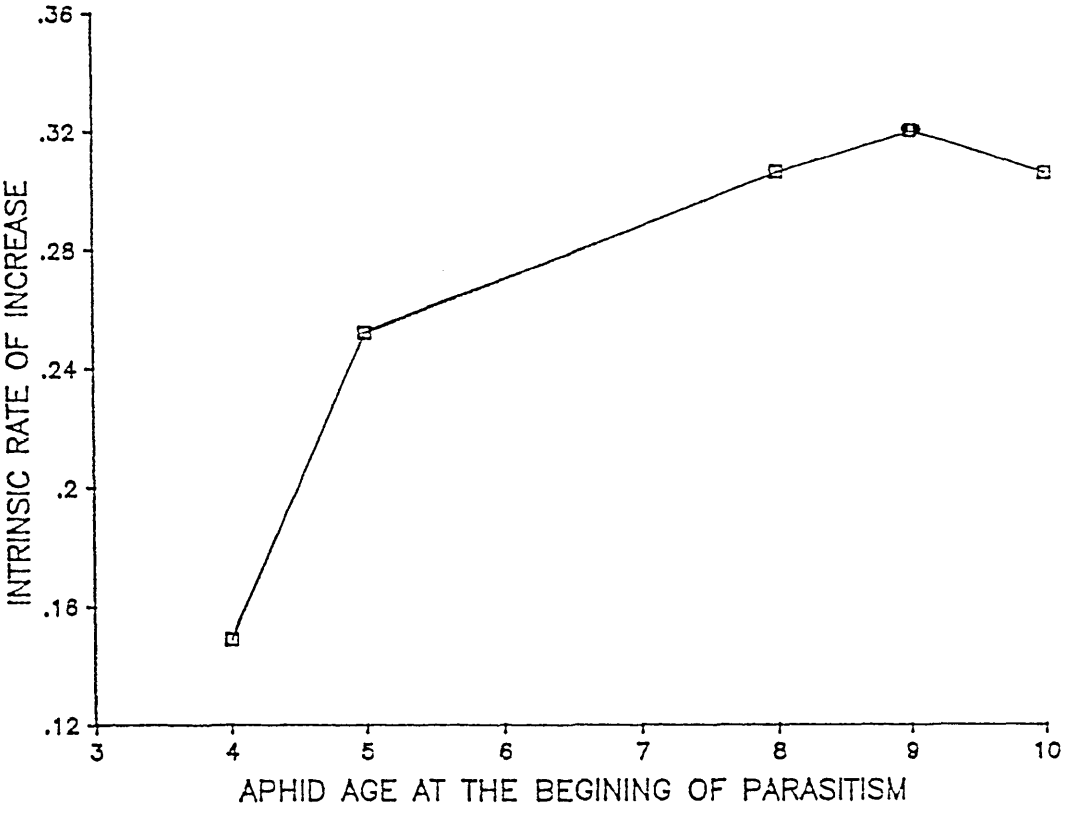


Figure 6.5 THE RELATIONSHIP BETWEEN THE INTRINSIC RATE OF INCREASE OF M. persicae AND APHID AGE AT THE BEGINNING OF PARASITISM BY A. matricariae

6.2.4 DISCUSSION

The rate of development, longevity and reproductive pattern of unparasitized M. persicae under the present study compare well with published data (Barlow, 1962; DeLoach, 1974; Shalaby & Rabasse, 1979; Hagvar & Hofsvang, 1986). Natural populations of aphids typically show a broad overlap of generations, and thus results in individuals of several or all instars and morphs simultaneously available to attack by the parasitoid. So particular examination of the significance of host age at the time of initial parasitization is important. The present results agree well with the general picture found in such studies with aphidiids. Parasitization in the 1st and 2nd instars totally inhibits the aphids from producing offspring. Whereas a reduced aphid progeny production results from parasitization in later nymphal instars and in newly emerged adult aphids. In most studies, only hosts parasitized from the 4th instar on reproduce. Although occasional reproduction from those parasitized in the 3rd instar has been observed by some authors (Campbell & Mackauer, 1975b; Liu Shu-sheng & Hughes, 1984b) and in the present results. But Hagvar & Hofsvang (1986) reported that M. persicae may reproduce when parasitized by Ephedrus cerasicola Stary from the 2nd instar on. This difference is partly explained by the slower rate of egg development in E. cerasicola compared with other aphidiid species in M. persicae (Hagvar & Hofsvang, 1986). The present results show that about 8.8%, 16%, 27.7% and 42.3% of the average progeny of unparasitized aphids is produced, when aphids are parasitized in the 3rd instar, 4th instar, adult of 7-8 days and adult of 8-9 days old respectively.

Parasitism of M. persicae by A. matricariae results in host organs and tissues being slowly destroyed and consumed by the developing parasitoid larvae. Therefore there is a lag period between the beginning of parasitization which is decided by the act of oviposition and the time at

which the effects of parasitism become obvious. The time elapsed from oviposition by A. matricariae to the mummification of M. persicae was about 6 days for all age classes. This means that such time is independent on the host age at which the egg was laid. Such independence is also witnessed for termination of the reproduction of the host, indicating that the rate of development of the parasite is little affected by the host age at the time of initial attack. Such results are in line with what Liu Shu-sheng & & Hughes, 1984b) found for Aphidius sonchi Marshall parasitizing different stages of its host the sowthistle aphid Hyperomyzus lactucae (L.). But it differs from what Mackauer & Kambhampati (1984) reported for D. rapa parasitizing different ages of the cabbage aphid Brevicoryne brassicae (L.) and Sequeira & Mackauer (1988) on Praon pequodorum Viereck attacking different ages of the pea aphid A. pisum. They found that the time from parasitization to host death resulting from destructive feeding by the 4th instar parasitoid larvae varied between cohorts. They suggested a relationship between the parasitoid's rate of growth and development and the host's capacity to satisfy the nutritional demands of the immature parasite stages. In newly deposited 1st instars it is the initially small size whereas in adult aphids it is the presence of large number of embryos that may limit the parasitoid's potential growth rate.

During the lag period the parasitized M. persicae continued to develop relatively normally. When part or all of the lag period occured within the aphid reproductive stage, the aphid would continue to produce offspring, thereby contributing to population growth.

Table (6.5) shows that the finite rate of increase of an aphid population, when parasitized at the age of 7-8 days old, was not significantly different from that of unparasitized aphids. Figure (6.5) shows that the intrinsic rate of increase rises rapidly as the aphid age at the beginning of parasitization increases until an adult of 7-8 days old is reached. Aphids

which are parasitized as adults of 7-8 days old or later show almost similar potential for population increase to that of unparasitized aphids. A. matricariae seems to develop and feed with initially no effects on the rate of development, survival and fecundity of the host. This could result from homostatic mechanisms of the host in response to the feeding of the parasitoid (Vinson, 1975). This allows the host to grow and develop and reproduce normally until the parasitoid reaches a well defined destructive feeding stage usually after about a third of its total development (Vinson & Iwantsch, 1980b). Table (6.4) indicates that the reproduction of M. persicae is unaffected until the parasitoid inside has completed about 4.3 days which is about 33% of its total development time. The time needed by A. matricariae to reach the destructive stage is almost constant independent of the age of the host at the time of parasitization. This means that the harshness of parasitogenic effects depends entirely on the age of host at the time of attack. The younger the host the more severe the effects. Therefore the degree of parasitoid impact on M. persicae population growth depends mainly on the pattern of host instar selection by the A. matricariae female. The present results show that aphids parasitized in the 1st and 2nd instars did not reach the adult stage. Thus if A. matricariae attacks only such young instars, it can probably eliminate M. persicae populations in an isolated area. However, A. matricariae did not parasitize only 1st and 2nd instars but also other nymphal instars as well as adults. The overall impact of parasitism by A. matricariae in the glasshouse seems to largely depend on the age structure of M. persicae populations and on the parasitoid preference for available host ages. The pattern of relative probability of being parasitized among aphids of different instars and morphs is crucial in determining the degree of the parasite's impact on the population dynamics of the host and thus the potential of the parasite as a biological control agents (Liu Shu-sheng & Hughes, 1984b). Other factors being equal, a parasite's preference pattern for particular host ages

determines its potential impact on the host population (Campbell & Mackauer, 1975b; Sequeira & Mackauer, 1988). A parasite that attacks the younger host stages is likely to be more effective than one that attacks the older stages.

CONCLUSION

An understanding of the dynamical behaviour of M. persicae and its parasitoid A. matricariae populations is important in designing control programmes. By combining mathematical models with empirical studies in laboratory and glasshouse, it has been shown how specific components of the parasitoid response to different densities of their host, temperature and sex ratio, influence biological control. Life tables are used extensively as a device for expressing the change in density. However, caution must be taken in applying such methods because in biology events do not always follow mathematical predictions as they do in physics (Coppel & Mertins, 1977).

The processes involved in the regulation of the population density of M. persicae are really quite complex. The temperature requirements of parasitoids are a little higher than that of their hosts. Because of the difference in threshold values the parasitoid takes a little longer to develop than host. This is advantageous for the parasitoid and ensure its survival on emergence. A strong inverse relationship between temperature and longevity was found for the aphid and the parasitoid. The optimum temperature for longevity appears to be 16°C for A. matricariae and 12°C for M. persicae. Longevity of A. matricariae was not much affected by the type of host plant. Honey solution drastically increased longevity of the parasitoid. Longevity data is best described using the Weibull function. There was a strong relationship between the time taken to develop for both species and temperature at which development occurs. In general the aphid takes much less time to develop than the parasitoid. The logistic curve and thermal summation only described the linear portion (12-24°C) of the relationship between rate of development and temperature. A polynomial regression was found to be the more accurate method for describing the temperature-velocity relationship within whole range of (12-30°C). Optimum

temperature range for fecundity is between 16-20°C for both the aphid and the parasitoid. Fecundity decreased outside this range. A. matricariae has a regular oviposition pattern, with one peak of oviposition the second day followed by a gradual decline. Preoviposition and postoviposition periods are extremely short for the parasitoid. The percentage emergence from cocoons was consistent and high but was much less at high temperatures of 28 and 30°C. The development rate of parasitoid progeny was independent of parental age. The sex ratio was almost 1:1 at all temperatures except at 30°C where the proportion of males was much higher. The proportion of female progeny decreased in a linear manner with the age of parent.

The cycling temperature regimes appear to have reduced the lower threshold. The exposure to fluctuating temperatures under the experimental conditions did not have an accelerative effect on development. The thermal limits are widened considerably under cycling and fluctuating conditions. Day degree models predicted development rates reasonably well for both species except where temperature fluctuation went outside the linear range for long periods in May and June. The polynomial regression model predicted development reasonably well and remained consistent under all temperature regimes tested.

Both the aphid and the parasitoid exhibited capacities for increase at all temperatures tested, as all values of rm were positive. The maximum value of rm for A. matricariae was found at 20°C, while it was at 24°C for M. persicae. Most of the contribution to the value of rm was made during the first few days of adult life. At any given temperature between 12-20°C, values of rm for A. matricariae were higher than those for M. persicae. Although aphids develop to maturity faster and survive longer, the parasitoid has a greater total fecundity as well as greater initial fecundity rates. The model of Siddiqui et al., (1973) predicted the values of rm for M. persicae and A. matricariae satisfactorily only within the

linear portion 12-24°C. The Tanigoshi et al., (1975) model would not give any significant improvement over the Siddiqui et al., (1973) model. The proposed polynomial model gave an excellent fit and gave a very good empirical technique to examine the influence of temperature on rm. The rm can be used as a numerical rating index, to measure the effectiveness of the parasitoid, as a climatic index to examine climatic limits of existence and as a growth rate index as rm varies with temperature.

Such studies may provide the basis for future studies of factors regulating populations of both in the field. So the overall mortality of populations can be measured by working out the difference between the potential rate of increase obtained from laboratory conditions and the observed rate of increase in the field. This should take into consideration that, in the field the rate of increase of both populations is influenced by many factors other than temperature. Other environmental factors e.g. humidity, photoperiod, wind, rain, light intensity, etc., preclude the population from reaching the maximum rate of increase. In addition to that, for aphids, other factors such as the suitability of host plants and the different rates of migration and attack by natural enemies may be important as well. Other factors influencing the parasitoid A. matricariae could be the suitability and availability of hosts, searching efficiency, hyperparasitism and competition with other natural enemies. These factors are largely excluded from laboratory experiments.

The host aphid density appears to have no effect on longevity and consequently generation time of the parasitoid. Difference in values of rm is caused mainly by differences in fecundity at different densities. The intrinsic rate of increase, increases with host density, reaching the highest at the highest density of 200. The value of rm was largely determined by the first few days of adult life. The rm values provided a direct comparison of population increase at different densities, so it can be used

as a bio-index.

In nature these biotic factors such as density, crowding, mating, female age and superparasitism interact with each other and with other climatic factors like temperature, humidity and photoperiod in influencing the species development, longevity and fecundity and hence rm. So rm can be used as a quantitative measure of the response of the species to the collective bio and climatic factors as a bioclimatic index.

A curvilinear Holling's type 2 response was found for A. matricariae. The value of handling time indicates that the total egg complement is the limiting factor for maximum parasitization. The type of functional response curve did not change through time. The random parasitoid equation described the data well for the first five days of adult life.

There is evidence that the parasitoid was able to discriminate between parasitized and nonparasitized hosts. However, they do not consistently avoid superparasitism especially when the parasitoid-host ratio is high.

The leaf morphology influenced searching behaviour components. Walking speeds were inversely proportional to hairiness while the rate of turning was positively correlated. The parasitoid exhibited an arrestment behaviour when encountering a honey-dew contaminated leaf. A concentrated search pattern was begun when the parasitoid encounters honey-dew or aphids. Plant structure influenced time spent searching. Much less time was spent on stem, petioles and heart in comparison to leaves. They also spent more time in aphid infested, honey-dew or aphid-exuviae contaminated leaves than clean ones. A higher percentage of parasitization was found on the upper than on the lower surface of leaves.

Olfactometer studies showed that A. matricariae females were strongly attracted by odours from living host aphids, honey-dew and host aphid exuviae but they showed negative response to host plant odours. In dual

choice tests the parasitoid response to transmitted colour light varied with the colour presented, but a preference for green was dominant followed by yellow.

Response to green most likely serves as a long range attraction which direct flying parasitoids toward vegetation, while aphids do so in response to yellow. The positive response to green, irrespective to plant taxonomic status, would serve the function of host finding in general way. This suggests that habitat colour is used by the parasitoid in its initial location of its host aphid. This means that the visual stimuli from the habitat is associated with a higher level of foraging. As no evidence for olfactory attraction to plants was found, the sense of smell can exert an influence on the choice of the flying female once in the habitat. The chemical stimuli from the host or its honey-dew or exuviae is most likely associated with a comparatively lower level of foraging. Therefore, A. matricariae most likely uses visual cues for habitat finding and then olfactory cues for host finding. This is in accordance with the generally accepted sequence that parasitoids orient first towards their host habitat and secondly towards their host.

The female parasitoids showed a positive aggregative response, leading to an inverse density dependent relationship between per cent parasitism and host density per patch. As the parasitoid uses odour cues emanating from M. persicae, honey-dew, then the higher the densities of their host the higher the concentration of kairomones, the stronger the attraction and the more parasitoid aggregation. The positive aggregative response by female parasitoids may also result from stronger arrestment behaviour in which more time is spent searching in plants with high host densities. The aggregation by parasitoids in high host densities is advantageous in allowing them to maximize their oviposition rates.

It seems that foraging behaviour in A. matricariae is advanced. Female

parasitoids make systematic use of plant habitat colour followed by olfaction of the immediate host environment as they survey plant structure in a preplanned programme.

The consequences of parasitism by A. matricariae showed that only aphids parasitized from the 3rd instar on produced offspring. The longevity of the aphid, the length of reproductive period, the mean number of progeny produced, and hence the intrinsic rate of increase increased with the age of aphid at the time of parasitoid attack.

Biological control involves the manipulation of resident natural enemies native and exotic to increase their regulating capabilities by providing favourable conditions. This biological control tactic is much older than the one involving importation of species (Hagen & van den Bosch, 1968). Since the optimum temperature for parasitoid survival was at 16°C and the maximum rate of increase attained at 20°C, and the rate of increase for the parasitoid was higher than that of its host aphid between 12-20°C, therefore maintaining temperatures below 24°C would be advantageous for the parasitoid. As oviposition occurs during day light, and honey solution greatly increased parasitoid longevity, then increasing photoperiod and spraying honey solution will increase chances of parasitism. The use of kairomones, by spraying honey-dew could promote arrestment behaviour, more parasitoids would spend more time in plants but it may reduce effectiveness by arresting parasitoids on surfaces which do not contain hosts. Polynomial regression models can be used to predict M. persicae population trends in glasshouses based on weather forecast data to time A. matricariae releases. In glasshouse biological control, seasonal inoculative releases of parasitoids constitutes a strategy intermediate between classical and inundative release (Hussey & Bravenboer, 1971). The parasitoid populations must be protected by using only selective chemicals, only when necessary and with utmost caution.

A. matricariae appears to be a good prospect for biological control of M. persicae in glasshouses. Still, many questions wait to be answered, among them, the impact of hyperparasitism, multiparasitism and competition with other natural enemies especially fungi needs investigation.

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APPENDICES

Appendix 2.1 FUNCTIONAL PART OF PROGRAMME WRITTEN IN "BASIC" TO PREDICT DEVELOPMENTAL PERIODS BY ACCUMULATING DAY DEGREES

```
10 REM PART OF A PROGRAM TO CALCULATE ACCUMULATING DAY DEGREES
20 REM COMMODORE BASIC
30 INPUT"THERMAL CONSTANT";TC:REM                E.G. 3159 HOUR DEGREES
40 INPUT"LOWER THRESHOLD";LT:REM                 E.G. 5.28°C
50 PRINT"INPUT STARTING RECORD POSITION":INPUT RP:HT=1
60 DOPEN#2,"GLASSDATA",L35:REM DISC FILE WITH GLASSHOUSE DATA
70 RECORD#2,(RP)
80 INPUT#2,MT:HT=HT+1:REM INPUT MONITORED TEMP FROM DISC  E.G.  24°C
90 EH=(MT-LT):REM HOUR DEGREES ACCUMULATED IN ONE HOUR
100 ET=ET+EH:REM HOUR DEGREES TOTAL
110 IFET<TCTHEN80
120 DCLOSE#2
130 PRINT"LIFE CYCLE COMPLETE IN";HT/24;"DAYS":END
```

Appendix 2.2 FUNCTIONAL PART OF PROGRAMME IN "BASIC" TO PREDICT DEVELOPMENTAL PERIODS AT DIFFERENT TEMPERATURES FROM POLYNOMIAL REGRESSION FITS TO CONSTANT TEMPERATURE DATA

```
10 REM PART OF A PROGRAMME TO PREDICT LIFE CYCLE IN THE GLASSHOUSE
20 REM COMMODORE BASIC
30 DIM PR(12):REM DIMENSION POLYNOMIAL COEFFICIENTS
40 DOPEN#1,"BUGFILE",L10:REM OPEN DISC FILE CONTAINING POLYNOMIAL DATA
50 INPUT#1,PR(1):REM POLYNOMIAL ORDER            E.G.   5
60 INPUT#1,PR(2):REM COEFFICIENT A               E.G.  -0.0522587776
70 INPUT#1,PR(3):REM COEFFICIENT B               E.G.   0.0258665253
80 INPUT#1,PR(4):REM COEFFICIENT C               E.G.  -0.00367472692
90 INPUT#1,PR(5):REM COEFFICIENT D               E.G    0.000275501649
100 INPUT#1,PR(6):REM COEFFICIENT E              E.G   -0.00000860192545
110 INPUT#1,PR(7):REM COEFFICIENT F              E.G.   0.00000091555165
120 INPUT#1,PR(8):REM COEFFICIENT G              E.G.   0
130 INPUT#1,PR(9):REM COEFFICIENT H              E.G.   0
140 INPUT#1,PR(10):REM COEFFICIENT I             E.G.   0
150 INPUT#1,PR(11):REM LOWER TEMPERATURE LIMIT   E.G.   4°C
160 INPUT#1,PR(12):REM UPPER TEMPERATURE LIMIT   E.G.   38°C
170 DCLOSE#1
180 PRINT"INPUT STARTING RECORD POSITION":INPUT RP:HT=1
190 DOPEN#2,"GLASSDATA",L35:REM DISC FILE WITH GLASSHOUSE DATA
200 RECORD#2,(RP)
210 INPUT#2,MT:HT=HT+1:REM INPUT MONITORED TEMP FROM DISC  E.G. 24°C
220 IFMT<PR(11)ORMT>PR(12)THENEH=0:GOTO250:REM SKIP IF OUTSIDE THRESHOLDS
230 FORK=PR(1)TOSTEP-1:EH=EH+(PR(K+2)*MT^K):NEXTK:REM CALC REGRESSION
240 EH=(1/EH)*.0416:REM AMOUNT OF LIFE CYCLE IN ONE HOUR
250 ET=ET+EH:REM ACCUMULATING LIFE CYCLE
260 IFET<1THEN210
270 DCLOSE#2
280 PRINT"LIFE CYCLE COMPLETE IN";HT/24;"DAYS":END
```

Appendix 3.1 FUNCTIONAL PART OF PROGRAMME WRITTEN IN "BASIC" FOR COMPUTING THE VALUE OF rm BY ITERATIVE SUBSTITUTION OF VALUES OF rm

---

```
5   i = 100
10  dim x (i),1(i),m(i)
30  read n
40  read r
50  for i = 1 to n
60  read x (i),1(i),m(i)
110 a = 1(i)*m(i)
120 b = x(i)*r
130 c = 5-b
140 d = exp(c)
150 e = a*d
160 m = M+a
170 t = t+e
230 nexti
250 print"Cum Ro ="m,"Cum Rm ="t
251 list 281
260 rem * x-------i-------m *
270 rem *--------------------*
280 data n value
281 data rm value
282 data x, Lx, Mx
283 data x, Lx, Mx
---  -- --
---  -- --
Ready
run
```

By changing the value in 281 until Cum Rm = 148.4131591, then 281 data ? is the real rm.

Appendix 3.2 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR M. persicae AT 12C

x	Lx	Mx	LxMx	xLxMx
20.5	1.00	0.6	0.6	12.3
21.5	1.00	0.7	0.7	15.05
22.5	1.00	0.8	0.8	18.00
23.5	1.00	1.3	1.3	30.55
24.5	1.00	1.1	1.1	26.95
25.5	1.00	1.2	1.2	30.6
26.5	0.98	1.4	1.372	36.358
27.5	0.98	1.3	1.274	35.035
28.5	0.96	1.3	1.248	35.568
29.5	0.96	1.8	1.728	50.976
30.5	0.95	2.08	1.976	60.268
31.5	0.93	2.2	2.046	64.449
32.5	0.91	2.1	1.911	62.108
33.5	0.91	2.5	2.275	76.213
34.5	0.88	2.3	2.024	69.828
35.5	0.88	2.4	2.112	74.976
36.5	0.86	2.1	1.806	65.919
37.5	0.83	1.9	1.577	59.138
38.5	0.83	2.1	1.743	67.106
39.5	0.80	2.1	1.68	66.36
40.5	0.76	1.4	1.064	43.092
41.5	0.75	1.8	1.35	56.025
42.5	0.70	1.5	1.05	44.625
43.5	0.66	1.3	0.858	37.323
44.5	0.66	1.4	0.924	41.118
45.5	0.63	1.2	0.756	34.398
46.5	0.62	1.2	0.744	34.596
47.5	0.58	1.1	0.638	30.305
48.5	0.50	1.1	0.55	26.675
49.5	0.48	1.2	0.576	28.512
50.5	0.48	1.3	0.624	31.512
51.5	0.46	1.1	0.506	26.059
52.5	0.45	1.1	0.495	25.988
53.5	0.43	1.1	0.473	25.306
54.5	0.43	1.0	0.43	23.435
55.5	0.41	1.1	0.451	25.031
56.5	0.40	0.9	0.36	20.34
57.5	0.40	0.9	0.36	20.7
58.5	0.40	0.8	0.32	18.72
59.5	0.40	0.9	0.36	21.42
60.5	0.38	0.8	0.304	18.392
61.5	0.36	0.7	0.252	15.498
62.5	0.35	0.8	0.28	17.5
63.5	0.33	0.8	0.246	15.621
64.5	0.30	0.8	0.24	15.48
65.5	0.28	0.8	0.224	14.672
66.5	0.26	0.6	0.156	10.374
67.5	0.26	0.6	0.156	10.53
68.5	0.25	0.6	0.15	10.275
69.5	0.23	0.6	0.138	9.591
70.5	0.23	0.5	0.115	8.108
71.5	0.20	0.5	0.1	7.15
72.5	0.20	0.6	0.12	8.7
73.5	0.18	0.6	0.108	7.938
74.5	0.17	0.5	0.085	6.333
75.5	0.15	0.5	0.075	5.663
76.5	0.15	0.5	0.075	5.738
77.5	0.15	0.4	0.06	4.65
78.5	0.13	0.3	0.039	3.062
79.5	0.13	0.1	0.013	1.034
80.5	0.11	0.1	0.011	0.886
81.5	0.11	0.1	0.011	0.897
82.5	0.11	0.08	0.0088	0.726
83.5	0.08	0.0	0.0	0.0
		Σ Mx = 68.56	Σ LxMx = 46.3278	Σ xLxMx = 1787.6

Appendix 3.3 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR *M. persicae* AT 16°C

x	Lx	Mx	LxMx	xLxMx
12.5	1.00	0.9	0.9	11.25
13.5	1.00	1.1	1.1	14.85
14.5	1.00	1.2	1.2	17.4
15.5	1.00	1.1	1.1	17.05
16.5	0.98	1.3	1.274	21.021
17.5	0.96	2.5	2.4	42.0
18.5	0.95	3.8	3.61	66.785
19.5	0.88	3.6	3.168	61.776
20.5	0.86	3.8	3.268	66.994
21.5	0.83	3.8	3.154	67.811
22.5	0.80	3.08	2.464	55.44
73.5	0.76	3.1	2.356	55.366
24.5	0.68	3.3	2.244	54.978
25.5	0.58	2.8	1.624	41.412
26.5	0.50	2.5	1.25	33.125
27.5	0.48	2.4	1.152	31.68
28.5	0.46	2.3	1.058	30.153
29.5	0.45	2.1	0.945	27.878
30.5	0.43	1.8	0.774	23.607
31.5	0.43	1.4	0.602	18.963
32.5	0.41	1.2	0.492	15.99
33.5	0.41	1.3	0.533	17.856
34.5	0.40	1.4	0.56	19.32
35.5	0.40	1.3	0.52	18.46
36.5	0.38	1.3	0.494	18.031
37.5	0.36	1.2	0.432	16.2
38.5	0.35	1.2	0.42	16.17
39.5	0.35	1.1	0.385	15.2075
40.5	0.33	0.9	0.279	12.0285
41.5	0.30	0.6	0.18	7.47
42.5	0.28	0.9	0.252	10.71
43.5	0.26	0.7	0.182	7.917
44.5	0.26	0.6	0.156	6.942
45.5	0.25	0.5	0.125	5.6875
46.5	0.23	0.4	0.092	4.278
47.5	0.20	0.4	0.08	3.8
48.5	0.17	0.1	0.017	0.8245
49.5	0.15	0.08	0.012	0.594
50.5	0.11	0.08	0.0088	0.4444
51.5	0.06	0.06	0.0036	0.1854
52.5	0.05	0.05	0.0025	0.13125
53.5	0.03	0.05	0.0015	0.08025
54.5	0.01	0.05	0.0005	0.02725
55.5	0.01	0.01	0.0001	0.00555
56.5	0.01	0.01	0.0001	0.00565
57.5	0.01	0.01	0.0001	0.00575

Σ Mx =	Σ LxMx =	Σ xLxMx =
63.38	40.8892	957.9105

Approx. generation time (T) = 23.42698, approx. rm = 0.1584

Appendix 3.4 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR *M. persicae* AT 20°C

x	Lx	Mx	LxMx	xLxMx
8.5	1.00	2.2	2.2	18.7
9.5	1.00	2.5	2.5	23.75
10.5	0.98	3.6	3.528	37.044
11.5	0.95	4.4	4.18	48.07
12.5	0.91	4.08	3.713	46.4125
13.5	0.85	4.1	3.485	47.0475
14.5	0.73	4.3	3.139	45.5155
15.5	0.68	4.2	2.856	44.268
16.5	0.56	3.5	1.96	32.34
17.5	0.50	3.6	1.8	31.5
18.5	0.48	3.3	1.584	29.304
19.5	0.45	3.1	1.395	27.2025
20.5	0.43	3.1	1.333	27.3265
21.5	0.41	2.8	1.148	24.682
22.5	0.40	2.8	1.12	25.2
23.5	0.38	2.6	0.988	23.218
24.5	0.36	2.7	0.972	23.814
25.5	0.35	2.3	0.805	20.5275
26.5	0.33	2.1	0.693	18.3645
27.5	0.31	2.1	0.651	17.9025
28.5	0.28	1.8	0.504	14.364
29.5	0.25	1.4	0.35	10.325
30.5	0.23	1.4	0.322	9.821
31.5	0.23	1.3	0.299	9.4185
32.5	0.22	1.3	0.286	9.295
33.5	0.21	1.1	0.231	7.7385
34.5	0.20	1.2	0.24	8.28
35.5	0.18	0.9	0.162	5.751
36.5	0.18	0.9	0.162	5.913
37.5	0.15	0.8	0.12	4.5
38.5	0.15	0.8	0.12	4.62
39.5	0.13	0.7	0.091	3.5945
40.5	0.11	0.8	0.088	3.564
41.5	0.08	0.6	0.048	1.992
42.5	0.05	0.5	0.025	1.0625
43.5	0.05	0.1	0.005	0.2175
44.5	0.03	0.1	0.003	0.1335
45.5	0.01	0.06	0.0006	0.0273
46.5	0.01	0.01	0.0001	0.00465
		Σ Mx = 79.15	Σ LxMx = 43.1067	Σ xLxMx = 712.81095

Approx. generation time (T) = 16.53597, approx. rm = 0.2276

Appendix 3.5 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR M. persicae AT 24°C

x	Lx	Mx	LxMx
7.5	1.00	2.6	2.6
8.5	0.91	4.1	3.731
9.5	0.88	4.3	3.784
10.5	0.80	4.2	3.36
11.5	0.78	4.2	3.272
12.5	0.62	3.3	2.046
13.5	0.50	3.1	1.55
14.5	0.45	3.1	1.395
15.5	0.40	2.8	1.12
16.5	0.38	2.1	0.798
17.5	0.36	1.8	0.648
18.5	0.33	1.4	0.462
19.5	0.28	1.1	0.308
20.5	0.25	1.1	0.275
21.5	0.23	0.9	0.207
22.5	0.18	0.8	0.144
23.5	0.15	0.8	0.12
24.5	0.13	0.7	0.091
25.5	0.11	0.6	0.066
26.5	0.11	0.6	0.066
27.5	0.01	0.08	0.0008
		Σ Mx = 43.68	Σ LxMx = 26.0438

Appendix 3.6 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR M. persicae AT 28°C

x	Lx	Mx	LxMx
8.5	1.00	3.1	3.1
9.5	0.91	3.5	3.185
10.5	0.88	3.6	3.168
11.5	0.85	3.3	2.805
12.5	0.76	2.9	2.204
13.5	0.68	2.5	1.7
14.5	0.62	1.4	0.868
15.5	0.50	1.4	0.7
16.5	0.43	1.2	0.516
17.5	0.38	1.1	0.418
18.5	0.35	0.9	0.315
19.5	0.33	0.8	0.264
20.5	0.28	0.6	0.168
21.5	0.25	0.4	0.1
22.5	0.23	0.4	0.092
23.5	0.18	0.1	0.018
24.5	0.13	0.03	0.0039
25.5	0.05	0.01	0.0005
		Σ Mx = 27.24	Σ LxMx = 19.6254

Appendix 3.7 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR M. persicae AT 30°C

x	Lx	Mx	LxMx	xLxMx
9.5	1.00	2.8	2.8	26.6
10.5	0.76	2.4	1.824	19.152
11.5	0.50	3.08	1.04	11.96
12.5	0.35	1.8	0.63	7.875
13.5	0.26	1.1	0.286	3.861
14.5	0.13	1.1	0.143	2.0735
15.5	0.11	0.01	0.0011	0.01705
		Σ Mx = 12.29	Σ LxMx = 6.7241	Σ xLxMx = 71.53855

Approx. generation time (T) = 10.63913, approx. rm = 0.1791

Appendix 3.8 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT 12°C

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			Sex ratio 1:1		
34.5	1.00	29.4	29.4	1014.3	14.7	14.7	507.15
35.5	1.00	41.6	41.6	1476.8	20.8	20.8	738.4
36.5	0.91	29.2	26.572	969.878	14.6	13.286	484.939
37.5	0.87	24.0	20.88	783.0	12.0	10.44	391.5
38.5	0.79	16.7	13.193	507.9305	8.35	6.597	253.9845
39.5	0.70	12.9	9.03	356.685	6.45	4.515	178.3425
40.5	0.58	8.7	5.046	204.363	4.35	2.523	102.1815
41.5	0.50	5.7	2.85	118.275	2.85	1.425	59.1375
42.5	0.33	5.3	1.749	74.3325	2.65	0.875	37.1875
43.5	0.20	1.2	0.24	10.44	0.6	0.12	5.22
44.5	0.04	0.0	0.0	0.0	00.0	0.0	0.0
		147.7	150.56	5516.004	87.35	75.281	2758.0425
		Approx. T = 36.6366			approx. T = 36.6366		
		Approx. rm = 0.1369			approx. rm = 0.1179		

Appendix 3.9 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT 16°C

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
20.5	1.00	40.7	40.7	834.35	20.35	20.35	417.175
21.5	1.00	50.3	50.3	1081.45	25.15	25.15	540.725
22.5	0.95	34.4	32.68	735.3	17.2	16.34	367.65
23.5	0.87	28.1	24.447	574.5045	14.05	12.224	287.264
24.5	0.75	16.5	12.375	303.1875	8.25	6.188	151.606
25.5	0.62	12.4	7.688	196.044	6.2	3.844	98.022
26.5	0.50	6.1	3.05	80.825	3.05	1.525	40.4125
27.5	0.37	3.1	1.147	31.5425	1.55	0.574	15.785
28.5	0.12	1.1	0.132	3.762	0.55	0.066	1.881
		192.7	172.519	3840.9655	96.35	86.261	1920.5205
		Approx. T = 22.2640			approx T = 22.2641		
		Approx. rm = 0.2313			approx. rm = 0.2002		

Appendix 3.10 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT 20°C

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	51.7	51.7	697.95	25.85	25.85	348.975
14.5	1.00	69.1	69.1	1001.95	34.55	34.55	500.975
15.5	0.83	44.8	37.184	576.352	22.4	18.592	288.176
16.5	0.66	26.3	17.358	286.407	13.15	8.679	143.2035
17.5	0.58	19.5	11.31	197.925	9.75	5.655	98.9625
18.5	0.50	10.1	5.05	93.425	5.05	2.525	46.7125
19.5	0.16	3.1	0.496	9.672	1.55	0.248	4.836
		224.6	192.198	2863.681	112.3	96.099	1431.8405
		Approx. T = 14.8996			approx. T =14.8996		
		Approx. rm = 0.3529			approx. rm = 0.306		

Appendix 3.11 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT 24°C

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
11.5	1.00	34.5	34.5	396.75	17.25	17.25	198.375
12.5	0.70	41.4	28.98	362.25	20.7	14.49	181.125
13.5	0.50	21.2	10.6	143.1	10.6	5.3	71.55
14.5	0.25	14.1	3.525	51.1125	7.05	1.763	25.5635
15.5	0.04	4.3	0.172	2.666	2.15	0.086	1.333
		115.5	77.777	955.8785	57.75	38.889	477.7465
		Approx. T = 12.2899			approx. T = 12.2848		
		Approx. rm = 0.3543			approx. rm = 0.2980		

Appendix 3.12 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT 28°C

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	9.1	9.1	122.85	4.55	4.55	61.425
14.5	0.66	16.8	11.088	160.776	8.4	5.544	80.388
15.5	0.50	9.2	4.6	71.3	4.6	2.3	35.65
16.5	0.04	3.8	0.152	2.508	1.9	0.076	1.254
		38.9	24.94	357.434	19.45	12.47	178.717
		Approx. T = 14.3317			approx. T = 14.3317		
		Approx. rm = 0.2244			approx. rm = 0.1761		

Appendix 3.13 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT 30°C

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m		sex ratio 1:1			
15.5	1.00	7.1	7.1	110.05	3.55	3.55	55.025
16.5	0.50	3.3	1.65	27.225	1.65	0.825	13.6125
17.5	0.04	0.0	0.0	0.0	0.0	0.0	0.0
		10.4	8.75	137.275	5.2	4.375	68.6375
		Approx. T = 15.68857			approx. T = 15.689		
		Approx. rm = 0.1383			approx. rm = 0.0941		

Appendix 3.14 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR M. persicae AT 12°C

x	$LxMx^{5-rm\ x}$	% contribution
20.5	8.14	5.48
21.5	8.45	5.69
22.5	8.59	5.79
23.5	12.43	8.38
24.5	9.36	6.31
25.5	9.08	6.12
26.5	9.24	6.23
27.5	7.64	5.15
28.5	6.66	4.49
29.5	8.20	5.53
30.5	8.35	5.63
31.5	7.69	5.18
32.5	6.39	4.31
33.5	6.77	4.56
34.5	5.36	3.61
35.5	4.98	3.36
36.5	3.79	2.55
37.5	2.94	1.98
38.5	2.89	1.95
39.5	2.48	1.67
40.5	1.40	0.94
41.5	1.58	1.06
42.5	1.09	0.73
43.5	0.795	0.54
44.5	0.762	0.51
45.5	0.555	0.37
46.5	0.486	0.33
47.5	0.371	0.25
48.5	0.273	0.18
49.5	0.265	0.18
50.5	0.255	0.17
51.5	0.184	0.12
52.5	0.160	0.11
53.5	0.136	0.09
54.5	0.110	0.07
55.5	0.103	0.07
56.5	0.07	0.05
57.5	0.07	0.05
58.5	0.05	0.03
59.5	0.05	0.03
60.5	0.04	0.03
61.5	0.03	0.02
62.5	0.03	0.02
63.5	0.02	0.01
64.5	0.02	0.01
65.5	0.02	0.01
66.5	0.01	0.007
67.5	0.009	0.006
68.5	0.008	0.005
69.5	0.006	0.004
70.5	0.005	0.003
71.5	0.004	0.003
72.5	0.004	0.003
73.5	0.003	0.002
74.5	0.002	0.001
75.5	0.002	0.001
76.5	0.001	0.0007
77.5	0.001	0.0007
78.5	0.0006	0.0004
79.5	0.0002	0.0001
80.5	0.0001	0.00007
81.5	0.0001	0.00007
82.5	0.00009	0.00006
	148.41109	99.9871

Appendix 3.15 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR *M. persicae* AT 16°C

x	$L_xM_x^{5-rm\,x}$	% contribution
12.5	16.63	11.20
13.5	13.88	9.35
14.5	12.49	8.41
15.5	9.53	6.42
16.5	9.29	6.26
17.5	14.58	9.82
18.5	18.28	12.31
19.5	13.36	9.0
20.5	11.48	7.73
21.5	9.23	6.22
22.5	6.01	4.05
23.5	4.79	3.23
24.5	3.80	2.56
25.5	2.29	1.54
26.5	1.47	0.99
27.5	1.13	0.76
28.5	0.863	0.58
29.5	0.642	0.43
30.5	0.438	0.30
31.5	0.284	0.19
32.5	0.193	0.13
33.5	0.174	0.12
34.5	0.153	0.10
35.5	0.1181	0.08
36.5	0.093	0.06
37.5	0.068	0.05
38.5	0.055	0.04
39.5	0.042	0.03
40.5	0.027	0.02
41.5	0.014	0.009
42.5	0.016	0.01
43.5	0.0096	0.006
44.5	0.0068	0.005
45.5	0.0046	0.003
46.5	0.0028	0.002
47.5	0.002	0.001
48.5	0.0004	0.0003
49.5	0.0002	0.0001
50.5	0.0001	0.00007
51.5	0.00004	0.00003
52.5	0.00003	0.00002
53.5	0.00001	0.000007
54.5	0.000004	0.000003
55.5	0.0000006	0.0000004
56.5	0.0000005	0.0000003
57.5	0.0000004	0.00000003
	148.44669	102.0165

Appendix 3.16 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR M. persicae AT 20°C

x	$L_xM_x^{5-rm\ x}$	% contribution	
8.5	28.64	19.27	
9.5	24.45	16.45	
10.5	25.91	17.43	
11.5	23.05	15.51	
12.5	15.38	10.35	
13.5	10.84	7.29	
14.5	7.33	4.93	^ 91.23%
15.5	5.01	3.37	
16.5	2.58	1.74	
17.5	1.78	1.20	
18.5	1.18	0.794	
19.	0.779	0.524	
20.5	0.559	0.376	
21.5	0.362	0.244	
22.5	0.265	0.178	
23.5	0.175	0.118	
24.5	0.130	0.087	
25.5	0.081	0.054	
26.5	0.052	0.035	
27.5	0.039	0.026	
28.5	0.021	0.014	
29.5	0.011	0.0074	
30.5	0.0077	0.0052	
31.5	0.005	0.0034	
32.5	0.004	0.0027	
33.5	0.002	0.0013	
34.5	0.002	0.0013	
35.5	0.0009	0.0006	
36.5	0.0007	0.00047	
37.5	0.0004	0.00027	
38.5	0.0003	0.0002	
39.5	0.0002	0.0001	
40.5	0.0001	0.00007	
41.5	0.00005	0.00003	
42.5	0.00002	0.00001	
43.5	0.000003	0.000002	
44.5	0.000001	0.0000007	
45.5	0.0000002	0.0000001	
46.5	0.00000002	0.00000001	
	148.64737	100.0130	

Appendix 3.17 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR M. persicae AT 24°C

x	$LxMx^{5-rm\ x}$	% contribution
7.5	36.40	24.57
8.5	38.13	25.73
9.5	28.22	19.05
10.5	18.29	12.34
11.5	13.00	8.77
12.5	5.94	4.01
13.5	3.28	2.21
14.5	2.16	1.46
15.5	1.26	0.850
16.5	0.657	0.443
17.5	0.390	0.263
18.5	0.20	0.135
19.5	0.099	0.067
20.5	0.064	0.043
21.5	0.035	0.024
22.5	0.018	0.012
23.5	0.011	0.007
24.5	0.006	0.004
25.5	0.003	0.002
26.5	0.002	0.001
27.5	0.00002	0.00001
	148.16502	99.99101

Appendix 3.18 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR M. persicae AT 28°C

x	$LxMx^{5-rm\ x}$	% contribution
8.5	45.15	30.45
9.5	35.30	23.81
10.5	26.72	18.02
11.5	18.01	12.15
12.5	10.77	7.26
13.5	6.32	4.26
14.5	2.46	1.66
15.5	1.51	1.02
16.5	0.846	0.571
17.5	0.521	0.351
18.5	0.299	0.202
19.5	0.191	0.129
20.5	0.092	0.06
21.5	0.042	0.028
22.5	0.029	0.020
23.5	0.0044	0.003
24.5	0.00072	0.0005
25.5	0.00007	0.00005
	148.26519	99.99455

Appendix 3.19 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR M. persicae AT 30°C

x	$LxMx^{5-rm\ x}$	% contribution
9.5	74.10	49.94
10.5	40.26	27.13
11.5	19.14	12.90
12.5	9.67	6.52
13.5	3.66	2.47
14.5	1.53	1.03
15.5	0.0098	0.0066
	148.3698	99.9966

Appendix 3.20 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT 12°C

x	$LxMx^{5-rm\ x}$ Sex ratio 1f:0m	% contribution	$LxMx^{5-rm\ x}$ sex ratio 1:1	% contribution
34.5	37.73	25.41	36.58	24.57
35.5	46.51	31.32	45.98	30.89
36.5	25.89	17.43	26.09	17.53
37.5	17.73	11.94	18.21	12.23
38.5	9.76	6.57	10.22	6.87
39.5	5.82	3.92	6.21	4.17
40.5	2.83	1.91	3.08	2.069
41.5	1.39	0.936	1.55	1.04
42.5	0.746	0.502	0.844	0.567
43.5	0.089	0.06	0.10	0.067
	148.495	99.998	148.864	100.003

Appendix 3.21 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT 16°C

x	$LxMx^{5-rm\ x}$ Sex ratio 1f:0m	% contribution	$LxMx^{5-rm\ x}$ sex ratio 1:1	% contribution
20.5	49.86	33.55	47.75	32.19
21.5	48.76	32.81	48.20	32.50
22.5	25.07	16.87	25.58	17.25
23.5	14.84	9.99 ^ (93.22)	15.63	10.54 ^ (92.48)
24.5	5.95	4.00	6.46	4.36
25.5	2.92	1.96	3.28	2.21
26.5	0.918	0.618	1.06	0.715
27.5	0.273	0.184	0.327	0.220
28.5	0.025	0.0168	0.031	0.021
	148.616	99.9988	148.318	100.006

Appendix 3.22 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR *A. matricariae* AT 20°C

x	$LxMx^{5-rm}$ x	% contribution	$LxMx^{5-rm}$ x	% contribution
13.5	60.36	40.52	57.62	38.70
14.5	56.35	37.82	56.42	37.89
15.5	21.18	14.22 ^ (92%)	22.25	14.94 ^(90%)
16.5	6.90	4.63	7.61	5.11
17.5	3.14	2.11	3.63	2.44
18.5	0.980	0.658	1.28	0.860
19.5	0.067	0.045	0.086	0.078
	148.977	100.003	148.896	100.018

Appendix 3.23 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR *A. matricariae* AT 24°C

x	$LxMx^{5-rm}$ x Sex ratio 1f:0m	% contribution	$LxMx^{5-rm}$ x sex ratio 1:1	% contribution
11.5	83.91	56.37	80.81	54.55
12.5	49.30	33.12	50.26	33.93
13.5	12.61	8.47	13.61	9.19
14.5	2.93	1.97	3.35	2.26
15.5	0.10	0.067	0.12	0.081
	148.85	99.999	148.15	100.010

Appendix 3.24 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT 28°C

x	$LxMx^{5-rm\ x}$ Sex ratio 1f:0m	% contribution	$LxMx^{5-rm\ x}$ sex ratio 1:1	% contribution
13.5	64.42	43.42	62.24	41.91
14.5	62.65	42.23	63.56	42.80
15.5	20.75	13.99	22.10	14.88
16.5	0.547	0.369	0.612	0.412
	148.367	100.009	148.512	100.002

Appendix 3.25 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT 30°C

x	$LxMx^{5-rm\ x}$	% contribution	$LxMx^{5-rm\ x}$	% contribution
15.5	123.72	83.17	122.916	82.54
16.5	25.04	16.83	26.00	17.46
	148.76	100.00	148.916	100.00

Appendix 3.26 DERIVATIONS OF THE VALUES OF y0, a and T USING PRADHAN METHOD FOR THE RELATIONSHIP BETWEEN RATE OF DEVELOPMENT AND TEMPERATURE FOR M. persicae

For fitting equation $Y = AX^2 + BX + C$,to the observations on development period, where P = development period, X = values of temperature corresponding to different values of P, the procedure is as follows:

x	x^2	x^3	x^4	p	Y = log y y = 100/p	xY	x^2Y
12	144	1728	20736	20.22	0.694283288	8.331399467	99.9769736
16	256	4096	65536	12.2	0.913640169	14.61824271	233.8918833
20	400	8000	160000	8.65	1.062983893	21.25967785	425.193557
24	576	13824	331776	7.167	1.144680775	27.4723386	659.3361263
28	784	21952	614656	8.017	1.096004368	30.68812231	859.2674247
30	900	27000	810000	9.067	1.042550754	31.27652262	938.2956785
130	3060	76600	2002704		5.954143247	133.6463036	3215.961643

$A\,\Sigma(x)^4 + B\,\Sigma(x)^3 + C\,\Sigma(x)^2 = \Sigma x^2y$

(a) A2002704 + B76600 + C3060 = 3215.961643

$A\,\Sigma(x)^3 + B\,\Sigma(x)^2 + Cx = \Sigma xy$

(b) A76600 + B3060 + C130 = 133.6463036

$A\,\Sigma(x)^2 + B\,\Sigma(x) + NC = \Sigma y$

(c) A3060 + B130 + 6C = 5.954143247

(d) A459600 + B18360 + C780 = 801.8778216 — multiply (b) x 6

(e) A397800 + B16900 + C780 = 774.0386221 — multiply (c) x 130

(f) A61800 + B1460 + 0 = 27.8391995 — (d) - (e)

(g) A12016224 + B459600 + C18360 = 19295.76986 — (a) x 6

(h) A9363600 + B397800 + C18360 = 18219.67834 — (c) x 3060

(i) A2652624 + B61800 + 0 = 1076.09152 — (g) - (h)

(j) A3819240000 + B90228000 = 1720462.529 — (f) x 61800

(k) A3872831040 + B90228000 = 1571093.619 — (i) x 1460

(l) -53591040A + 0 = 149368.91 — (j) - (k)

A = -0.0027871993

By substituting the value of A in (f) we have B

-172.2489177 + B1460 = 27.8391995

B = 200.0881172/1460 = 0.137046655

Substituting the values of A and B in (c) we have C

-8.528829905 + 17.81606515 + 6C = 5.954143247

17.81606515 + 6C = 14.48297315

6C = -3.333092

C = -0.555515333

$t_0 = B/2A = 0.137046655/2x0.0027871993 = 24.585$

$\log y_0 = \log k = C - AT^2$

$= -0.555515333 - -0.0027871993\ (24.585)^2$

$\log y_0 = 1.129129688$

$y_0 = 13.4626$

$a = A/0.4343 = 0.0064176813$

Appendix 3.27 DERIVATIONS OF THE VALUES OF y0, a and T USING PRADHAN METHOD FOR THE RELATIONSHIP BETWEEN RATE OF DEVELOPMENT AND TEMPERATURE FOR A. matricariae

For fitting equation $Y = AX^2 + BX + C$,to the observations on development period, where P = development period, X = values of temperature corresponding to different values of P, the procedure is as follows:

x	x^2	x^3	x^4	p	Y = log y y = 100/p	xY	x^2Y
12	144	1728	20736	33.067	0.480605204	5.767262455	69.20714946
16	256	4096	65536	19.25	0.715569266	11.44910826	183.1857321
20	400	8000	160000	12.58	0.900215803	18.00431607	360.0863213
24	576	13824	331776	10.65	0.972650392	23.34360941	560.2466259
28	784	21952	614656	12.233	0.912467024	25.54907668	715.374147
30	900	27000	810000	14.333	0.843662899	25.30988697	759.2966092
130	3060	76600	2002704		4.825170588	109.4232598	2647.396585

$A\,\Sigma(x)^4 + B\,\Sigma(x)^3 + C\,\Sigma(x)^2 = \Sigma(x)^2 y$

(a) $A2002704 + B76600 + C3060 = 2647.396585$

$A\,(x)^3 + B\,(x)^2 + C\,(x) = \Sigma xy$

(b) $A76600 + B3060 + C130 = 109.4232598$

$A\,(x)^2 + B\,(x) + NC = \Sigma y$

(c) $A3060 + B\,130 + 6C = 4.825170588$

(d) $A459600 + B18360 + C780 = 656.5395588$ multiply (b) x 6

(e) $A397800 + B16900 + C780 = 627.2721764$ multiply (c) x 130

(f) $A61800 + B1460 + 0 = 29.2673824$ (d) - (e)

(g) $A12016224 + B459600 + C18360 = 15884.37951$ (a) x 6

(h) $A9363600 + B397800 + C18360 = 14765.022$ (c) x 3060

(i) $A2652624 + B61800 + 0 = 1119.35751$ (g) - (h)

(j) $A3819240000 + B90228000 + 0 = 1808724.232$ (f) x 61800

(k) $A3872831040 + B90228000 + 0 = 1634261.965$ (i) x 1460

(l) $-53591040A + 0 = 174462.267$ (j) - (k)

$A = -0.0032554372$

Substituting the value of A in (f)

$-201.186021 + B1460 = 29.2673824$

$B = 0.157844796$

Substituting the values of A and B in (c)

$-9.961637935 + 20.51982348 + 6C = 14.78680852$

$6C = -5.73301496 \qquad C = -0.955502493$

$t_0 = B/2A = 0.157844796/2x0.0032554372 = 24.24$

$\log y0 = \log k = C - AT^2$

$= -0.955502493 - -0.0032554372 \times (24.24)^2 = 0.957319366$

$y0 = 9.0639 \qquad (\log_{10} 2.7183 = 0.4343)$

$a = A/0.4343 = -0.0032554372/0.4343 = -0.0074958254$

Appendix 4.1 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT THE APHID HOST DENSITY OF 5

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	4.1	4.1	55.35	2.05	2.05	27.675
14.5	1.00	4.4	4.4	63.8	2.2	2.2	31.9
15.5	0.83	4.2	3.486	54.033	2.1	1.743	27.0165
16.5	0.70	4.3	3.01	49.665	2.15	1.505	24.8325
17.5	0.66	4.1	2.706	47.355	2.05	1.353	23.6775
18.5	0.58	3.3	1.914	35.409	1.65	0.957	17.7045
19.5	0.50	2.4	1.2	23.4	1.2	0.6	11.7
20.5	0.25	2.1	0.525	10.763	1.05	0.263	5.3815
21.5	0.04	0.0	0.0	0.0	0.0	0.0	0.0
		28.9	21.341	339.775	14.45	10.671	169.8875

Appendix 4.2 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT THE HOST APHID DENSITY OF 10

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	8.8	8.8	118.8	4.4	4.356	59.4
14.5	1.00	9.1	9.1	131.95	4.55	4.505	65.975
15.5	0.95	6.5	6.175	95.713	3.25	3.088	47.8565
16.5	0.79	7.2	5.688	93.852	3.6	2.844	46.926
17.5	0.75	6.1	4.575	80.063	3.05	2.288	40.0315
18.5	0.70	5.1	3.57	66.045	2.55	1.785	33.0225
19.5	0.50	4.4	2.2	42.9	2.2	1.1	21.45
20.5	0.33	3.1	1.023	20.972	1.55	0.512	10.486
		50.3	41.131	650.295	25.15	20.478	325.1475

Appendix 4.3 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT THE APHID HOST DENSITY OF 15

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	11.4	11.4	153.9	5.7	5.7	76.95
14.5	1.00	13.1	13.1	189.95	6.55	6.55	94.975
15.5	1.00	11.6	11.6	179.8	5.8	5.8	89.9
16.5	0.83	9.2	7.636	125.994	4.6	3.818	62.997
17.5	0.70	8.1	5.67	99.225	4.05	2.835	49.6125
18.5	0.50	9.2	4.6	85.1	4.6	2.3	42.55
19.5	0.20	7.3	1.46	28.47	3.65	0.73	14.235
20.5	0.16	0.0	0.0	0.0	0.0	0.0	
		69.9	55.466	862.439	34.95	27.733	431.2195

Appendix 4.4 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT THE APHID HOST DENSITY OF 20

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	12.1	12.1	163.35	6.05	6.05	81.675
14.5	1.00	15.2	15.2	220.4	7.6	7.6	110.2
15.5	0.83	12.1	10.043	155.667	6.05	5.022	77.8335
16.5	0.70	11.1	7.77	128.205	5.55	3.885	64.1025
17.5	0.70	9.3	6.51	113.925	4.65	3.255	56.9625
18.5	0.58	8.2	4.756	87.986	4.1	2.378	43.993
19.5	0.50	6.2	3.1	60.45	3.1	1.55	30.225
20.5	0.25	3.3	0.825	16.913	1.65	0.413	8.4565
		77.5	60.304	946.976	38.75	30.153	473.448

Appendix 4.5 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT THE HOST APHID DENSITY OF 30

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	19.4	19.4	261.9	9.7	9.7	130.95
14.5	1.00	22.3	22.3	323.35	11.15	11.15	161.675
15.5	0.79	19.4	15.326	237.553	9.7	7.663	118.7765
16.5	0.75	14.4	10.8	178.2	7.2	5.4	89.1
17.5	0.62	11.4	7.068	123.69	5.7	3.534	61.845
18.5	0.50	8.2	4.1	75.85	4.1	2.05	37.925
19.5	0.25	6.1	1.525	29.738	3.05	0.7625	14.869
20.5	0.20	3.1	0.62	12.71	1.55	0.31	6.355
		104.3	81.139	1242.991	52.15	40.5695	621.4955

Appendix 4.6 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae At THE APHID HOST DENSITY OF 50

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	24.4	24.4	329.4	12.2	12.2	164.7
14.5	1.00	34.1	34.1	294.45	17.05	17.05	147.225
15.5	0.91	30.2	27.482	425.971	15.1	13.741	212.9855
16.5	0.87	26.0	22.62	373.23	13.0	11.31	186.615
17.5	0.70	22.1	15.47	270.725	11.05	7.735	135.3625
18.5	0.62	18.5	11.47	212.195	9.25	5.735	106.0975
19.5	0.50	16.2	8.1	157.95	8.1	4.05	78.975
20.5	0.37	9.1	3.367	69.024	4.55	1.684	34.512
21.5	0.12	2.2	0.264	5.676	1.1	0.132	2.838
		182.8	147.273	2138.621	91.4	73.637	1069.3105

Appendix 4.7 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT THE APHID HOST DENSITY OF 100

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	39.1	39.1	527.85	19.55	19.55	263.925
14.5	1.00	58.2	58.2	843.9	29.1	29.1	421.95
15.5	0.87	44.3	38.541	597.386	22.15	19.2705	298.693
16.5	0.79	24.2	19.118	315.447	12.1	9.559	157.7235
17.5	0.75	17.2	12.9	225.75	8.6	6.45	112.875
18.5	0.66	12.0	7.92	146.52	6.0	3.96	73.26
19.5	0.58	10.2	5.916	115.362	5.1	2.958	57.681
20.5	0.50	3.1	1.55	31.775	1.55	0.775	15.8875
21.5	0.16	0.0	0.0	0.0	0.0	0.0	
		208.3	183.245	2803.99	104.15	91.6225	1401.995

Appendix 4.8 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR A. matricariae AT THE APHID HOST DENSITY OF 200

x	Lx	Mx	LxMx	xLxMx	Mx	LxMx	xLxMx
		Sex ratio 1f:0m			sex ratio 1:1		
13.5	1.00	37.4	37.4	504.9	18.7	18.7	252.45
14.5	1.00	61.2	61.2	887.4	30.6	30.6	443.7
15.5	0.95	40.3	38.285	593.418	20.15	19.143	296.709
16.5	0.79	26.1	20.619	340.214	13.05	10.310	170.107
17.5	0.75	16.2	12.15	212.625	8.1	6.075	106.3125
18.5	0.58	15.5	8.99	166.315	7.75	4.495	83.1575
19.5	0.50	7.5	3.75	73.125	3.75	1.875	36.5625
20.5	0.20	7.4	1.48	30.34	3.7	0.74	15.17
21.5	0.04	0.0	0.0	0.0	0.0	0.0	
		211.6	183.874	2808.337	105.8	91.938	1404.1685

Appendix 4.9 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT THE APHID HOST DENSITY OF 5

x	$LxMx^{5-rm}$ x Sex ratio 1f:0m	% Contribution	$LxMx^{5-rm}$ x sex ratio 1:1	% Contribution
13.5	42.99	28.88	39.46	26.60
14.5	37.97	25.51	36.40	24.54
15.5	24.68	16.58	24.79	16.71 ^(80%)
16.5	17.51	11.76	18.40	12.40
17.5	12.94	8.69	14.22	9.59
18.5	7.52	5.05	8.65	5.83
19.5	3.87	2.60	4.66	3.14
20.5	1.39	0.934	1.76	1.19
	148.87	100.004	148.34	100.00

Appendix 4.10 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT THE APHID HOST DENSITY OF 10

x	$LxMx^{5-rm}$ x Sex ratio 1f:0m	% Contribution	$LxMx^{5-rm}$ x sex ratio 1:1	% Contribution
13.5	50.12	33.81	46.76	31.41
14.5	40.71	27.46	39.78	26.72
15.5	21.70	14.64	22.21	14.92 ^(84%)
16.5	15.70	10.59	16.82	11.30
17.5	9.92	6.69	11.13	7.48
18.5	6.08	4.10	7.14	4.80
19.5	2.94	1.98	3.62	2.43
20.5	1.07	0.722	1.39	0.934
	148.24	99.99	148.85	99.99

Appendix 4.11 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT THE APHID HOST DENSITY OF 15

x	$LxMx^{5-rm\ x}$ Sex ratio 1f:0m	% Contribution	$LxMx^{5-rm\ x}$ sex ratio 1:1	% Contribution
13.5	47.92	32.33	44.95	30.20
14.5	42.29	28.53	41.56	27.92
15.5	28.76	19.40	29.61	19.89
16.5	14.54	9.81	15.68	10.53
17.5	8.29	5.59	9.37	6.29
18.5	5.17	3.49	6.12	4.11
19.5	1.26	0.850	1.56	1.05
	148.23	100.00	148.85	99.99

Appendix 4.12 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT THE APHID HOST DENSITY OF 20

x	$LxMx^{5-rm\ x}$ Sex ratio 1f:0m	% Contribution	$LxMx^{5-rm\ x}$ sex ratio 1:1	% Contribution
13.5	48.26	32.44	44.96	30.28
14.5	46.37	31.17	45.24	30.47
15.5	23.44	15.75	23.95	16.13
16.5	13.87	9.32	14.84	10.00
17.5	8.89	5.98	9.96	6.71
18.5	4.97	3.34	5.83	3.93
19.5	2.48	1.67	3.04	2.05
20.5	0.504	0.339	0.65	0.438
	148.784	100.009	148.47	100.008

Appendix 4.13 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT THE APHID HOST DENSITY OF 30

x	$LxMx^{5-rm\ x}$ Sex ratio 1f:0m	% Contribution	$LxMx^{5-rm\ x}$ sex ratio 1:1	% Contribution
13.5	54.84	36.95	51.92	34.85
14.5	47.00	31.67	46.66	31.32
15.5	24.09	16.23	25.07	16.83
16.5	12.66	8.53	13.81	9.27
17.5	6.18	4.16	7.07	4.75
18.5	2.67	1.80	3.21	2.15
19.5	0.741	0.499	0.932	0.626
20.5	0.225	0.152	0.296	0.199
	148.406	99.99	148.968	99.995

Appendix 4.14 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT THE APHID HOST DENSITY OF 50

x	$LxMx^{5-rm\ x}$ Sex ratio 1f:0m	% Contribution	$LxMx^{5-rm\ x}$ sex ratio 1:1	% Contribution
13.5	45.39	30.51	42.34	28.45
14.5	45.86	30.83	44.80	30.10
15.5	26.72	17.96	27.34	18.37
16.5	15.90	10.69	17.04	11.45 ^(88%)
17.5	7.86	5.28	8.82	5.93
18.5	4.21	2.83	4.95	3.33
19.5	2.15	1.45	2.65	1.78
20.5	0.647	0.435	0.834	0.560
21.5	0.037	0.025	0.05	0.03
	148.774	100.01	148.824	100.00

Appendix 4.15 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT THE APHID HOST DENSITY OF 100

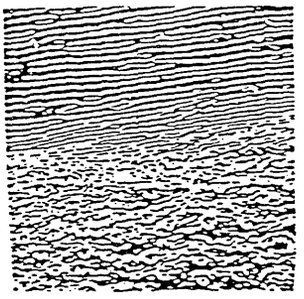
x	$LxMx^{5-rm\ x}$ Sex ratio 1f:0m	% Contribution	$LxMx^{5-rm\ x}$ sex ratio 1:1	% Contribution
13.5	52.25	35.07	49.34	33.22
14.5	54.86	36.82	54.31	36.56 ^(87%)
15.5	25.63	17.20	26.60	17.91 ^(94%)
16.5	8.97	6.02	9.76	6.57
17.5	4.27	2.87	4.87	3.28
18.5	1.85	1.24	2.21	1.49
19.5	0.974	0.654	1.22	0.821
20.5	0.180	0.121	0.237	0.160
	148.984	99.995	148.547	100.011

Appendix 4.16 THE CONTRIBUTION OF EACH AGE GROUP TO THE VALUE OF rm FOR A. matricariae AT THE APHID HOST DENSITY OF 200

x	$LxMx^{5-rm\ x}$ Sex ratio 1f:0m	% Contribution	$LxMx^{5-rm\ x}$ sex ratio 1:1	% Contribution
13.5	49.57	33.40	46.94	31.62
14.5	57.19	38.54	56.78	38.25 ^(88%)
15.5	55.22	16.99	26.25	17.68 ^(95%)
16.5	9.58	6.46	10.45	7.04
17.5	3.98	2.68	4.55	3.06
18.5	2.08	1.40	2.49	1.68
19.5	0.610	0.411	0.768	0.517
	148.4	99.996	148.452	99.998

Citrus lemon

with almost no trichomes

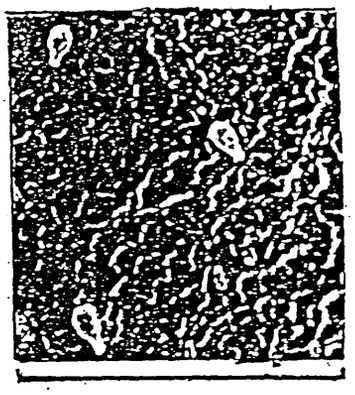


500 µm

0 per 500 µm^2

Faba bean

with few trichomes

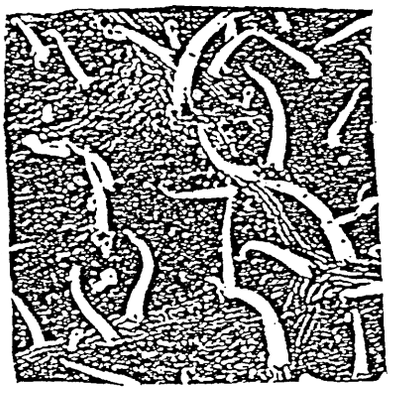


500 µm

6 per 1000 µm^2

Potato

with dense trichomes



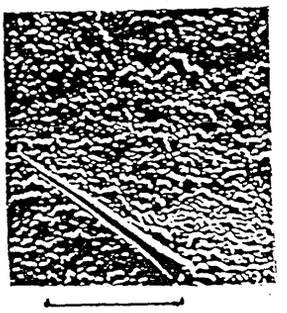
500 µm

23 per 1000 µm^2

Appendix 5.1 S.E.M. of lower surfaces of experimental plant leaves to show different densities of trichomes

Turnip

with few trichomes

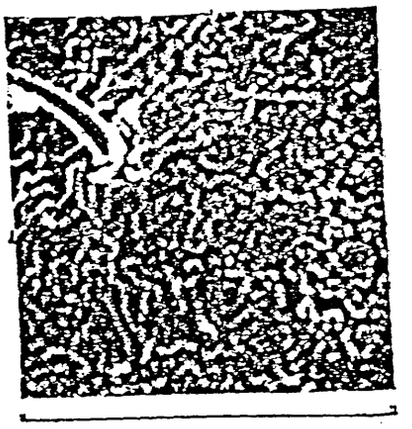


500 µm

1 per 1000 µm^2

Peach

with few trichomes

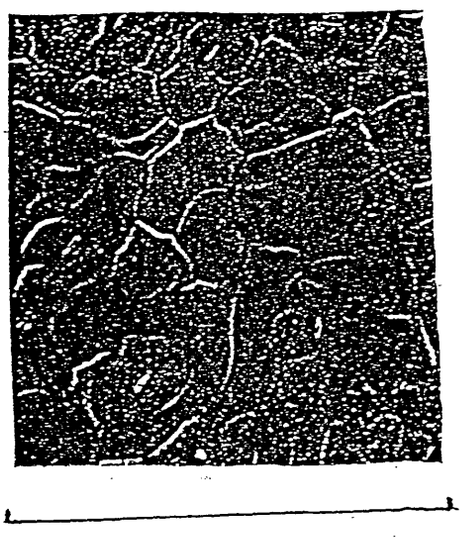


500 µm

2 per 1000 µm^2

Cauliflower

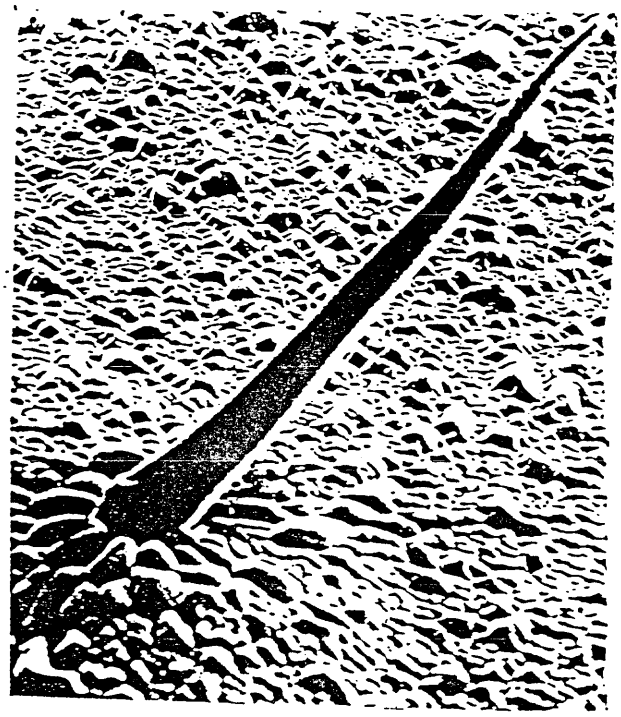
with almost no trichomes



500 µm

0 per 500 µm^2

Appendix 5.2 S.E.M. of lower surfaces of experimental plant leaves to show different densities of trichomes



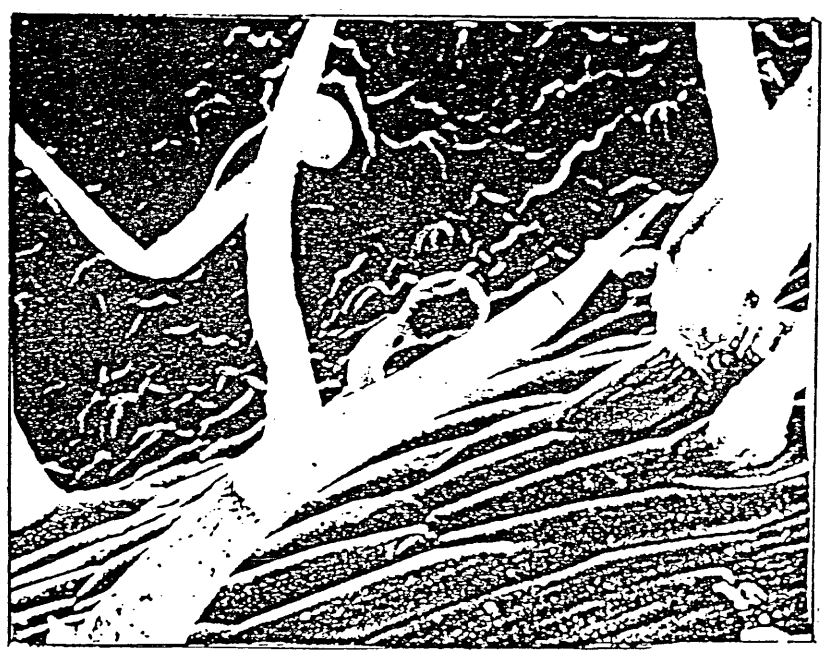
50 µm

Turnip trichome



50 µm

Faba bean trichome



50 µm

Potato trichome

Appendix 5.3 S.E.M. of 3 forms of trichome observed on 3 experimental plants

Appendix 6.1 THE AGE SPECIFIC FECUNDITY RATES (mx) OF UNPARASITIZED M. persicae AND OF APHIDS PARASITIZED BY A. matricariae AT VARIOUS AGES

x	Age specific fecundity rates							
	Control	Host age at parasitization, days						
		8-9 day	7-8 day	4-5 day	3-4 day	2-3 day	1-2 day	0-1day
0.5	00	00	00	00	00	00	00	00
1.5	00	00	00	00	00	00	00	00
2.5	00	00	00	00	00	00	00	00
3.5	00	00	00	00	00	00	00	00
4.5	00	00	00	00	00	00	00	00
5.5	00	00	00	00	00	00	00	00
6.5	00	00	00	00	00	00	00	00
7.5	4.2	4.1	4.2	4.1	3.4	00	00	00
8.5	4.4	4.3	4.3	4.2	2.8	00	00	00
9.5	5.1	5.1	5.3	3.1	00	00	00	00
10.5	6.1	6.1	4.1	00	00	00	00	00
11.5	6.2	5.2	2.2	00	00	00	00	00
12.5	6.1	3.1	00	00	00	00	00	00
13.5	6.2	2.1	00	00	00	00	00	00
14.5	5.3	00	00	00	00	00	00	00
15.5	4.3	00	00	00	00	00	00	00
16.5	4.0	00	00	00	00	00	00	00
17.5	4.0	00	00	00	00	00	00	00
18.5	4.1	00	00	00	00	00	00	00
19.5	3.1	00	00	00	00	00	00	00
20.5	2.2	00	00	00	00	00	00	00
21.5	2.1	00	00	00	00	00	00	00
22.5	1.7	00	00	00	00	00	00	00
23.5	00	00	00	00	00	00	00	00

Appendix 6.2 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR M. persicae PARASITIZED AT THE THIRD INSTAR (3-4 DAY OLD)

x	Lx	Mx	LxMx	xLxMx
0.5	1.00	00	00	00
1.5	1.00	00	00	00
2.5	1.00	00	00	00
3.5	0.97	00	00	00
4.5	0.95	00	00	00
5.5	0.95	00	00	00
6.5	0.91	00	00	00
7.5	0.70	3.4	2.38	17.85
8.5	0.30	2.8	0.84	7.476
9.5	0.09	00	00	00
		6.2	3.22	25.326

T = 7.865, rm = 0.149

Appendix 6.3 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR M. persicae PARASITIZED AT THE FOURTH INSTAR (4-5 DAY OLD)

x	Lx	Mx	LxMx	xLxMx
0.5	1.00	00	00	00
1.5	1.00	00	00	00
2.5	1.00	00	00	00
3.5	1.00	00	00	00
4.5	0.96	00	00	00
5.5	0.96	00	00	00
6.5	0.93	00	00	00
7.5	0.93	4.1	3.813	28.5975
8.5	0.76	4.2	3.192	27.132
9.5	0.23	3.1	0.713	6.7735
10.5	0.09	00	00	00
		11.4	7.718	62.503

T = 8.098, rm = 0.252

Appendix 6.4 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR M. persicae PARASITIZED AT THE ADULT STAGE (7-8 DAY OLD)

x	Lx	Mx	LxMx	xLxMx
0.5	1.00	00	00	00
1.5	1.00	00	00	00
2.5	1.00	00	00	00
3.5	1.00	00	00	00
4.5	0.98	00	00	00
5.5	0.96	00	00	00
6.5	0.96	00	00	00
7.5	0.92	4.2	3.864	28.98
8.5	0.92	4.3	3.956	33.626
9.5	0.92	5.3	4.876	46.322
10.5	0.58	4.1	2.378	24.969
11.5	0.26	2.2	0.572	6.578
12.5	0.06	00	00	00
		20.1	15.646	140.475

T = 8.978, rm = 0.306

Appendix 6.5 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR M. persicae PARASITIZED AT THE ADULT STAGE (8-9 DAY OLD)

x	Lx	Mx	LxMx	xLxMx
0.5	1.00	00	00	00
1.5	1.00	00	00	00
2.5	1.00	00	00	00
3.5	1.00	00	00	00
4.5	1.00	00	00	00
5.5	0.95	00	00	00
6.5	0.92	00	00	00
7.5	0.92	4.1	3.772	28.29
8.5	0.90	4.3	3.87	32.895
9.5	0.90	5.1	4.59	43.605
10.5	0.90	6.1	5.49	57.645
11.5	0.65	5.2	3.38	38.87
12.5	0.47	3.1	1.457	18.2125
13.5	0.25	2.1	0.525	7.0875
14.5	0.07	00	00	00
		30.00	23.084	226.605
		T = 9.8, rm =	0.320	

Appendix 6.6 THE AGE SPECIFIC FECUNDITY AND SURVIVAL RATES FOR THE NONPARASITIZED (CONTROL) M. persicae

x	Lx	Mx	LxMx	xLxMx
0.5	1.00	00	00	00
1.5	1.00	00	00	00
2.5	1.00	00	00	00
3.5	1.00	00	00	00
4.5	1.00	00	00	00
5.5	1.00	00	00	00
6.5	0.98	00	00	00
7.5	0.98	4.2	4.116	30.87
8.5	0.98	4.4	4.312	36.652
9.5	0.98	5.1	4.998	47.481
10.5	0.98	6.1	5.978	62.769
11.5	0.93	6.2	5.766	66.309
12.5	0.93	6.1	5.673	70.9125
13.5	0.90	6.2	5.58	75.33
14.5	0.86	5.3	4.558	66.091
15.5	0.86	4.3	3.698	57.319
16.5	0.81	4.0	3.24	53.46
17.5	0.80	4.0	3.2	56
18.5	0.80	4.1	3.28	60.68
19.5	0.79	3.1	2.449	47.7555
20.5	0.69	2.2	1.518	31.119
21.5	0.64	2.1	1.344	28.896
22.5	0.62	1.7	1.054	23.715
23.5	0.57	00	00	00
24.5	0.57	00	00	00
25.5	0.51	00	00	00
26.5	0.47	00	00	00
27.5	0.42	00	00	00
28.5	0.39	00	00	00
29.5	0.33	00	00	00
30.5	0.31	00	00	00
31.5	0.29	00	00	00
32.5	0.26	00	00	00
33.5	0.19	00	00	00
34.5	0.17	00	00	00
35.5	0.11	00	00	00
36.5	0.09	00	00	00
37.5	0.09	00	00	00
38.5	0.05	00	00	00
39.5	0.02	00	00	00
40.5	0.01	00	00	00
		69.1	60.764	815.359

T = 13.418, rm = 0.306