An Investigation of Ecological Relationships

— Experimental Studies of the Interactions Between the Sowthistle Aphid, *Hyperomyzus lactucae* and its Parasite, *Aphidius sonchi*

Liu Shu—sheng

A thesis submitted for the degree of Doctor of Philosophy of the Australian National University

July 1983
DECLARATION

The research carried out in the course of this investigation and the results presented in this thesis are, except where acknowledged, my original work.

Liu Shu-sheng

July, 1983
ACKNOWLEDGEMENTS

Many people helped me with the work described in this thesis and the
preparation of the thesis:

Dr R.D. Hughes supervised my work throughout this study. He gave me
encouragement, constructive criticism and tireless help in all stages of
the study.

Dr M. Carver acted as a joint supervisor, and was generous with assistance
and criticism throughout the study.

Dr W.L. Nicholas supervised my work during the final year of the study and
was helpful with assistance and advice.

The late Dr J.R.T. Short gave me encouragement and help during the earlier
part of the study.

Dr R.E. Jones gave me guidance and extensive help with the construction of
the computer simulation models.

Mr R. Morton gave me statistical advice on many occasions.

Dr G.H.L. Rothschild, Mr N. Gilbert and Dr B.C. Longstaff offered useful
suggestions during the writing up period. Dr G.H.L. Rothschild also read
through a draft of the thesis and made many useful comments.

Mr L.T. Woolcock offered technical help especially during the initial
stages. He was also very cooperative in the use of equipment and space in
the glasshouse and insectary. In addition, he took the photos presented in
Figures 6.1 and 8.1.

Ms Anne Bryce helped in looking after the aphid and parasite stock cultures
during my ten weeks' recreation leave in 1982.
Mr D.N. Crawford offered technical assistance at various stages of the study.

Ms I. Pumpurs typed the drafts of most chapters.

Mr J.P. Green and his assistants produced most of the photos presented.

Ms Robyn Clegg offered generous help with the illustrations of the thesis.

The staff of the Black Mountain Library, CSIRO, were very cooperative and helpful at all stages.

To all of these people I extend my deepest gratitude.

The research was carried out in the CSIRO Division of Entomology, Canberra. During the course of this study, I was financially supported by a postgraduate student scholarship of the Ministry of Education of the People's Republic of China.

I am grateful to colleagues in the Division of Entomology, fellow students at the Australian National University and members of the Australia-China Friendship Society for making my stay in Canberra a pleasant one.

Finally, I wish to convey a word of gratitude to Chen Li-hua for her warm and consistent support during my three years' stay in Australia.
CHAPTER 5. BASIC DEMOGRAPHIC TECHNIQUES: A DISCUSSION ON THE DESCRIPTION, CONSTRUCTION AND ANALYSIS OF LIFE AND FERTILITY TABLES

5.1 Introduction
5.2 Description and Construction of Life and Fertility Tables
5.3 Calculation of Intrinsic Rate of Increase and Other Population Parameters
5.4 Discussion

PART III. STUDIES ON HYPEROMYZUS LACTUCAE

CHAPTER 6. PERFORMANCE OF THE APHID IN RELATION TO ITS HOST PLANT, WITH PARTICULAR EMPHASIS ON THE DEVELOPMENT OF REARING SYSTEMS

6.1 Introduction
6.2 Materials and Methods
6.2.1 Host Plant Materials
6.2.2 Aphids
6.3 Experiments with Individual Aphids
6.3.1 Experimental Procedures
6.3.2 Results
6.4 Experiments with Small Populations
6.5 Discussion

CHAPTER 7. BIOCLIMATIC STUDIES

7.1 Introduction
7.2 Influence of Constant and Alternating Temperatures
7.2.1 Experimental Procedures
7.2.2 Rate of Development
7.2.3 Life Span and Age-Specific Survival
7.2.4 Fecundity and Age-Schedule of Births
7.2.5 Intrinsic Rate of Increase
7.2.6 Performance at 12.5°C Constant Temperature
7.2.7 Deleterious Effects of High Temperatures
7.3 Influence of Photoperiod
7.3.1 Larviposition Rate in Relation to Light and Darkness
7.3.2 Effects of Photoperiod on Other Population Parameters
7.4 Production and Performance of Alatae
7.4.1 Stages Sensitive to Crowding
7.4.2 Population Parameters of Alatae
7.5 Additional Observations on Rate of Nymphal Development
7.6 Discussion

CHAPTER 8. POPULATIONS OF THE APHID IN A FIELD CAGE

8.1 Introduction
8.2 The Field Cage
8.3 The Experiments
8.4 Results and Preliminary Analysis
8.4.1 Growth of S. oleracea
8.4.2 Changes in Aphid Numbers
8.4.3 Occurrence of Apterous and Alate Forms
CHAPTER 9. MODELLING THE APHID POPULATIONS IN THE FIELD CAGE 106

9.1 Introduction 106
9.2 Formulation of the Basic Model 106
  9.2.1 Physiological Time Scale 106
  9.2.2 Rate of Nymphal Development 107
  9.2.3 Survival and Fecundity Rates 108
  9.2.4 Crowding and Production of Alatae 113
  9.2.5 Synopsis of the Basic Model 114
9.3 Simulation Experiments and Results 116
  9.3.1 Initial Application of the Basic Model to the Field Cage Data 116
  9.3.2 Simulation Experiments with the Data of First Cage Experiment 117
  9.3.3 Application of the Model to Second Cage Experiment 119
9.4 Discussion 119

PART IV. STUDIES ON APHIDIUS SONCHI AND THE HOST-PARASITE INTERRELATIONSHIPS

CHAPTER 10. BIOLOGY of APHIDIUS SONCHI 127

10.1 Introduction 127
10.2 Development of Immature Stages 127
10.3 Emergence of Adults 128
10.4 Reproduction and Reproductive Capacity 128
10.5 Mating 129
10.6 Oviposition 131
  10.6.1 Oviposition Behaviour and Reaction of Aphids 131
  10.6.2 Oviposition Activity 133
  10.6.3 Superparasitization 133
  10.6.4 Oviposition in Relation to Light and Darkness 133
10.7 Adult Life Span 138
10.8 Adult Integumental Coloration in Relation to Temperature 141
10.9 Diapause 142
10.10 Hyperparasites 143
10.11 Host Specificity 143

CHAPTER 11. HOST-PARASITE INTERRELATIONSHIPS 145

11.1 Introduction 145
11.2 Effects of Parasitization on the Aphid 145
  11.2.1 Effects of Parasitization on Development, Survival and Reproduction 145
  11.2.1.1 Materials and Methods 145
  11.2.1.2 Results and Analysis 147
  11.2.2 Effects of Parasitization on Wing Development 155
  11.2.2.1 Materials and Methods 155
  11.2.2.2 Experiments and Results 155
11.3 Effects of Parasitization of Different Instars/Morphs of the Host on the Parasite 159
  11.3.1 Materials and Methods 159
  11.3.2 Results and Analysis 160
11.4 Host Instar Selection by and Searching Behaviour of the Parasite 167
11.4.1 Introduction 167
11.4.2 Materials and Methods 167
11.4.3 Results and Analysis 170
11.5 Discussion 176
11.5.1 Effects of Parasitization of Different Instars/Morphs on the Relative Fitness of the Aphid and the Parasite 176
11.5.2 Evidence for Host Instar Preference of the Parasite in Relation to Searching Behaviour 178
11.5.3 Production of Random Distributions of Parasite Eggs 179

Chapter 12. EFFECT OF HOST DENSITY ON FECUNDITY, REPRODUCTIVE RATE AND ADULT LIFE SPAN OF APHIDIUS SONCHI, WITH AN ADDITIONAL ANALYSIS ON THE FUNCTIONAL RESPONSE OF THE PARASITE TO HOST DENSITY 181
12.1 Introduction 181
12.2 Materials and Methods 181
12.3 Results and Analysis 182
12.3.1 Fecundity 182
12.3.2 Reproductive Rate 187
12.3.3 Adult Life Span 187
12.3.4 Functional Response 187
12.4 Discussion 193
12.4.1 Effect of Host Density on Fecundity, Reproductive Rate and Life Span 193
12.4.2 Functional Response to Host Density 194

Chapter 13. BIOCLIMATIC AND LIFE-FERTILITY TABLE STUDIES OF APHIDIUS SONCHI 198
13.1 Introduction 198
13.2 Development, Body Size and the Number of Eggs in the Ovaries Under Various Temperature-Light Regimes 198
13.2.1 Materials and Methods 198
13.2.2 Results and Analysis 199
13.3 Lower Temperature Threshold for Oviposition 207
13.3.1 Materials and Methods 207
13.3.2 Results 208
13.4 Oviposition Rate Under Various Temperature-Light Regimes 208
13.4.1 Materials and Methods 208
13.4.2 Results 209
13.5 Realized Fecundity and Progeny Sex Ratio Under Two Different Temperature-Light Regimes 211
13.5.1 Materials and Methods 211
13.5.2 Results 211
13.6 Life and Fertility Tables and Intrinsic Rate of Increase 214
13.6.1 Methods 215
13.6.2 Results and Analysis 216
13.7 Discussion 223

Chapter 14. TWO FIELD CAGE EXPERIMENTS WITH HYPEROMYZUS LACTUCAE AND APHIDIUS SONCHI 227
14.1 Introduction 227
14.2 Materials and Methods 227
14.3 Results and Preliminary Analysis 230
14.3.1 Growth of S. oleraceus 230
14.3.2 Changes of Aphid Numbers and Impact of the Parasite on the
Aphid Population in Third Cage Experiment 233
14.3.3 Changes of Aphid Numbers and Impact of the Parasite on the
Aphid Population in Fourth Cage Experiment 234

CHAPTER 15. PRELIMINARY MODELLING OF THE HOST-PARASITE SYSTEM AND ANALYSIS OF
THE HOST-PARASITE INTERACTIONS IN THE FIELD CAGE 237
15.1 Introduction 237
15.2 Incorporation of the Population Processes of Aphidius sonchi
into the Aphid Model 237
15.2.1 Physiological Time Scale 237
15.2.2 Rate of Development 238
15.2.3 Survival Rates 239
15.2.4 Effects of Host Instars/Morphs Attacked 240
15.2.5 Sex Ratio 241
15.2.6 Fecundity Rates 241
15.2.7 Consequences of Parasitization on the Aphid 245
15.2.8 Synopsis of the Host-Parasite Model 246
15.3 Comparison of Model Output with Field Cage Data 248
15.4 Analyses and Discussion 252

PART V. GENERAL DISCUSSION

CHAPTER 16. GENERAL DISCUSSION 258
16.1 Speculation Concerning the Effectiveness of A. sonchi as a
Biological Control Agent of H. lactucae in South-Eastern
Australia 258
16.2 Temperature Relationships: Effect of Constant and Fluctuating
Temperatures on the Development of Insects 261

APPENDIX 1. Effects of Crowding on the Production of Alatae in Hyperomyzus
lactucae: Stages Sensitive to Crowding 266

APPENDIX 2. The Aphid Model 271

APPENDIX 3. Preliminary Studies on Diapause of Aphidius sonchi 275

APPENDIX 4. Development, Body Size and Number of Eggs in the Ovaries of the
Japanese Strain of Aphidius sonchi Under Various Temperature-
Light Regimes 278

APPENDIX 5. The Aphid-Parasite Model 288

APPENDIX 6. Simulation Experiments on the Interactions Between Hyperomyzus
lactucae and Aphidius sonchi 295

REFERENCES 302
ABSTRACT

(1) The population biology of the sowthistle aphid, *Hyperomyzus lactucae* (L.), and its hymenopterous parasite, *Aphidius sonchi* Marshall, and the interactions between the aphid and the parasite were studied under laboratory and large field cage conditions. The aphid is cosmopolitan, mainly infests the sowthistle, *Sonchus oleraceus* L. and had previously been established as the principal vector of lettuce necrotic yellows virus. The parasite was recently introduced into Australia as a biological control agent against the aphid.

(2) The basic method was to examine quantitatively the important biological processes and put them together in computer simulation models. The models were then used to explore various ecological relationships.

(3) Laboratory experiments on *H. lactucae* showed that speed of development and reproductive rate of the aphid increase as temperature rises, while both life span and total fecundity decline gradually at higher temperatures. The performance of the aphid at the lower temperatures tested showed that the aphid can survive through relatively cold weather without recourse to sexual reproduction. At 22°C, changes of photoperiod within the range of 12L:12D to 16L:8D had little effect on the performance of the aphid.

(4) Analyses of the dynamics of the aphid populations in a large field cage indicated that (a) on its own physiological time scale the aphid multiplies more quickly at lower than at higher temperatures; (b) the proportion of winged forms increases with population density; and (c) the aphid adjusts its number to plant conditions mainly through density-related emigration, the effect of population density on reproductive rate *per se* being insignificant.

(5) Detailed observations were made on the biology of *A. sonchi* and the relevant descriptions were given.
(6) Parasitization of different instars/morphs of the aphid influences the relative fitness of both the host and the parasite. The degree of parasite impact on the population increase of the aphid depends foremost on the pattern of host instar selection by the females of the parasite.

(7) Although *A. sonchi* females generally search for hosts at random and attempt to oviposit in any aphid encountered, the differences in size and antagonistic response between aphid instars/morphs result in more eggs being laid in aphids of instars 2 and 3, which also endow the parasite with greater fitness. The analyses of the distributions of parasite eggs showed that the conditions leading to random egg distributions are more flexible than previously proposed.

(8) Both fecundity and reproductive rates of *A. sonchi* increase with host density. At host densities of less than 50 aphids per caged pot per day, the effective fecundity of the parasite decreases dramatically with decrease in host density. By contrast, adult life span of the parasite is little affected by host density.

(9) Overall, *A. sonchi* shows a typical convex functional response to host density, but both the attack rate, *a'* , and the handling time, *T_h*, vary through the adult life of the parasite.

(10) *A. sonchi* develops more slowly but shows a greater fecundity than *H. lactucae* over the mid temperature range (12.5°-22°C). As a result, the potential for population increase of the parasite is very similar to that of the aphid under these conditions. But the data obtained at extreme conditions indicated that the aphid is more tolerant of high temperatures.

(11) The comparison of the dynamics of the host-parasite interactions observed in the laboratory with those observed in the field cage showed that the parasite was able to lay only a small proportion of its complement of eggs under the latter conditions. This situation resulted mainly from the low searching efficiency of the parasite, which was subject to further reductions at those low temperature levels (i.e. about 8-10°C) where the aphid can still develop and reproduce normally.
(12) The overall analyses of the aphid-parasite system suggest that (a) the strain of *A. sonchi* examined has limited potential to be an effective biological control agent of *H. laotucae* in south-eastern Australia, and (b) *H. lactucae*, in its role as a virus vector, is favourable for successful biological control by effective natural enemies.

(13) The data of the development of *H. lactucae* and *A. sonchi* under constant and alternating temperatures showed that (a) healthy development can proceed during regular exposures to extremes which would be harmful or even lethal if experienced continuously and (b) temperature fluctuations neither stimulate nor retard the rate of development.
LIST OF ABBREVIATIONS AND SYMBOLS

A al. alate aphid adult
A apt. apterous aphid adult
D^\circ C day-degrees above the threshold temperature t in Celsius
BYSV beet yellow stunt virus
LNYV lettuce necrotic yellows virus
N_1 first instar aphid nymph
N_2 second instar aphid nymph
N_3 third instar aphid nymph
N_4 al. fourth instar alatiform aphid nymph
N_4 apt. fourth instar apteriform aphid nymph
quip a quarter of an aphid instar period (a physiological time unit)
\( r_m \) intrinsic rate of increase
\( R_0 \) net reproductive rate
T mean generation time
PART I

INTRODUCTION AND LITERATURE REVIEW
1.1 BACKGROUND AND PERSPECTIVE

The role played by natural enemies in the dynamics of natural populations has long been one of the most controversial subjects in insect population ecology. Although natural enemies have been successfully used to control pest populations on many occasions, the history of biological control of pests shows that unrewarding attempts have been very frequent. Thorough, long-term studies of pests and their natural enemies before, during and after introductions in classical biological control programs have been rarely made. As a result, the properties of the species involved (especially the interactions between them) which may have been the causes of success or failure are poorly understood. While today, thanks to some outstanding successes achieved by biological control (see Huffaker and Messenger 1976), natural enemies are viewed by an increasing number of ecologists as highly significant natural forces contributing to the regulation of many insect populations, there still remains a need for a series of detailed, long-term studies on particular predator-prey systems (including parasite-host systems) to gain a better understanding of their functioning and ultimately of predator-prey relationships in general (Huffaker, Simmonds and Laing 1976; Waage and Hassell 1982).

In the course of an attempt to biologically control the sowthistle aphid, Hyperomyzus lactucae (L.), in Australia, a specific hymenopterous parasite, Aphidius sonchi Marshall, was introduced, mass-reared and released in the field in 1981. This host-parasite system was considered suitable for detailed studies for the following reasons:
(i) The sowthistle aphid life system has many features which make it favourable for an attempt at biological control by natural enemies (see 2.6) - so that the causes of any success or failure are likely to be in the interactions of the aphid with the introduced parasite.

(ii) Although sowthistle is a weed of no economic importance in its own right, it has been demonstrated to be the principal reservoir of lettuce necrotic yellows virus. The virus can be transmitted to lettuce by *H. lactucae* and seriously damage the crop (see 2.5.2*). As a virus vector, the aphid is a serious pest and already has been studied for some years. Those studies and the work reported in this thesis will provide background for further studies by CSIRO and State Departments of Agriculture when the parasite has reached its full potential in Australia.

1.2 GENERAL METHODOLOGY

A detailed study of a predator-prey system is a daunting task, because the relationships between the predator and prey may be affected by all the ecological events and processes affecting the population numbers of both animals. Indeed, after studying coccinellid-pea aphid relationships, Frazer and Gilbert (1976) and Baumgaertner et al. (1981) concluded that any complete study of a predator-prey relationship must include the population dynamics of both predator and prey.

Three approaches to the study of a host-parasite system seem possible:

(i) Laboratory experiments to identify and measure basic attributes of the host and of the parasite under a range of conditions. Such

*Throughout the thesis, references to other sections, figures and tables within are indicated by a decimal code, the first figure indicating the chapter.*
attributes include developmental rate, life span, fecundity, sex ratio, dispersal, and so on. Other experiments analyse the components of the host–parasite interactions, such as the effects of host density, population structure and distribution. Such data may be validated by observing the fate of host–parasite cultures in the laboratory and/or by simulating the interactions of populations using computer models.

This approach allows important processes to be examined closely under controlled conditions to determine numerical relationships precisely. It has the major weakness that relationships observed under simplified laboratory conditions may not apply or may be incomplete under the more complex conditions of the field.

(ii) Field cage experiments to observe and monitor over long periods the growth and interactions of host and parasite populations under conditions approximating those of the field. Detailed analysis of the data including the use of simulation models is only possible if the important components have been quantified in laboratory experiments. The main weakness of this approach is that it is very much subject to chance, particularly in the initial stages (e.g. difficulties of establishing known numbers of insects of known ages at the beginning; presence of unwanted insects and/or insect diseases; and so on). Furthermore, modification of local conditions by the structure of the field cage may result in events which do not occur under natural conditions and thus obscure the normal interactions between host and parasite; and

(iii) Field studies of host and parasite populations in their natural field environment. These involve frequent sampling over prolonged
periods and a representative range of habitats and seasons. Again detailed analysis of the data including the use of simulation models is only possible if the important components of the host-parasite interactions have been quantified. The main weakness of this approach results from the general imprecision of field estimates of populations and from natural stochastic variations in the attributes of the protagonists and their interactions.

Since each of the approaches has its inherent advantages and weaknesses, for a detailed study of a host-parasite system some kind of integration of the above approaches may be the ideal. In this study of *H. lactucae* and *A. sonchi* the relatively recent introduction and release of the parasite in Australia currently precludes any meaningful field study of the host-parasite relationship.

1.3 SCOPE AND OBJECTIVES OF THIS STUDY

The work described in this thesis concerns the interactions between *H. lactucae* and *A. sonchi* under laboratory and field cage conditions. Various laboratory experiments were carried out to describe and measure properties of both the aphid and the parasite thought to be important in the aphid-parasite system. In the laboratory studies, particular effort was also made to elucidate the effects of constant and alternating temperatures on development, survival and reproduction of the subject species. This was considered important because of the prime role of temperature in the biology of all insects and the need to determine the most realistic temperature relationships for the analysis of field data. With the data obtained, a series of laboratory age-specific life and fertility tables were constructed and their implications to the
insects' ecological relationships were discussed. Parallel to the laboratory studies, four large field cage experiments were run, two with the aphid alone and two with the aphid and the parasite. Data on components of plant/aphid/parasite relationships collected in the laboratory were transformed and integrated to compile "variable life-tables" (i.e., computer simulation models) first for the aphid and then for the aphid and the parasite to analyse the population trends observed in the field cage. In this way, the validity of laboratory data were further discussed, and the analyses of the field cage data offered the opportunity to gain some insight into various aspects of the population dynamics of the aphid and the host-parasite interrelationships in a more natural environment.

The thesis is composed of five parts. In Part I, following the introduction, two chapters review the literature on the aphid and the parasite respectively. In Part II, the research facilities used, and the materials and methods common to all experiments are presented. In addition, there is a chapter dealing with the life and fertility table techniques used in this thesis. This account is included because of the confusion concerning the descriptions, construction and analysis of life and fertility tables in the literature. Part III describes the laboratory and field cage experiments on the aphid, *H. lactucae*, ending with a chapter on the synthesis of the available information and detailed analysis of the field cage data. Part IV includes the various studies on *A. sonchi* and the host-parasite interrelationships. It starts with a chapter presenting the results of the observations on the biology of the parasite. The next three chapters describe the experiments on various components of the host-parasite interrelationships and also bioclimatic studies on the parasite. Two more chapters present the field cage
trials involving the aphid and the parasite and analysis of the data obtained. All the experimental results presented in Part III and Part IV are discussed in detail in the chapters where they are presented. Then in Part V, an attempt is made to speculate on the potential of the parasite for the control of the aphid as a virus vector in south-eastern Australia in the light of the data obtained in this study, and an overall discussion of the data on the responses of the two species to constant and alternating temperatures is presented.
CHAPTER 2
REVIEW OF LITERATURE ON HYPEROMYZUS LACTUCAE

2.1 INTRODUCTION

The sowthistle aphid, Hyperomyzus lactucae (L.) (Homoptera: Aphididae), was first noted as a serious pest of Ribes spp. (Saxifragaceae) (Hille Ris Lambers 1949; Keep & Briggs 1971; Keep 1977) and then in 1963 was recognized as the principal vector of two important plant virus diseases associated with its main secondary host plant Sonchus oleraceus L. (Duffus 1963; Stubbs & Grogan 1963). Extensive studies of the aphid have thus been carried out by both virologists and entomologists in various parts of the world.

Much of the earlier work on this aphid was reviewed by Leong (1977) and less extensively by Martin (1979). The present review, while comprehensive, emphasizes recent developments and gives more detailed accounts of aspects more relevant to the present investigation, e.g. biology and population ecology. References are also made to findings on other aphids whenever appropriate.

2.2 TAXONOMY AND GEOGRAPHICAL DISTRIBUTION

H. lactucae was first described by Linnaeus in 1758 and its synonyms were listed by Hille Ris Lambers (1949) and by Eastop and Hille Ris Lambers (1976). This aphid was originally a palaearctic species, and although now cosmopolitan (Hille Ris Lambers 1949; Eastop 1958, 1966), it is still most common in temperate climates (Eastop 1966; Hughes et al. 1964, 1965; Miyazaki 1971).

2.3 GENERAL BIOLOGY

2.3.1 Life Cycles

Like many other aphids, e.g. Myzus persicae (van Emden et al. 1969;
Blackman 1974), *H. lactucae* has evolved complex life cycles which vary from holocyclic, anholocyclic, to a combination of both, depending upon the environmental conditions encountered in different regions of the world. Thus, in areas with a continental climate and characterized by very cold winters, such as some parts of the USSR (Ponomareva 1969), *H. lactucae* is typically holocyclic, alternating between primary and secondary hosts (Hille Ris Lambers 1949). In temperate regions where conditions may allow some parthenogenetic populations to persist during the winter months, both holocycle and anholocycle occur. This situation has been reported from New Zealand (Cottier 1953; Leong 1977), Tasmania (e.g. Hardy et al. 1978) and other cooler parts of Australia, e.g. Canberra (M. Carver, unpublished data). Hille Ris Lambers (1949) also mentioned briefly that such a combination of life cycles occurs in parts of Europe, though he did not specify the regions involved. In warm temperate to subtropical regions, *H. lactucae* is exclusively anholocyclic, reproducing parthenogenetically and viviparously all year round on its secondary hosts (Eastop 1966; Martin 1979; Passlow & Roubicek 1967).

Apart from climate, the availability of appropriate host plants for overwintering is undoubtedly a factor limiting the occurrence of different life cycles.

Since virtually all experimental work on *H. lactucae* has been done with parthenogenetic populations, in the following review the terms apterae and alatae are used for apterous and alate virginoparae on *S. oleraceus* unless otherwise stated.

2.3.2 Host Plants

*H. lactucae* has a restricted range of host plants. Its primary hosts belong to the genus *Ribes*, the blackcurrant, *Ribes nigrum* L., being the
most important. The main secondary hosts of this aphid are species of *Sonchus* (Asteraceae), with the sowthistle, *S. oleraceus*, being the most common host (Cottier 1953; Hille Ris Lambers 1949). Parthenogenetic populations of *H. lactucae* have also been recorded from two related composites, i.e. *Reichardia tingitana* L. and *Embergeria megalocarpa* (Hook. f.) (Randles & Carver 1971).

2.3.3 Developmental Rate

The developmental rate of *H. lactucae* in relation to temperature has been studied by Boakye (1973) in South Australia and Leong (1977) in New Zealand. Both authors used constant temperatures and a leaf disc technique in their experiments, and obtained similar results (Table 2.1). It is obvious that under such conditions the optimum temperature for development is about 25°C, with temperatures above 28°C retarding development of the aphid.

<table>
<thead>
<tr>
<th>Data source</th>
<th>Temperature (°C)</th>
<th>Develop. threshold</th>
<th>Thermal constant† (Day-degrees °C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>15</td>
<td>20</td>
<td>25</td>
</tr>
<tr>
<td>Boakye (1973)</td>
<td>10.9</td>
<td>7.4</td>
<td>5.6</td>
</tr>
<tr>
<td>Leong (1977)</td>
<td>10.8</td>
<td>7.6</td>
<td>5.7</td>
</tr>
</tbody>
</table>

* Values estimated by the original authors.
† Values estimated by the present author, in both cases the coefficient of determination (r²) for the linear regressions exceeds 0.99.

When interpreting their data, both Boakye and Leong assumed a linear relationship between temperature and developmental rate. Unfortunately, both of them extrapolated their own data wrongly to give an estimated developmental threshold of 10°C (Table 2.1). A threshold temperature as high as 10°C is unlikely for an aphid like *H. lactucae* in which anholocyclic
populations survive relatively cold winters. Nevertheless, the erroneous estimate was used by Boakye himself to interpret results of his later experiments and was also quoted by Francki and Randles (1979). For practical purposes, developmental threshold and thermal constant have been shown to be very useful in ecological studies (Hughes 1963; Messenger 1970; Campbell et al. 1974). Using the data of Boakye and Leong up to the optimum temperature of 25°C, the developmental threshold was estimated by the present author to be near 4°C (Table 2.1).

2.3.4 Life Span, Survival and Reproduction

Published laboratory data on the life span and reproduction of *H. lactucae* are mostly consistent (Boakye & Randles 1974; Leong 1977; Sylvester 1969, 1973), the exception being those reported by Martin (1979).

The total duration of the nymphal and adult life of *H. lactucae* is about 40-50 days at 15°C, 25-35 days at 20°C, and 20 days at 25°C (Boakye & Randles 1973; Leong 1977; Sylvester 1973). Mortality during the immature stages was shown to be negligible (Duffus 1963; Sylvester 1973) or virtually none (Leong 1977). Constant temperatures of 30°C or above are obviously deleterious to the survival of the aphid (Duffus 1963; Leong 1977). The life span of aphids infected with lettuce necrotic yellows virus (LNYV) was reduced at 28°C and 20°C but not at 15°C (Boakye & Randles 1974). Sylvester (1973), working with sowthistle yellow vein virus (SYVV), found that the life span of aphids infected with this virus at 25°C was also reduced. However, these authors reported that death usually did not occur until the end of maximal larviposition period, so the intrinsic rate of increase ($r_m$) was not affected.
Both apterous and alate *H. lactucae* can produce young at any temperature between 5°C and 30°C (Duffus 1963). While mean total fecundity per female was higher at relatively lower temperatures (15°C), the highest fecundity rates were achieved at temperatures between 20°C and 25°C (Duffus 1963; Leong 1977). The population statistics, such as the intrinsic rate of increase \( r_m \), net reproduction rate \( R_0 \), differ considerably in the literature. Such differences were, however, sometimes caused by different or incorrect methods of calculation (see Chapter 5). For example, Leong (1977) used the "time-to-first-birth" as generation time \( T \) to estimate other statistics. Although "time-to-first-birth" is one kind of measure of generation time which may be very useful under certain circumstances (Maelzer 1981), it is irrelevant to the calculation of \( r_m \) and \( R_0 \). Therefore, all the values of \( r_m \) and \( R_0 \) estimated by Leong are incorrect.

The results obtained by Martin (1979) are remarkably different from those mentioned above. In his study, mortality during the nymphal stages of both apterae and alatae was 20% or higher at temperatures from 15°C to 25°C, and the total life span of apterae was only about half that obtained by other workers. Both length of reproductive life and number of young produced were also greatly reduced. Although Martin's experimental methods were somewhat different from those of other authors, an appraisal of his unique results is, however, very difficult.

The effect of population density on the rate of reproduction of *H. lactucae* was studied by Boakye (1973) under field cage conditions in Adelaide. In his randomized factorial experiment, Boakye infested sowthistle plants of three different sizes (small, medium and large) with four different densities (2, 4, 8 and 16 per plant) of fourth instar apteriform *H. lactucae*. The experiment was run in a relatively warm
season for 32 days during which the populations were estimated to have completed 3.4 generations (the estimated number of generations is unreliable, as the temperature coefficients used in the calculations were incorrect, see 2.3.3.). During the course of the experiment, all cages were examined daily and any emigrants (mostly alate and apterous adults) found on the cage screens were collected with an aspirator and counted. All plants were cut at the end of the experiment and the aphids on each plant were retrieved separately and also counted. The totals of aphids that emigrated from each plant and those collected at the end were pooled and used to calculate the mean numbers of aphids produced by each initial fourth instar apteriform nymph. The results can be summarized in the following table (Table 2.2):

Table 2.2 Mean number of *H. lactucae* produced per apteriform nymph at various initial population densities on three plant sizes (after Boakye 1973)

<table>
<thead>
<tr>
<th>Plant size</th>
<th>Initial population density (No. aphids/plant)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>16</td>
</tr>
<tr>
<td>Small</td>
<td>972(167)*</td>
</tr>
<tr>
<td>Medium</td>
<td>462(43)</td>
</tr>
<tr>
<td>Large</td>
<td>409(84)</td>
</tr>
<tr>
<td></td>
<td>335(236)</td>
</tr>
<tr>
<td></td>
<td>245(115)</td>
</tr>
<tr>
<td></td>
<td>287(58)</td>
</tr>
<tr>
<td></td>
<td>188(310)</td>
</tr>
<tr>
<td></td>
<td>109(171)</td>
</tr>
<tr>
<td></td>
<td>196(146)</td>
</tr>
<tr>
<td></td>
<td>140(547)</td>
</tr>
<tr>
<td></td>
<td>66(259)</td>
</tr>
<tr>
<td></td>
<td>93(221)</td>
</tr>
</tbody>
</table>

*Figures in parentheses indicate the mean numbers of aphids (mostly alatae and apterae, a few nymphs) that emigrated from each plant.

Although the data show that the mean total number of aphids per original nymph was inversely correlated with the initial aphid density on every plant size, the conclusion reached by Boakye that the rate of reproduction of *H. lactucae* was significantly reduced at higher host densities in his experiment must be treated with caution. As the numbers of emigrants per plant were higher on plants with higher initial aphid densities and these emigrants were probably largely newly-moulted adults.
(see Hughes & Gilbert 1968), the lower number of aphids per original nymph recorded could have been caused mainly by the increasing emigration. However, this point cannot be clarified without further experimentation.

2.3.5 Production of Alatae and Emigration

The study of the production of alate forms and emigration in *H. lactucae* is of particular interest both in terms of its population dynamics and its economic importance (see below). In *H. lactucae*, the incidence of alatiform nymphs increases with the increase of population density (Boakye 1973; Martin 1979). Martin (1979) found that at any given density more alatiform nymphs were produced at a relatively low temperature, e.g. 15°C, and suggested that such a finding would help to explain why more alatae were trapped at lower temperatures in the field (e.g. Hughes *et al.* 1964, 1965; Randles & Crowley 1970; Martin 1979).

Little information is yet available on the factors affecting the rate of emigration in *H. lactucae*. The preliminary experiments conducted by Boakye (1973) showed that more adults (both apterae and alatae) leave the host plants as the population density increases, while emigration of nymphs is negligible regardless of population density as well as host plant condition. However, movements of nymphs between flower heads within each plant are frequent (Martin 1979).

2.4 POPULATION DYNAMICS

The understanding of the population dynamics of a species requires the knowledge of (a) the numerical changes that occur in its populations in both space and time, and (b) the factors causing these changes and how they act and interact to produce the observed patterns of change. Obviously, any study of this sort must be based on comprehensive, quantitative information on many generations of several populations. So far, no such
an attempt has been made on populations of *H. lactucae*.

Nevertheless, in the past twenty years, pieces of information on the dynamics of *H. lactucae* populations have been published, with the sources mainly from the investigations carried out in Australia and New Zealand.

*H. lactucae* is an introduced aphid in Australia and is known from all States (Eastop 1966). Passlow & Roubicek (1967) have reported that in Queensland large colonies of *H. lactucae* occurred on *S. oleraceus* virtually wherever this plant was present. However, a survey of aphids flying over eastern Australia indicated that *H. lactucae* shows a trend in relative abundance from south to north, no alatae being caught in all six traps north of latitude 21°S over two successive years (Hughes *et al.*, 1964, 1965). In these warm temperate and subtropical regions, the prolonged hot seasons are undoubtedly hazardous to the survival of *H. lactucae*.

The critical low temperature for the survival of anholocyclic population of *H. lactucae* is not known. However, examination of data available shows that *H. lactucae* can overwinter as active stages on *S. oleraceus* in areas where the mean monthly temperature remains above 4°C for the three coldest months. This occurs in Canberra, for example, where the mean monthly temperatures are around 5-6°C and the mean monthly minimum below 1°C for three months each year. In fact, the minimum daily temperature goes down below -5°C quite frequently during these months in this area (see Yearbook of Australia, No.66, 1982).

In the field, *H. lactucae* usually aggregates on and immediately below the young flower heads of *S. oleraceus* but moves away as the seed head pappi and achenes appear (Martin 1979; Stubbs & Grogan 1963). As the aphids usually do not colonize old leaves of *S. oleraceus*, the fluctuations of the numbers of young flower heads strongly influence the development of aphid populations (Martin 1979). Thus, in the field, two peaks of aphid
numbers are usually observed each year, one in spring and one in autumn, when the mean weekly temperatures are 15-17°C and flowering host plants are relatively abundant (Martin 1979). Martin (1979) also showed that peak numbers of alatiform 4th instar nymphs usually coincide with the peaks in total aphid numbers. This pattern of seasonal abundance of the aphid is also reflected by the fact that alate *H. lactucaea* are always trapped in greatest numbers during spring and autumn in south-eastern Australia (Hughes *et al.* 1965; Martin 1979; O'Loughlin 1963) and in New Zealand (Leong 1977).

In pointing out the close correlation between the seasonal fluctuations of *H. lactucaea* and the phenology of *S. oleraceus*, Martin (1979), and later Maelzer (1981), particularly stressed that, under relatively low temperature and short photoperiod, the new plant tissues mature more slowly relative to the increase of aphid numbers, so that the aphids are offered relatively more time to increase in numbers than under high temperatures and long photoperiods.

Leong (1977) made observations of holocyclic populations of *H. lactucaea* on its primary host over one year at Lincoln, New Zealand. Egg hatch was found to be well synchronized with bud burst of *Ribes*. Peak hatching was observed to occur in early September, thereafter aphid numbers increased progressively to reach a peak in early November. The alatae of the third generation first appeared in late October and flew off when mature. In autumn, the aphid was observed to return to *Ribes* to start a new cycle.

Several species of ladybeetles (Coleoptera: Coccinellidae) have been observed to prey on *H. lactucaea* in Australia (Martin 1979) and New Zealand (Leong 1977). Fungus diseases have also been found to occur frequently in populations of *H. lactucaea* (Leong 1977; Milner *et al.* 1980). However the impact of these natural enemies on the population dynamics of *H. lactucaea*
appear to be insignificant. In fact, as the mortality caused usually occurs when the population density is high, it is possible that their effect is compensated for by a reduction in intraspecific competition.

2.5 PEST STATUS

2.5.1 As a Pest of Ribes

In areas where holocycly of this aphid occurs, *H. lactucae* may cause serious damage to its primary host plants, *Ribes* spp. In Britain, for example, *H. lactucae* is the most common and serious aphid pest of *Ribes* spp. (Keep & Briggs 1971; Keep 1977). Infestations of *Ribes* spp. (mainly *R. nigrum*) have also been reported to occur in Tasmania (e.g. Hardy et al. 1978) and New Zealand (Leong 1977). Damage caused by the direct effect of its feeding may be severe, including leaf-curling or blistering, and checking and deformation of the shoot growth (Keep 1977; Leong 1977). Field surveys of *Ribes* spp. for resistance to *H. lactucae* and subsequent breeding have been pursued for some years in Britain, but so far results are far from satisfactory (Keep & Briggs 1971; Keep 1977).

2.5.2 As a Vector of Virus Diseases

The economic significance of *H. lactucae* arises more importantly from the virus diseases transmitted by this aphid. On a world scale, its main host plant, *S. oleraceus*, the common sowthistle, is of virtually no economic importance as a weed. However, it is the principal reservoir of several virus diseases which are transmitted to lettuce and other crops mainly by *H. lactucae* (Duffus 1963, 1973; Stubbs & Grogan 1963).

After LNYV was recognized in lettuce crops in 1954, nine years of investigations led, in 1963, to the conclusion that *H. lactucae* was the only vector of this virus disease in Australia (Stubbs & Grogan 1963). This conclusion is supported by subsequent observations that flights of
this aphid were followed by the high incidence of the disease in lettuce crops 4-5 weeks later (Martin 1979; Randles & Crowley 1970). Although *H. lactucae* can neither colonize lettuce nor can it transmit LNYV from infected lettuce, migrating alatae and crawling adults from *S. oleraceus* sometimes alight on and probe lettuce, and in doing so, may transmit LNYV (Stubbs & Grogan 1963; Randles & Crowley 1970). The virus, though symptomless in its main natural host, *S. oleraceus*, produces serious necrotic disease in lettuce crops, and thus causes severe losses of this crop in Australia (Martin 1979; Randles & Crowley 1970; Stubbs & Grogan 1963) and New Zealand (Fry *et al.* 1973).

*H. lactucae* is also the only effective vector of sowthistle yellow vein virus in the United States and England (Duffus 1963; Duffus & Russell 1969). Although the virus produces conspicuous symptoms in its main host *S. oleraceus*, it causes only a very low level of infection in lettuce (Duffus *et al.* 1970; Richardson & Sylvester 1968).

Another virus disease of major economic importance transmitted mainly by *H. lactucae* is the beet yellow stunt virus (BYSV), a potentially destructive, yellows-type, virus disease of sugar beet and lettuce (Duffus 1972, 1973). This virus, though associated with a number of plant species in parts of the Northern Hemisphere, is frequent only in *S. oleraceus*. The virus is transmitted by *H. lactucae*, readily to lettuce, but only inefficiently to beet (Duffus 1972). An epidemic in the Salinas Valley, California, caused between 50 to 80% losses in affected lettuce fields (Duffus 1972). However, since *H. lactucae* does not feed on lettuce, and transmits BYSV in a typical semipersistent manner, i.e., most aphids being infective only on the first day or so after virus acquisition, spread of the virus in the crop tends to be marginal and serious infections of the virus disease can occur only in areas where large concentrations
of *S. oleracea*us are present (Duffus 1972, 1973).

*H. lactucae* is reported to transmit a number of stylet-borne viruses (Kennedy, Day & Eastop 1962). More recently two other viruses, i.e. peanut mottle and sugar-cane mosaic, have been added to this list (Abbott & Charpentier 1962; Behncken 1970). Since all these viruses are each transmitted by a number of different aphid species, they have limited significance in terms of the pest status of *H. lactucae*.

2.6 POTENTIAL FOR ITS BIOLOGICAL CONTROL

*H. lactucae* has many features which make it a promising target for biological control (especially by hymenopterous parasites) in Australia: (i) *H. lactucae* is an exotic aphid species and prior to the initiation of the biological control program, was not recorded to be parasitized by any hymenopterous parasites in Australia (Carver & Stary 1974). However, the aphid is known to have hymenopterous parasites and other natural enemies in the Old World (Table 2.3). Although there is little quantitative data on their ecology and impact on the population dynamics of *H. lactucae*, the geographical distribution of the parasites covers a variety of climates, some of which are homoclimatic to parts of Australia; (ii) In most regions of Australia, including the areas where LNYV occurs in epiphytotic proportions, *H. lactucae* is anholocyclic and mostly restricted to *S. oleracea*us (Randles & Carver 1971). This obviates the need to find parasites adapted to both its primary and alternative host plants and their habitats; (iii) Plants of all stages of *S. oleracea*us occur throughout the year (Martin 1979), and as they are not cultivated, no insecticides are applied directly to them. Thus, the ecosystem of *S. oleracea*us is more than usually favourable to the establishment of a permanent aphid-parasite relationship;
(iv) *H. lactucae* is present as active stages throughout the year, though in relatively small numbers in mid summer and winter, and populations are always available for attack by parasites, i.e. a parasite niche is normally vacant; and

(v) Since the alatae are mainly responsible for the spread of the virus disease, the pest status of *H. lactucae* would be largely removed if the parasites can reduce the aphid numbers on *S. oleraceus* below the density at which large numbers of alatae form (M. Carver, personal communication).

Table 2.3 Recorded natural enemies of *H. lactucae*

<table>
<thead>
<tr>
<th>PARASITES</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aphidiidae</strong></td>
<td></td>
</tr>
<tr>
<td><em>Aphidius sonchi</em> Marshall (Mackauer and Stary 1967)</td>
<td></td>
</tr>
<tr>
<td><em>Ephedrus cerasicola</em> Stary (Halme 1977)</td>
<td></td>
</tr>
<tr>
<td><em>E. plagiator</em> (Nees) (Mackauer and Stary 1967)</td>
<td></td>
</tr>
<tr>
<td><em>Lysiphlebus fabarum</em> (Marshall) (Mackauer and Stary 1967)</td>
<td></td>
</tr>
<tr>
<td><em>L. testaceipes</em> (Cresson) (Stary 1981)</td>
<td></td>
</tr>
<tr>
<td><em>Praon orientale</em> Stary &amp; Schlinger (Mackauer and Stary 1967)</td>
<td></td>
</tr>
<tr>
<td><em>P. volucre</em> (Haliday) (Mackauer and Stary 1967)</td>
<td></td>
</tr>
<tr>
<td><em>P. dorsale</em> (Haliday) recorded from Greece (M. Carver, personal communication)</td>
<td></td>
</tr>
</tbody>
</table>

| **Aphelinidae** |                  |
| *Aphelinus abdominalis* Dalman (Kalina and Stary 1976) |                  |
| *A. asychis* Walker, recorded from South Africa (M. Carver, personal communication) |                  |

| **PREDATORS** |                  |
| **Anthocoridae** |                  |
| *Anthocoris pilosus* (Yakovlev) (Korcz 1968) |                  |

(Table 2.3 continue/...
Coccinellidae

*Harmonia axyridis* (Pall.) (Hukusima and Ohwaki 1972)

*Leis conformis* (Boisd.)* (Leong 1977, Hardy et al. 1978)

*Coccinella undecimpunctata* L. (Leong 1977)

Neuroptera

*Micromus tasmaniae* Walker (Leong 1977; Martin 1979)

Syrphidae

*Baccha elongata* (Fab.) (Kozlowska 1978)

*Pipiza bimaculata* Meig. (Wnuk 1972)

*Platychirus albimanus* (Fab.)* (Kozlowska 1978)

*P. scutatus* (Meig.) (Kozlowska 1978; Wnuk 1972)

*Scæva pyrastrī* (L.)* (Kozlowska 1978)

*Simosyrphus grandicornis* (Macquart) recorded from Australia (M. Carver, personal communication)

*Sphaerophoria rueppellii* (Wied.) (Kozlowska 1978)

*S. scripta* (L.) (Wiackowska 1963)

*Syrphus balteatus* (Deg.) (Kozlowska 1978; Wnuk 1972)

*S. bifasciatus* Fab. (Kozlowska 1978; Wnuk 1972)

*S. cinctellus* (Zett.)* (Kozlowska 1978)

*S. corollae* Fab.* (Kozlowska 1978; Wnuk 1972)

*S. euchromus* Kow.* (Kozlowska 1978)

*S. latifasciatus* Macq.* (Kozlowska 1978)

*S. luniger* Meig.* (Kozlowska 1978; Wnuk 1972)

*S. nitens* (Zett.)* (Kozlowska 1978)

*S. nitidicollis* Meig.* (Kozlowska 1978)

*S. ribesii* (L.) (Kozlowska 1978; Wnuk 1972)

(Table 2.3 continue/...
S. torvus O.-S. (Kozlowska 1978)
S. triangulifera (Zett.) (Kozlowska 1978; Wnuk 1972)
S. vitripennis Meig. (Kozlowska 1978; Wnuk 1972)

FUNGAL PATHOGENS**

Erynia neoaphidis Remaudiere and Hennebert (Entomophthora aphidis Hoffman in Fresenius sensu Thaxter) (Milner et al. 1980; Thoizon 1970)
Neozygites fresenii (Nowakowski) Remaudiere & Keller (E. fresenii (Nowakowski) Gustafsson) (Thoizon 1970)
Entomophthora planchoniana Cornu (Thoizon 1970)
E. thaxteriana Petch (Thoizon 1970)

* All species with an asterisk are now known under a different generic name (M. Carver, personal communication).

** A recent major taxonomic revision of the genus Entomophthora has resulted in many changes in the nomenclature in this group (Milner 1981). For each species listed, the name in the parentheses is the one used by the original authors.
CHAPTER 3
REVIEW OF LITERATURE ON *APHIDIUS SONCHI*

3.1 INTRODUCTION

*Aphidius sonchi* Marshall, 1896 (Hymenoptera: Aphidiidae), is a specialised parasite of *Hyperomyzus* species, and is palaearctic in distribution. Stary (1973) and Takada and Yamauchi (1979) have redescribed the species. The published, non-taxonomic, information on the parasite concerns only its host range and geographic distribution.

3.2 HOST RANGE

The host range of *A. sonchi* is restricted to the genus *Hyperomyzus* Börner (Mackauer and Stary 1967), the following four species have been recorded:

- *H. carduellinus* (Theobald) (Takada & Yamanchi 1979)
- *H. lactucae* (L.) (Stary 1966, 1976, 1979)
- *H. lampsanae* (Börner) (Stary, Remaudiere & Leclant 1977)
- *H. picridis* (Börner & Blunck) (Stary, Remaudiere & Leclant 1971)

All the authors above recorded *A. sonchi* from *Hyperomyzus* on their secondary host plants, *Sonchus* spp. So far, the parasite has not been reported from the host aphids on their primary host plants, *Ribes* spp.

3.3 GEOGRAPHIC DISTRIBUTION

*A. sonchi* has been recorded from England, Poland, Czechoslovakia, Italy and USSR (Mackauer & Stary 1967); Finland (Halme 1977); Holland (Evenhuis 1978); France, Sicily, Egypt and Israel (Stary 1976); Kazakhstan (Stary 1979) and Japan (Takada & Yamauchi 1979). Evenhuis (1978) has recorded the cynipid, *Phaenoglyphis xanthochroa* Förster as a parasite of *A. sonchi* in Holland.
PART II

MATERIALS AND METHODS
CHAPTER 4
GENERAL MATERIALS AND METHODS

4.1 THE GLASSHOUSE AND THE INSECTARY

All plants used in this study were cultured in a glasshouse. Temperature in the glasshouse was controlled by electric fans and evaporative coolers. During the period of this study, the glasshouse was set to 23 ± 1°C all year round. However, the system was influenced by high ambient temperatures (26°C or above). As a result, mid-day temperatures in the glasshouse could rise up to 30°C or above in hot weather. A 13 h photoperiod provided by natural and fluorescent lights was maintained.

The insectary used comprised three 2 x 4 x 2 m nylon mesh-covered cubicles within a glasshouse similar to the one above. The temperature in the insectary was set to 22 ± 1°C, but as in the glasshouse, was also affected by mid-day heat. However, the excess temperature was reduced considerably by white-washing (i.e. by painting all the glass panels white with oil-based, water soluble paint during the warm months), so that only in very hot weather did the temperature reach 30°C. "Punkah" fans hung from the ceiling and small turbofans in the cubicles provided a continuous and fairly rapid air circulation. A 14 h photoperiod provided by natural light and artificial illumination (supplied by twin 80 watt fluorescent tubes 18 cm above the rearing units) was maintained all year round. Measurements showed that the general level of relative humidity in the cubicles was 50 ± 10%.

4.2 THE ENVIRONMENTAL CABINETS AND THE TEMPERATURE-CONTROLLED ROOM

The four environmental cabinets used in this study were placed together in a laboratory maintained at 20 ± 2°C (Fig. 4.1). Temperatures in each of the cabinets were controlled by a dual-thermostat which provided
two different temperature settings each 24 h period. Each cabinet contained its own cooling and heating systems and air flow in the working space was vertical. The equipment permitted the maintenance of the temperatures used to within ± 0.5°C. When an alternating temperature regime was used, the time required to change gradually from one temperature to the other varied with the amplitude of alternation, e.g. approximately one hour was required for 15°C change.

The required photoperiods in each cabinet were provided by two 40 watt fluorescent lamps operated by time switches. No attempt was made to regulate the humidity in the cabinets during this study.

The temperature-controlled room used was situated in the same laboratory. With its own temperature-regulating system, the room provided constant temperatures within ± 0.5°C. The illumination on each 1 x 0.5 m shelf was provided by two 30 watt fluorescent lamps located 42 cm above the surface on which experimental material was placed. A time switch allowed regulation of the photoperiod. Again, humidity was not controlled.

Hygrothermograph records were kept for all experiments.

4.3 GROWING AND HANDLING THE HOST PLANT

4.3.1 Obtaining Seeds

The plant used throughout this study was the aphid's main secondary host, *S. oleraceus*. As its seed was not commercially available, the large amount required was collected from the field in early to mid summer when large numbers of flowering plants could easily be found. Preliminary experiments showed that seeds on cut plants ripened successfully if the flower heads were already open at the time of cutting (also see Gill 1938). Good germination was almost invariably obtained with seed collected at all times of the year. The seed germinated more uniformly, however,
if it was stored at ordinary room temperature for two months or longer before use (T.L. Woolcock, unpublished data).

The actual procedures of collecting seed were as follows: Flowering stems (usually 30-40 cm long) were cut and tied into bundles of 20 to 30 stems each. Two or three bundles were suspended within a large plastic dustbin. A sheet of newspaper placed on the bottom of the bin absorbed the moisture accumulating from aphids and plants. Bins were kept dry and warm for about seven days after which the majority of fertile seeds had fallen. The bundles were shaken carefully to release further seed. The collected seed was stored in paper bags.

4.3.2 Selection of Substratum

The morphology, biology and ecology of *S. oleraceus* have been described in detail by Lewin (1948). The plant grows very well on clay-rich, sandy, or loamy soils, showing wide tolerance, although its morphology, especially its size, varies widely with soil conditions.

Table 4.1 Constitution of three different types of experimental soil

<table>
<thead>
<tr>
<th>Type of soil</th>
<th>Material</th>
<th>Fertilizer per 0.028 m³</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;Compost&quot;</td>
<td>50% Recycled soil</td>
<td>70 g N.P.K. (complete fertilizer)</td>
</tr>
<tr>
<td></td>
<td>30% Leaf mould</td>
<td>50 g Lime</td>
</tr>
<tr>
<td></td>
<td>10% Straw</td>
<td>50 g Blood &amp; Bone</td>
</tr>
<tr>
<td></td>
<td>10% Perlite, vermiculite coarse sand</td>
<td></td>
</tr>
<tr>
<td>&quot;Potting mix&quot;</td>
<td>60% River loam</td>
<td>75 g N.P.K. (complete fertilizer)</td>
</tr>
<tr>
<td></td>
<td>20% Peat moss</td>
<td>50 g Lime</td>
</tr>
<tr>
<td></td>
<td>20% Perlite, vermiculite coarse sand</td>
<td>6 g Minor elements (esminell)</td>
</tr>
<tr>
<td>&quot;Special&quot;</td>
<td>80% Recycled soil composted with straw</td>
<td>75 g N.P.K. (complete fertilizer)</td>
</tr>
<tr>
<td></td>
<td>20% Peat moss</td>
<td>60 g Lime</td>
</tr>
</tbody>
</table>

Three types of experimental soil: "compost", "potting mix", and "special" (Table 4.1), available in large quantities at CSIRO, were
tested in September 1980. Ten 15 cm pots of each type of soil were seeded with *S. oleracea* (see below, for methods of planting) and all pots were placed together on one bench in the glasshouse. After germination, the young plants were watered whenever necessary. On the 10th day after planting, they were thinned to two seedlings per pot and fertilized with dilute Aquasol. Plant size was recorded twice, on the 24th and 35th day respectively (Table 4.2). The results showed that "potting mix" was clearly far inferior to the other two, presumably because it contains less organic material (see Table 4.1). "Compost" was marginally the best soil type, and was chosen to grow the host plants for all subsequent experiments.

4.3.3 Planting and Growing

The basic units for growing the host plant were 30 x 40 cm glasshouse flats filled with compost soil. The seed required was distributed evenly on the surface of the soil and then covered with sheets of wet sponge material. The flats were placed in metal trays for basal watering.

In the glasshouse germination usually took 2-3 days during the warmer months but up to 4-5 days in winter. The sponge sheets were removed as soon as most of the seed had germinated. The soil was kept moist by basal watering every second day.

For rearing aphids, seedlings grown under crowded conditions were ready for use 2-4 weeks after germination depending again on the time of the year.

For the production of flower heads, the plants were thinned to two seedlings per flat. The main stems were tipped to induce the plants to produce a large number of flower heads which usually required seven weeks or longer to develop.
### Table 4.2 Mean growth characteristics of *S. oleraceus* after 24 and 35 days growth in three different types of experimental soil†

<table>
<thead>
<tr>
<th>Type of soil</th>
<th>24 days</th>
<th>35 days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. leaves*</td>
<td>Length of largest leaf (cm)</td>
</tr>
<tr>
<td>Compost</td>
<td>9.3</td>
<td>9.0</td>
</tr>
<tr>
<td>Potting mix</td>
<td>4.2</td>
<td>3.4</td>
</tr>
<tr>
<td>Special</td>
<td>9.5</td>
<td>10.2</td>
</tr>
</tbody>
</table>

† For each type of soil, 10 plants were sampled;

* Stipules and leaves shorter than 1 cm are not included.
4.4 ESTABLISHMENT AND MAINTENANCE OF THE APHID STOCK CULTURE

The aphid stock culture used in this study was initiated with 60 apterous (parthenogenetic, viviparous female) adults taken from *S. oleraceus* at Canberra, A.C.T. and at Wangaratta, Victoria, in September, 1980. The culture was reared continuously in the insectary on crowded seedlings of *S. oleraceus*. A flat of seedlings covered by a gauze-covered frame cage was infested with about 150 aphids of mixed stages. Fourteen days later, the foliage was cut and the aphids thereon were shaken off into a large sieve (3 mm - 5 mm mesh size). Aphids required for continuation of both the aphid culture and the parasite cultures were removed, as were those required for experimental purposes, the rest were discarded. Usually, two or more culture flats were maintained simultaneously so that a large number of aphids were available whenever required.

4.5 ESTABLISHMENT AND MAINTENANCE OF THE PARASITE STOCK CULTURES

Two strains of *A. sonchi* were involved in this study: one from the Drôme Department, the Mediterranean region of France, sent by Dr Jean-Paul Aeschlimann in July 1981; the other was introduced from Kyoto, Japan, in May 1980, with the help of Dr H. Takada.

A stock culture of each of the two strains was established. The two stock cultures were maintained in separate cubicles in the insectary. Caged flats of seedlings were infested each with about 1 ml. of aphids of mixed instars and morphs obtained from the aphid stock culture. After four days, when the aphids had increased considerably in numbers, 50 mated female parasites (1-3 days after emergence) were introduced into each cage. Six days later, the mummies (i.e. the dead, mummified, silk-lined aphid remains enclosing the developing parasite) began to appear. Emergence of adult parasites usually started on the 12th day, thus the cultures were
Fig. 4.1 Environmental cabinets

Fig. 4.2 Three basic rearing units (from left to right): the caged pot, the jar and the vial.
maintained on a two-week cycle. Adult parasites were always provided with honey and water when they were not allowed access to host aphids.

The stock originating from France (French strain hereafter) was used in the investigation of the aphid-parasite system. Experiments were also carried out on the stock from Japan (Japanese strain hereafter) whenever a comparison between the two strains seemed desirable. The nouns "parasite" and "A. sonchi" denote the French strain in all subsequent chapters unless otherwise stated.

4.6 GENERAL EXPERIMENTAL REARING METHODS FOR BOTH THE APHID AND THE PARASITE

Three basic rearing units (Fig. 4.2) were used to rear both the aphid and the parasite in experimental work. When cut shoots of flower heads were used, they were supported in a caged pot containing modified Hoagland-Snyder culture solution (see Hughes & Woolcock 1965). The caged pot was assembled from a plastic jar, a glass bottle containing the culture solution, the jar lid and a clear plastic cylinder with gauze top. A 20 mm diameter hole was made half way on the cylinder and closed with a removable gauze lid.

When detached young leaves were used, they were laid upper surface down on the surface of nutrient agar contained either in a plastic jar or in 25 x 50 mm vials. The nutrient agar was made with the same culture solution as the one above. The surface of agar was wetted with water to ensure leaf adherence. After aphids were put on the leaves, the jars or vials were inverted onto a flat surface of a tray or a box so that the aphids fed on the underside of the leaves.

The period during which the cut plant material remained favourable to the aphid varied with the experimental conditions and with the number
Fig. 4.3 Suction devices for handling adult parasites.

A, suction device operated by a compressed air venturi system;
B, mouth suction tube. a, small perspex tube; b, bronze gauze tube;
c, perspex tube; d, detachable rubber cock; e, flexible polythene tube connected to the air venturi system; f, soft sponge material covered by terylene gauze (to reduce the impact when parasites are sucked in); g, small perspex tube; h, terylene gauze; i, flexible polythene tube. The arrows show the direction of air flow.
of aphids feeding on it. Experiments showed that cut shoots of flower heads in the caged pot grew actively and stayed suitable for the aphid for almost as long as they did when still attached to the plant under comparable conditions. For example, within the temperature range from 8°C to 28°C, 20 or more aphids could be reared satisfactorily from birth to maturity on one flowering shoot. Detached young leaves, on the other hand, deteriorated more quickly than undetached ones. For example, at 20°C detached young leaves usually became unsuitable to the aphids within three or four days. In the course of experiments, any flowering shoots or young leaves showing signs of unsuitability for the aphid were replaced with freshly cut ones. The influence of these excised plant materials on the performance of the aphid will be described in detail in Chapter 6.

In all experiments, aphids were handled with moistened small paint brushes. Adult parasites were transferred either with a suction device connected to a compressed air venturi system or with a suction tube operated by mouth (Fig. 4.3).

4.7 DETERMINATION OF INSTARS OF *H. lactucae*

Aphids of different instars of *H. lactucae* were obtained by maintaining adult aphids on young leaves and separating their progeny when newly born and after each moult. The aphids thus obtained were carefully compared under a binocular microscope. As a result, the following simple key was derived for identifying the different instars in this study:

1. Antennae 4-segmented ........................................ Instar 1
   Antennae 5 or 6-segmented ........................................ 2
2. Antennae 5-segmented ........................................... Instar 2
   Antennae 6-segmented ............................................. 3
3. Cauda length less than twice as long as its basal width...........4  
   Cauda at least twice as long as its basal width,  
   wings absent (apterae) or present (alatae)....................Adults  

4. Antennal segment III equal to or slightly longer than  
   segment IV, well-developed wings absent......................Instar 3  
   Antennal segment III at least 1.25 times as long as  
   segment IV; if apteriform, wingpads absent; if  
   alatiform, wingpads well-developed.......................Instar 4  

Since the above key was derived from aphids reared under standard,  
 favourable conditions, it does not cover the variations that may occur  
 under different environmental conditions or between different populations.  
 (see Eastop and van Emden 1972). However, for rapid identification in  
 population studies of the aphid, the key was considered very satisfactory.  
 (The results of the above observations suggest that the criteria used by  
 Martin (1979, p. 126) to distinguish between different instars of  
 *H. lactucae* were incorrect.)  

In all subsequent chapters, descriptions of aphids belonging to  
 different instars/morphs are abbreviated, whenever appropriate, as  
 follows:  
   \[ N_1 = \text{first instar nymph}; \quad N_2 = \text{second instar nymph}; \]
   \[ N_3 = \text{third instar nymph}; \quad N_4 \text{ apt.} = \text{fourth instar apteriform nymph}; \]
   \[ N_4 \text{ al.} = \text{fourth instar alatiform nymph}; \quad A \text{ apt.} = \text{apterous adult}; \]
   \[ A \text{ al.} = \text{alate adult}. \]
5.1 INTRODUCTION

A life and fertility table is a convenient format for describing the death rate and the birth rate of a population living in a particular environment. From such a table, it is possible to calculate the intrinsic rate of increase $r_m$, which, by taking account of changes in birth and death rates with age, becomes a very meaningful parameter for describing the potential of the population to increase in numbers (Birch 1948). Since both the death rate and the birth rate in a population are determined by the interaction of the innate properties of the organism and its environmental components, the life and fertility table technique offers biologists a model with which the effects of different climatic and food conditions on the growth potential of a population can be meaningfully assessed (e.g. Howe 1953a, Watson 1964) and the innate competence for population increase of various species or of different biotypes of the same species can be compared (Barlow 1962; Frazer 1972a & b). Similarly, life and fertility table statistics for an insect and its natural enemies covering a range of experimental conditions can be used to aid the assessment of the potential effectiveness of the latter (Messenger 1964a; Force & Messenger 1964a & b; Mackauer 1983). Information obtained with the life and fertility table technique therefore can be very helpful in gaining an understanding of ecological relationships.

Because of its usefulness, the life and fertility table technique has been widely used in insect studies in the last three decades. Unfortunately, although the approach is relatively simple and the
assumptions involved are clear, some confusion concerning the description, construction and analyses of life and fertility tables have occurred in the literature. Since the life and fertility table technique is used extensively in this thesis, the problems involved will be discussed in some detail.

An example of the construction of a life and fertility table and the calculation of the intrinsic rate of increase \( (r_m) \) will be used to show the approximations that are usually introduced. In particular, the significance of age-interval grouping will be considered. Finally, the discussion will be directed to some of the constraints imposed on the interpretation of the parameters estimated from a life and fertility table.

5.2 DESCRIPTION AND CONSTRUCTION OF LIFE AND FERTILITY TABLES

Assuming that enough males occur in a population to mate the available females, only the latter essentially determine the rate of increase. A life and fertility* table therefore describes the mortality of females and the number of female births. Basically, a life and fertility table may be constructed with following columns (cf. Birch 1948):

- \( x \): pivotal age, the midpoint of age intervals in units of time (days, weeks, etc.)
- \( l_x \): the probability of a female surviving to the pivotal age \( x \), expressed on the basis of 1.00 at the start point
- \( m_x \): mean number of female births during age interval \( x \) per female aged \( x \).

The values in columns \( l_x \) and \( m_x \) are usually multiplied together to give a further column, \( l_x m_x \).

*This has often been termed the fecundity column, but since it refers to live female births, fertility is the appropriate term.
There are two ways of collecting data to construct a life and fertility table for a population with overlapping generations and the resultant tables will differ in form as well as in meaning (Krebs 1978). If the data on survival and reproduction over each age interval are based on an imaginary cohort with the age structure of a sample of individuals from the population, the life and fertility table constructed will be time-specific (or vertical). On the other hand, data of survival and reproduction can be collected by following a real cohort through successive short time intervals from birth to death. A life and fertility table constructed from the data obtained this way is termed age-specific (or horizontal). Obviously, these two types of tables will be identical only if mortality and reproduction in each age group of the subject population remain unchanged through time. Krebs (1978) and Southwood (1978) give detailed accounts on the differences between the two types of tables.

Table 5.1 gives a hypothetical example of the data obtained by maintaining 40 parthenogenetic females from birth to death under specific conditions where neither food nor space are limiting, and at the end of each day recording the number of females surviving and the total number of female offspring they produce during each day.

By following the methods and definitions given above, a life and fertility table for the animal can now be constructed (Table 5.2). The calculations involved are simple, e.g. to obtain $l_x$ and $m_x$ values for the pivotal age 6.5 in Table 5.2:

$$\frac{\text{No. survivors at the pivotal age } (N_{6.5})}{\text{No. survivors at the end of the 6th day}} = \frac{\text{No. survivors at the end of the 7th day}}{2}$$

$$= (28 + 26)/2 = 27$$
Table 5.1  Hypothetical recordings of survival and fecundity of a parthenogenetic population initiated with 40 newly born individuals

<table>
<thead>
<tr>
<th>Days</th>
<th>Number of survivors</th>
<th>Number of female births</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>40</td>
<td>-</td>
</tr>
<tr>
<td>1</td>
<td>38</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>36</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>34</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>32</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>30</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>28</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>26</td>
<td>270</td>
</tr>
<tr>
<td>8</td>
<td>24</td>
<td>250</td>
</tr>
<tr>
<td>9</td>
<td>22</td>
<td>230</td>
</tr>
<tr>
<td>10</td>
<td>20</td>
<td>210</td>
</tr>
<tr>
<td>11</td>
<td>18</td>
<td>190</td>
</tr>
<tr>
<td>12</td>
<td>16</td>
<td>170</td>
</tr>
<tr>
<td>13</td>
<td>14</td>
<td>150</td>
</tr>
<tr>
<td>14</td>
<td>12</td>
<td>130</td>
</tr>
<tr>
<td>15</td>
<td>10</td>
<td>110</td>
</tr>
<tr>
<td>16</td>
<td>8</td>
<td>90</td>
</tr>
<tr>
<td>17</td>
<td>6</td>
<td>70</td>
</tr>
<tr>
<td>18</td>
<td>4</td>
<td>50</td>
</tr>
<tr>
<td>19</td>
<td>2</td>
<td>30</td>
</tr>
<tr>
<td>20</td>
<td>0</td>
<td>10</td>
</tr>
</tbody>
</table>

Table 5.2  Life and fertility table constructed from the data given in Table 5.1

<table>
<thead>
<tr>
<th>Age interval in days</th>
<th>Pivotal age in days, x</th>
<th>$l_x$</th>
<th>$m_x$</th>
<th>$l_xm_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-1</td>
<td>0.5</td>
<td>0.975</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1-2</td>
<td>1.5</td>
<td>0.925</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2-3</td>
<td>2.5</td>
<td>0.875</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>3-4</td>
<td>3.5</td>
<td>0.825</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4-5</td>
<td>4.5</td>
<td>0.775</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5-6</td>
<td>5.5</td>
<td>0.725</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6-7</td>
<td>6.5</td>
<td>0.675</td>
<td>10</td>
<td>6.75</td>
</tr>
<tr>
<td>7-8</td>
<td>7.5</td>
<td>0.625</td>
<td>10</td>
<td>6.25</td>
</tr>
<tr>
<td>8-9</td>
<td>8.5</td>
<td>0.575</td>
<td>10</td>
<td>5.75</td>
</tr>
<tr>
<td>9-10</td>
<td>9.5</td>
<td>0.525</td>
<td>10</td>
<td>5.25</td>
</tr>
<tr>
<td>10-11</td>
<td>10.5</td>
<td>0.475</td>
<td>10</td>
<td>4.75</td>
</tr>
<tr>
<td>11-12</td>
<td>11.5</td>
<td>0.425</td>
<td>10</td>
<td>4.25</td>
</tr>
<tr>
<td>12-13</td>
<td>12.5</td>
<td>0.375</td>
<td>10</td>
<td>3.75</td>
</tr>
<tr>
<td>13-14</td>
<td>13.5</td>
<td>0.325</td>
<td>10</td>
<td>3.25</td>
</tr>
<tr>
<td>14-15</td>
<td>14.5</td>
<td>0.275</td>
<td>10</td>
<td>2.75</td>
</tr>
<tr>
<td>15-16</td>
<td>15.5</td>
<td>0.225</td>
<td>10</td>
<td>2.25</td>
</tr>
<tr>
<td>16-17</td>
<td>16.5</td>
<td>0.175</td>
<td>10</td>
<td>1.75</td>
</tr>
<tr>
<td>17-18</td>
<td>17.5</td>
<td>0.125</td>
<td>10</td>
<td>1.25</td>
</tr>
<tr>
<td>18-19</td>
<td>18.5</td>
<td>0.075</td>
<td>10</td>
<td>0.75</td>
</tr>
<tr>
<td>19-20</td>
<td>19.5</td>
<td>0.025</td>
<td>10</td>
<td>0.25</td>
</tr>
</tbody>
</table>
When a life and fertility table is completed the number of times the population will multiply per generation is described by the net reproductive rate, $R_0$, which is usually given by:

$$R_0 = \sum l_x m_x$$

$R_0$ is thus obtained by multiplying the $l_x$ and $m_x$ schedules together and summing over all age groups.

However, the term $l_x m_x$, though generally interpreted as the product of the age-specific survival rate ($l_x$) and the age-specific fertility rate ($m_x$), can be simply regarded as the number of female births per original female during the age interval. Likewise, the net reproductive rate, $R_0$, is simply the number of female births per original female during one generation, thus, in the calculations:

$$l_x^m x = \frac{\text{No. female births during age interval } x}{\text{No. original females}}$$

For example:

$$l_{6.5}^m_{6.5} = \frac{\text{No. female births during age interval } 6-7}{\text{No. original females}} = \frac{270}{40} = 6.75$$

$$R_0 = \frac{\text{No. female births during the first generation}}{\text{No. original females}} = \frac{1960}{40} = 49.00$$

It is obviously more convenient (and more accurate because of accumulation of round-off errors) to calculate values for $l_x m_x$ and $R_0$ this way.
5.3 CALCULATION OF INTRINSIC RATE OF INCREASE AND OTHER POPULATION PARAMETERS

Andrewartha and Birch (1954) discuss the use of the life and fertility table in calculating the intrinsic rate of increase. They define the intrinsic rate of increase as the actual rate of increase in a population with a stable age distribution under specified environmental conditions in which the amount of space and food are not limiting. The intrinsic rate of increase is \( r_m \) in the formula:

\[
\frac{dN}{dt} = r_m N
\]

That is, the increase in numbers (\( dN \)) with time (\( dt \)) is equal to the intrinsic rate of increase (\( r_m \)) multiplied by the number already present (\( N \)). The intrinsic rate of increase, \( r_m \), can also be expressed in the following formula:

\[
N_t = N_0 e^{r_m t}
\]

where \( N_t \) = number of individuals at time \( t \)

\( N_0 \) = number of individuals at time \( o \)

\( e \) = base of natural logarithms, 2.781828

\( r_m \) = intrinsic rate of increase

Theoretically, the precise value of \( r_m \) may be obtained by solving the following equation (Lotka 1925):

\[
\int_0^\infty e^{-r_m x} l_x m_x dx = 1
\]

In practice, given \( l_x m_x \) values from a life and fertility table, \( r_m \) may be estimated from the expression:

\[
\sum e^{-r_m x} l_x m_x = 1
\]

Determination of \( r_m \) in the above equation used to require either rather tedious trial-and-error calculations or elaborate graphic techniques (Birch 1948; Watson 1964). Thus, several authors attempted to
simplify the procedure (Howe 1953b; Wyatt and White 1977). However, modern calculators and computers have made the derivation of $r_m$ a matter of routine. As pointed out earlier, the values of $l_X m_X$ may be simply obtained by dividing the number of female births during each age interval by the number of females at time 0. Thus, for the determination of $r_m$, only (1) total number of original females at time 0; and (2) number of female births during each age interval, are needed.

In the present work, a simple program was written by the author for use in a Hewlett-Packard 97 calculator. Determination of $r_m$ for a life and fertility table in which $m_X$ is larger than 0 in fewer than 30 age intervals is a matter of minutes. The $r_m$ value for the imaginary population (Table 5.2) was estimated as 0.4323.

Once $r_m$ is known, the generation time ($T$) can be calculated from the following formula:

$$T = \frac{\log R_0}{r_m}$$

Where $R_0$, as defined earlier, $T$ is the mean time from birth of parents to birth of offspring in a population with stable age distribution that would eventually form if the prevailing life and fertility schedules remain unchanged through time. Thus the estimate of $T$ in the example is made as follows:

$$T = \frac{\log 49.00}{0.4323} = 9.00 \text{ (days)}$$

Another statistic, the finite rate of increase ($\lambda$), is also usually estimated. This is the multiplication per female in unit time and is defined by the equation: $\lambda = e^{r_m}$. This final statistic, when calculated, can be used to estimate the time required for a given population to double its numbers.
5.4 DISCUSSION

The value of $r_m$ estimated as above has normally been regarded as an accurate description of the population growth potential of animals with overlapping generations under given conditions. In fact, the accuracy of $r_m$ values depends entirely on the similarity between the actual population events and the life and fertility tables compiled. The life and fertility table technique assumes that $l_xm_x$ changes step-wise through the reproductive life of the population, the timing corresponding to each step value being taken as that at the mid point of the age interval. By contrast, the actual timing of deaths and births shows tremendous variation (Cole 1954). It is well-known that female births early in the reproductive life contribute far more to population increase than female births later (Cole 1954, Lewontin 1965; Wyatt & White 1977). This principle also applies to female births within each age interval, so $r_m$ must be an approximate statistic. Since the pivotal age is normally represented by the mid point of each age interval, in cases where deaths and births occur either regularly or with a monotonic trend as in aphids, mites, beetles and many other fast breeding insects, values of $r_m$ estimated from life and fertility tables are likely to be inaccurate and usually underestimated. The error of estimation will be accentuated where the age intervals are long relative to the whole reproductive life. Fig. 5.1 shows two significantly different population growth curves based on two life and fertility tables constructed from the same original recording (Table 5.1) but using different length of age intervals. The population predicted by the $r_m$ value derived from a life and fertility table with shorter age intervals has reached a much larger size in the same length of time.

To reduce the amount of error involved in the estimation of $r_m$, it
Fig. 5.1 Population growth curves resulting from two life and fertility tables which are constructed from the same data but with different length of age intervals. (A) Each age interval covers one day ($r_m = 0.4323$); (B) Each age interval covers three days ($r_m = 1.2657$).
is thus necessary to make observations on the pertinent population processes at the shortest possible intervals and then construct the life and fertility tables with the shortest interval between observations. This has sometimes been overlooked in the past. For example, Andrewartha and Birch (1954, p.37), when discussing the construction of life and fertility tables, wrote that "The intervals for the age-groups may be chosen quite arbitrarily and depend partly on the method by which the data were collected". Statements of this sort leave the unfortunate impression that the length of age intervals has little influence on the accuracy of \( r_m \) value estimated. Consequently, Barlow (1962) and Dean (1974), working with aphids, summed their data into weekly age intervals for their life and fertility tables, though they recorded daily observations on survival and reproduction. Because of the decreasing trend of population size predicted by \( r_m \) values estimated with longer age intervals, the population growth potential of the aphids under various experimental conditions could be much higher than that expressed by the values of intrinsic rate of increase calculated by these authors.

Several authors have attempted to compare \( r_m \) values estimated from life and fertility tables with those obtained empirically (Table 5.3). That various results were obtained was not surprising, given the problems expressed above. Furthermore, such comparisons assume that the empirical \( r_m \) values were estimated from populations initiated with the theoretical stable age distribution. In fact, all the authors started their populations with a number of animals chosen arbitrarily from a range of age classes. Since population increase at any moment varies with the age distribution (Collier et al. 1973, p. 153), populations with identical life and fertility schedules achieve significantly different growth curves through time if they are initiated with different age structure.
Thus, it is surprising that some of the results presented in Table 5.3 have been repeatedly claimed to be anomalous (Southwood 1966, pp. 289-290, 1978 p. 372).

Table 5.3 Comparison between empirical $r_m$ values and those computed from life and fertility tables by various authors

<table>
<thead>
<tr>
<th>Authors</th>
<th>Insects</th>
<th>Results of comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>Howe (1953a)</td>
<td>Ptinid beetles</td>
<td>Empirical values are higher in some species but lower in others</td>
</tr>
<tr>
<td>Lamb (1961)</td>
<td><em>Brevicoryne brassicae</em></td>
<td>Comparable</td>
</tr>
<tr>
<td>Lefkovitch (1963)</td>
<td><em>Lasioderma serricorne</em></td>
<td>Empirical values are higher</td>
</tr>
<tr>
<td>Messenger (1964b)</td>
<td><em>Theroaphis maculata</em></td>
<td>Empirical values are higher</td>
</tr>
</tbody>
</table>

Lefkovitch (1960, 1963) suggests that the higher empirical values of $r_m$ in his studies occurred because of the implicit assumption that the distribution of the time from birth to maturity was Gaussian. Values of $r_m$ will be slightly underestimated when the developmental times, which are usually found to be both leptokurtic and positively skewed (Lefkovitch 1960; Sharpe *et al.* 1977), are assumed to have a Gaussian distribution and represented by their means. While this may account for some of the discrepancy observed by various authors, it is important to remember that this assumption is involved only when the data for immature stages and those for adult life are collected separately.

Finally, the accuracy of $r_m$ is affected by the point within each age interval with which the pivotal age is represented. It is obvious that different values will be obtained if the deaths and births are assumed to occur at some point other than the mid point of each age interval, the highest value if the beginning of the age interval is used and the lowest
value if the end is used. Since the actual timing of the occurrence of deaths and births varies widely, there is no general rule to determine which is the best point to use. Justified by its simplicity, the midpoint has been customarily used in life and fertility tables. In literature, vague descriptions such as "$l_x$ is the probability at birth of a female being alive at age $x$" are frequently encountered (e.g. Price 1975, p. 130; Watson 1964). The reader can never be sure which point has been used as the pivotal age by such authors. Nevertheless, some authors' descriptions show that various methods have been used. For instance, Messenger (1964a) used the end of each age interval as the pivotal age. Therefore, compared to the standard technique all population events were postponed for half an age interval in his life and fertility tables, leading to the underestimation of $r_m$ values, i.e. as if calculation of $r_m$ was made from the following equation:

$$
\sum_e \frac{-r_m(x + 0.5)}{l_x m_x} = 1
$$

Similar errors may also have occurred in other papers, such as that of Clarke and Sardesai (1960).
PART III

STUDIES ON HYPEROMYZUS LACTUCAE
CHAPTER 6

PERFORMANCE OF THE APHID IN RELATION TO ITS HOST PLANT, WITH
PARTICULAR EMPHASIS ON THE DEVELOPMENT OF REARING SYSTEMS

6.1 INTRODUCTION

The performance of aphids (e.g. rate of development, survival, body size, reproductive rate, etc.) is directly affected by the condition of the host plant on which they feed (Adams & van Emden 1972). Important factors include age of plants and leaves (Dixon 1970; Kennedy & Booth 1951), feeding site (Llewellyn & Oureshi 1978, 1979; Lowe 1967a, b), and nutritive status (Banks & Macaulay 1970; van Emden 1966). Furthermore, when plant material is excised, it may undergo rapid and considerable physiological changes so as to alter its influence on the aphids compared to that of the same part of the whole plant (e.g. McCaffery 1982; Müller 1966).

H. lactucae is a typical example of an aphid feeding on the "flush" growth of its host plants. Natural anholocyclic populations feed preferentially on young flower heads, growing tips and young leaves of S. oleraceus (Hille Ris Lambers 1949; Martin 1979; Stubbs & Grogan 1963) and workers have used detached young leaves, young seedlings (e.g. Boakye & Randles 1974; Leong 1977; Sylvester 1969, 1973) and flowering plants (e.g. Martin 1979) in insectary and laboratory work on this aphid. However, no quantitative information was available on the performance of the aphid either in relation to the different stages of the host plant, or on the effect of detached plant material.

This chapter reports experiments to show how the performance of the aphid was affected by different plant materials. The development of different rearing systems for mass-production and experimental work is
examined in the light of the results obtained and their limitations are discussed.

6.2 MATERIALS AND METHODS

6.2.1 Host Plant Materials

In preliminary trials plants grown under crowded and uncrowded conditions showed different growth characteristics (Table 6.1). Under crowded conditions, upstanding, narrow leaves were produced, with few side shoots and flower heads. The leaves were bright green and appeared succulent. In contrast, under less crowded conditions the plants initially produced rosettes of wider, blue-green leaves but more flower heads. Only solitary plants produced an abundance of large flower heads. Thus, equivalent amounts of substrate for the aphid could be provided either by crowded seedlings or by large (older) solitary plants.

In the experiments, host plant material was derived either from three weeks old young seedlings grown in crowded conditions or from eight weeks old flowering plants grown in isolation. Seeds were sown in 15 cm pots in the glasshouse at different times, so that both young seedlings and flowering plants were in the right stages for use in the experiments at the same time. The growth characteristics of the young seedlings used were similar to those described in Table 6.1 for the seedlings of the same age, while the flowering plants were big, each bearing 20 or more young flowering shoots.

6.2.2 Aphids

All aphids used were taken from an experimental colony which was started with one apterous adult and had been maintained on young seedlings in the insectary. Performances of the aphids reared either individually or in small groups on different plant materials were then compared.
Table 6.1  Comparison of growth of *S. oleraceus* plants grown in crowded and uncrowded conditions

<table>
<thead>
<tr>
<th>Time in weeks after sowing</th>
<th>Condition*</th>
<th>No. leaves*</th>
<th>Growth characteristics (mean of 10 plants)</th>
<th>Predominant colour</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Length of longest leaf (cm)</td>
<td>Length of stem (cm)</td>
</tr>
<tr>
<td>2</td>
<td>crowded</td>
<td>3.6</td>
<td>3.6</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>uncrowded</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>crowded</td>
<td>6.2</td>
<td>12.7</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>uncrowded</td>
<td>7.1</td>
<td>7.4</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>crowded</td>
<td>10.3</td>
<td>10.5</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td>uncrowded</td>
<td>20.7</td>
<td>15.5</td>
<td>3.9</td>
</tr>
</tbody>
</table>

* Crowded and uncrowded conditions represent 30–40 and 2 plants in one 15 cm pot respectively.

* Stipules and leaves shorter than 1 cm are not included.
6.3 EXPERIMENTS WITH INDIVIDUAL APHIDS

6.3.1 Experimental Procedures

Six treatments including excised materials were derived for the experiment:

(1) inner leaves - newly emerged leaves of the crowded seedlings;
(2) outer leaves - the oldest leaves of the crowded seedlings;
(3) detached leaves - inner leaves cultured on agar in vials;
(4) hard leaves - mature leaves of the flowering plants;
(5) flower heads - young flower heads of the flowering plants; and
(6) cut flower heads - cut shoots of flower heads cultured in the caged pot.

To facilitate observations, young seedlings used were thinned to one plant in each pot just before the test aphids were introduced.

Caging individual aphids on the plant material of the six different treatments was fairly complicated. Preliminary observations showed that nymphs placed singly on the inner leaves of crowded seedlings usually remained there until they reached the adult stage, thus the whole seedling could be caged in a plastic cylinder with a gauze top. To keep aphids on outer leaves, hard leaves and flower heads, small cages made from 11 x 5 x 3 cm plastic boxes were used with a nylon mesh lid to allow illumination and air movement (Fig. 6.1). A hole was cut on one end of the box for inserting plant material. When plant material was inserted into the box, two small collar pieces of sponge placed in the hole prevented the aphids escaping. When used with a flower head, the whole cage was attached to two rods standing in the soil which could be raised gradually to match the growth of the stem during the experiment. The methods for rearing aphids on detached leaves and cut shoots of flower heads were the standard procedures described in Chapter 4. Detached leaves deteriorated quickly
Fig. 6.1 Cage for rearing aphids on flower heads; the same cage was also used for rearing aphids on outer leaves and hard leaves.
and thus were replaced with new ones every three days.

To minimize variations in experimental conditions, experiments for the six treatments were carried out in one cubicle of the insectary from October to November, 1980, starting on the same day. Daily mean temperature in the insectary during this period remained at 25 ± 1°C.

The plant material of each treatment was inoculated with first instar nymphs collected from the progeny of apterous adults (placed on detached leaves) within 24 h of birth. The nymphs were weighed singly on an electronic balance (accuracy 0.1 μg) just before they were placed onto the plant material. They were weighed again on the 6th day and also on the day when they became adult. Observations with outer leaves and detached leaves were then terminated. At the second weighing on the 6th day, aphids feeding on hard leaves were still very small and none of the nymphs had reached the adult stage. Observation of this treatment was stopped then.

Aphids feeding on inner leaves, flower heads and cut flower heads were all observed daily after they became adult. The plant material in each cage was examined thoroughly at a fixed time every day and any young found were removed and recorded until the adult died.

A small proportion (about 5-10%) of the aphids in the experiments developed into alatae. For simplicity, data on these aphids were not included in the results presented.

6.3.2 Results

(1) Growth of individuals

Weight increases of the aphids reared on the six treatments are shown in Table 6.2. The relative growth rate (the mean weight increment per unit time per initial weight over the period between two weighings) was calculated using the following formula (Radford 1967):
RGR (μg μg⁻¹ day⁻¹) = 
\[ \frac{\log_{10} \text{final weight (μg)} - \log_{10} \text{initial weight (μg)}}{\text{No. days over which weight increment is measured}} \]

Analysis of variance showed that there were significant differences between the mean relative growth rates of different treatments (F = 11.85, d.f. = 5/188, P < 0.01). The differences were further analyzed using Duncan's multiple range test (Duncan 1955) and the results are shown in Table 6.2.

(ii) Duration of nymphal development and adult weight

The aphids feeding on hard leaves developed much more slowly than aphids in other treatments: on the 6th day most of them were still very small (see Table 6.2) and appeared to be second or third instar nymphs. Among the remaining five treatments, although no significant differences were detected for either durations of nymphal development (F = 1.68, d.f. = 5/158, P > 0.05) or mean adult weights (F = 1.05, d.f. = 5/158, P > 0.05), Table 6.3 shows that aphids which showed higher relative growth rate (see Table 6.2) reached the adult stage earlier and were also heavier.

(iii) Survival and fecundity

Although the rates of growth and development of the aphids feeding on hard leaves were reduced considerably, every nymph in this treatment survived to the 6th day. In the remaining five treatments, no mortality during the immature stages occurred.

Observations on survival of adults and reproduction were only made on inner leaves, flower heads and cut shoots of flower heads. Aphids feeding on inner leaves generally lived longer and produced more young than aphids in the other two treatments (Fig. 6.2; Table 6.4). Although no significant differences were detected between the mean total numbers
Table 6.2  Mean relative growth rate of apterous *H. lactucae* reared on different treatments of young seedlings and flowering plants of *S. oleraceus*

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>Initial weight (µg)</th>
<th>Weight on day 6 (µg)</th>
<th>Relative growth rate*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>Range</td>
<td>S.D.</td>
</tr>
<tr>
<td>Inner leaves</td>
<td>30</td>
<td>46.5</td>
<td>31-69</td>
<td>12.0</td>
</tr>
<tr>
<td>Outer leaves</td>
<td>32</td>
<td>49.3</td>
<td>36-81</td>
<td>13.2</td>
</tr>
<tr>
<td>Detached leaves</td>
<td>35</td>
<td>48.5</td>
<td>32-78</td>
<td>14.0</td>
</tr>
<tr>
<td>Hard leaves</td>
<td>31</td>
<td>49.0</td>
<td>28-93</td>
<td>15.2</td>
</tr>
<tr>
<td>Flower heads</td>
<td>36</td>
<td>49.6</td>
<td>33-76</td>
<td>11.5</td>
</tr>
<tr>
<td>Cut flower heads</td>
<td>30</td>
<td>49.2</td>
<td>29-107</td>
<td>18.7</td>
</tr>
</tbody>
</table>

* µg µg⁻¹day⁻¹; Figures followed by the same lower case letter are not significantly different at the 5% level.
of young produced, the number of young produced during the first four
days of adult life was found to be significantly higher for the aphids
reared on inner leaves. Consequently, a much higher intrinsic rate of
increase was obtained by the aphids in this treatment.

Table 6.3 Duration of nymphal development and weight of apterous adults
of *H. lactucaea* reared on different treatments of young seedlings
and flowering plants of *S. oleraceus*

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>Develop. time in days</th>
<th>Weight within 24 h of adult moulting (µg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean ± S.D.</td>
<td>Mean ± Range ± S.D.</td>
</tr>
<tr>
<td>Inner leaves</td>
<td>30</td>
<td>6.2 ± 0.8</td>
<td>730.9 ± 323-1124 ± 242.2</td>
</tr>
<tr>
<td>Outer leaves</td>
<td>32</td>
<td>6.7 ± 0.7</td>
<td>646.4 ± 315-968 ± 175.2</td>
</tr>
<tr>
<td>Detached leaves</td>
<td>35</td>
<td>6.1 ± 0.6</td>
<td>795.2 ± 516-1175 ± 155.4</td>
</tr>
<tr>
<td>Flower heads</td>
<td>36</td>
<td>6.4 ± 0.6</td>
<td>667.7 ± 312-1084 ± 172.0</td>
</tr>
<tr>
<td>Cut flower heads</td>
<td>30</td>
<td>6.5 ± 0.7</td>
<td>688.8 ± 315-1182 ± 168.4</td>
</tr>
</tbody>
</table>

The age-specific survival and fecundity of the aphids feeding on
flower heads and cut flower heads were very similar (Fig. 6.2). In fact,
with the alternating positions of the two pairs of *l* and *m* curves, the
differences between them can be regarded safely as random variations.
This inference is supported by the similar values of intrinsic rate of
increase in the two treatments (Table 6.4).

6.4 EXPERIMENTS WITH SMALL POPULATIONS

To compare the rates of population increase of the aphids feeding on
young seedlings and flowering plants, five first instar nymphs collected
from the progeny of apterae within 2 h of birth were caged on a 15 cm pot
containing either 30-40 young seedlings or a flowering plant. There were
six replicates for each treatment and all twelve pots were placed on one
bench in the insectary. The experiments were done in October 1980, with
Fig. 6.2 Age specific survival and fertility rates of apterous *H. lactucae* reared on inner leaves, flower heads and cut shoots of flower heads of *S. oleraceus*.
Table 6.4  Survival and fecundity of apterous *H. lactucae* reared on inner leaves, flower heads and cut shoots of flower heads of *S. oleraceus*

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>Adult longevity in days Mean ± S.D.</th>
<th>No. young produced during first 4 days Mean ± S.D.*</th>
<th>No. young produced per female Mean ± S.D.</th>
<th>Intrinsic rate of increase $r_m$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inner leaves</td>
<td>30</td>
<td>17.6 ± 4.5</td>
<td>16.0 ± 5.9 a</td>
<td>45.9 ± 12.9</td>
<td>0.3596</td>
</tr>
<tr>
<td>Flower heads</td>
<td>36</td>
<td>14.8 ± 5.4</td>
<td>10.9 ± 5.1 b</td>
<td>37.9 ± 11.0</td>
<td>0.3198</td>
</tr>
<tr>
<td>Cut flower heads</td>
<td>30</td>
<td>14.5 ± 5.2</td>
<td>11.2 ± 5.0 b</td>
<td>40.4 ± 9.5</td>
<td>0.3225</td>
</tr>
</tbody>
</table>

* Figures followed by the same lower case letter are not significantly different at the 5% level (by Duncan's multiple range test).

Table 6.5  Mean number of aphids of *H. lactucae* after 16 days increase on crowded seedlings and flowering plants of *S. oleraceus* at 25 ± 1°C

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mean number of aphids in each instar and morph ± S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$N_1$</td>
</tr>
<tr>
<td>Young seedlings</td>
<td>466 ± 134</td>
</tr>
<tr>
<td>Flowering plants</td>
<td>513 ± 115</td>
</tr>
</tbody>
</table>
daily mean temperature being maintained at $25 \pm 1^\circ C$. At the end of the 16th day, plant material in each pot was cut and washed with water at 70°C. All aphids obtained were sorted into different instars and morphs and counted under microscope.

At the time when the plants were cut, there were still plenty of acceptable parts uncolonized by the aphids in each replicate of both young seedlings and flowering plants. In the treatment with flowering plants, the plants were big, actively growing and there were a number of new shoots and flower heads emerging as the experiment went on. Aphids in this treatment aggregated on the actively growing parts. However, in the treatment with young seedlings, many aphids were found feeding on the older leaves, presumably due to both the flexibility of the aphid in choosing feeding sites on such plants and the relative shortage of inner leaves.

Table 6.5 presents the mean number of aphids in each instar and morph at the end of the experiments. Although the number of aphids on flowering plants appeared higher, no significant difference was detected between the two treatments (in every case $P > 0.05$, by t-test).

6.5 DISCUSSION

Although all aphids used in the experiments were descendants of one apterous adult, there was considerable variation in all parameters measured within each treatment. Nevertheless, some significant differences were detected between treatments. Most of the observed differences were undoubtedly due to the effects of different plant materials, despite slight variations in temperature, humidity and light intensity within the cubicle, especially where cages of different types were used.

In the four treatments where plant material was kept intact, inner leaves were shown to be the most favourable food source for the aphid.
However, the quality of the leaves on crowded seedlings decreases as they age. This was shown by the lower relative growth rate, longer developmental time and smaller adult size of the aphids feeding on the outer leaves. As a result, although the aphids reared on inner leaves showed a higher intrinsic rate of increase than those feeding on flower heads, the gross population increases on young seedlings and flowering plants were very similar.

With flowering plants, the differences in performance between the aphids feeding on flower heads and those feeding on mature leaves were very obvious. Thus, the favourable feeding sites on such plants are restricted to the actively growing parts.

In the experiments with excised plant materials, the colour of most detached leaves changed from green to brownish in 2-3 days. By contrast, the cut shoots of flower heads continued their normal growth. In fact, the length of time during which the flowering shoots remained favourable to the aphid did not alter after separated from the parent plants.

Despite the rapid deterioration of the detached leaves, with the replacement of new leaves every three days the differences in growth and nymphal development of the aphid between inner leaves and detached leaves were not significant. However, since the leaves undergo obvious physiological changes as a result of excision, the performance of aphids reared with this method is likely to be altered by the frequency with which the detached leaves are replaced.

The data obtained with intact flower heads and cut flower heads suggest that the latter did not alter the aphid performance as far as developmental rate, survival and reproductive rate are concerned. Similar results have also been reported in other aphids. For instance, Graham (1959) and Messenger (1964b), working with the spotted alfalfa aphid,
*Theroaphis maculata* (Buckton), reported that alfalfa stems held in vials containing tap water proved satisfactory in their bioclimatic studies of the aphid without altering its response to different experimental conditions.

The data collected offer useful information for the development of rearing systems for *H. lactucae*. Since the aphid feeds readily on any actively growing part of *S. oleraceus*, both young seedlings grown in crowded conditions and flowering plants can be used for mass-rearing the aphid. However, compared to young seedlings, flowering plants take a relatively long time to grow and more of the plant material produced (i.e. mature leaves and old stems) is unsuitable for the development of the aphid. In addition, the large plant size creates inconvenience in insectary work. Thus the advantages of using young seedlings, in terms of time, space and ultimately efficiency are self-evident.

The method of culturing aphids on cut shoots of flower heads has great potential in the laboratory study on *H. lactucae*. It allows adequate replication in the laboratory, and facilitates the regular observations of aphids, either individually or in small groups, throughout their life spans. With this method, rigorous control of experimental environment and strict selection of consistent host plant conditions are quite feasible when required.

Detached young leaves can also be used in experimental work where substrate influences are not of particular interest and the main requirement is the uniformity of the substrate. However, possible deviations in aphid performance caused by the separation of the plant material from the original plants should be borne in mind when the experimental results are interpreted.
CHAPTER 7
BIOCLIMATIC STUDIES

7.1 INTRODUCTION

Much work on the life history characteristics and demographic performance of *H. lactucae* has been reported in the literature. However, the narrow range of environmental variables examined and the discrepancy in the results presented (see Chapter 2), make it clear that existing data are not a useful basis for quantitative studies of ecological relationships. Extensive and more precise laboratory experiments on various aspects of the biology of *H. lactucae* were necessary. Also of interest were the different reports in the literature of the effects of constant and fluctuating temperatures on insect performance (Bursell 1974). This chapter describes laboratory experiments in which the influences of climatic variables, particularly temperature, on the development, survival, reproduction and some aspects of life history characteristics of the aphid were examined.

7.2 INFLUENCE OF VARIOUS CONSTANT AND ALTERNATING TEMPERATURES

7.2.1 Experimental Procedures

Experimental populations were initiated with apterous adults obtained from the stock culture, and reared on cut shoots of flower heads unless otherwise stated. All experiments were conducted in the environmental cabinets with various temperature-light regimes (Table 7.1). These experimental conditions were chosen to encompass the normal range of the factors encountered in the field.

Experiments under each temperature-light regime were begun with first instar nymphs produced within 24 hours from adults which themselves had been born and reared, usually 5–10 individuals per flowering shoot, under
the same conditions. The test nymphs were transferred onto freshly cut flowering shoots, either one on each shoot in cases where the aphid was going to be observed until death, or 5-10 on each shoot if the aphids were going to be discarded on reaching maturity.

All the experiments listed in Table 7.1 were carried out from December 1980 to June 1981. Whenever possible, the experiments with the same mean temperatures (e.g. 17°C and 23.5°C-9.5°C) were started at about the same time. Development, mortality and reproduction of the aphids were recorded daily at a fixed time and any young found were removed. Dissection of the 56 adults reared under two experimental conditions (i.e. 28°C-13.5°C and 23.5°C-9.5°C) after their death revealed that almost all aphids died with embryos in their body. Adults which died early usually retained more embryos at death than those which lived longer. As "premature" or unnatural death could not be differentiated, all deaths that occurred were assumed to be natural.

Population performance was assessed using life-and fertility tables each constructed from data on 28 aphids reared individually under each set of experimental conditions. However, for the determination of developmental time, more aphids were observed and the sample sizes are shown at the appropriate places.

Results concerning different aspects of the aphid's life history are reported and analyzed separately below.

7.2.2 Rate of Development

The duration of nymphal development increased with a decrease in temperatures, either constant or alternating (Table 7.1). Except at 12.5°C, where an apparent morph "switch" occurred (see 7.2.6), no substantial differences were found between durations at each of the other two
Table 7.1 Population parameters of apterous *H. lactucae* reared on flowering shoots of *S. oleraceus* under various experimental conditions

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Photoperiod (light:dark; h)</th>
<th>R.H.% Mean</th>
<th>Range</th>
<th>Development time in days (Mean</th>
<th>Range)</th>
<th>% mortality in immature stages</th>
<th>Mean life span (from birth to death in days + S.D.)</th>
<th>Time to 50% mortality in days</th>
<th>Mean young produced per adult + S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>28</td>
<td>14 : 10</td>
<td>50</td>
<td>40-60</td>
<td>-</td>
<td>-</td>
<td>100.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>26</td>
<td>14 : 10</td>
<td>50</td>
<td>40-60</td>
<td>12.0(40) #</td>
<td>7-13</td>
<td>12.5</td>
<td>17.1± 4.9</td>
<td>17.0</td>
<td>1.6</td>
</tr>
<tr>
<td>24</td>
<td>14 : 10</td>
<td>70</td>
<td>60-80</td>
<td>6.7(48)</td>
<td>5-8</td>
<td>4.0</td>
<td>18.1± 5.4</td>
<td>19.0</td>
<td>41.3±19.9</td>
</tr>
<tr>
<td>22</td>
<td>14 : 10</td>
<td>70</td>
<td>60-80</td>
<td>7.1(77)</td>
<td>7-10</td>
<td>0.0</td>
<td>21.9± 6.8</td>
<td>21.0</td>
<td>44.8±22.2</td>
</tr>
<tr>
<td>28-13(22)*</td>
<td>14 : 10</td>
<td>70</td>
<td>60-90</td>
<td>7.2(77)</td>
<td>7-10</td>
<td>0.0</td>
<td>21.8± 5.6</td>
<td>22.9</td>
<td>48.3±20.7</td>
</tr>
<tr>
<td>17</td>
<td>13 : 11</td>
<td>70</td>
<td>60-80</td>
<td>9.5(80)</td>
<td>9-13</td>
<td>0.0</td>
<td>32.7± 9.6</td>
<td>35.0</td>
<td>57.2±22.8</td>
</tr>
<tr>
<td>23.5-9.5(17)*</td>
<td>13 : 11</td>
<td>70</td>
<td>50-80</td>
<td>9.4(45)</td>
<td>9-13</td>
<td>0.0</td>
<td>29.3± 7.3</td>
<td>30.0</td>
<td>58.0±20.0</td>
</tr>
<tr>
<td>12.5</td>
<td>12 : 12</td>
<td>75</td>
<td>60-90</td>
<td>17.3(39)</td>
<td>15-22</td>
<td>0.0</td>
<td>55.2±10.4</td>
<td>57.0</td>
<td>43.7±16.7</td>
</tr>
<tr>
<td>20-5(12.5)*</td>
<td>12 : 12</td>
<td>75</td>
<td>55-95</td>
<td>14.0(44) #</td>
<td>12-16</td>
<td>0.0</td>
<td>48.7±11.8</td>
<td>51.0</td>
<td>65.7±18.3</td>
</tr>
<tr>
<td>16-1(8.5)*</td>
<td>12 : 12</td>
<td>80</td>
<td>70-90</td>
<td>21.7(73)</td>
<td>18-25</td>
<td>8.8</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Higher temperature coincides with the light period in each 24 h, and the figure in parentheses is the corresponding mean temperature.

# Sample size for determining developmental time to maturity.
pairs of constant and alternating temperatures with the same mean.

It is well-known that the relationship between temperature and speed of development in insects is not linear but curvilinear over the whole range (Andrewartha & Birch 1954; Bursell 1974; Stinner, Gutierrez & Butler 1974). However, the sigmoid curve relating rate of development to temperature is almost straight over a range of some 10–15°C just below the optimum temperature for most species. Thus, for practical purposes, it is useful to fit a straight line to the middle segment of the curve (Campbell et al. 1974). The linear regression line, when extrapolated downwards, crosses the temperature axis at a notional developmental threshold (t). The estimated developmental threshold (t) may then be used to estimate the thermal constant (K), i.e. the total number of day-degrees (D°C) above the threshold temperature required to complete any aspect of development in an insect's life history. The temperature coefficients thus estimated will give good predictions of an insect's development where the temperature does not remain long outside the limits set by the linear zone of the sigmoid curve.

For nymphal development of apterous *H. lactucae*, the relationship between temperature and percent development per day under constant temperatures was nearly linear within the range 17–24°C ($r^2 = 0.9996$, d.f. = 2). The data obtained at 26°C were excluded from the linear analysis as the reversal in trend of development at this temperature was obvious. Similarly, the data obtained at 12.5°C were not included in the analysis because of the occurrence of the morph switch at this temperature (see 7.2.6). The regression line was $Y = 0.6962X - 1.2892$, with an extrapolated threshold temperature of 1.9°C. The thermal constant for the whole nymphal development was then calculated as 143.7D°.9C.

Reciprocals of the mean time in days to reach maturity at each
alternating temperature regime were multiplied by 100 and plotted against the mean daily temperature (Fig. 7.1) so that the values on the ordinate represent percent development per day. The relationship between the two variables was also nearly linear \((r^2 = 0.9985, \text{d.f.} = 3)\), and the regression line \(Y = 0.6965X - 1.3775\) was very similar to the one derived from constant temperature data. Thus, the threshold temperature and thermal constant estimated \((t = 2.0, K = 143.4^\circ C)\) were also very close to those shown above.

Partitioning of the estimated thermal constant of the whole nymphal development into \(K_i\) for each instar has been shown to be very useful in aphid studies (e.g. Hughes 1963; Gilbert et al. 1976). At each of the two temperature levels tested for \(H. lactucae\), the first three nymphal instars were of approximately equal duration, and the fourth instar had 1.25 times the duration of earlier instars (Table 7.2). Thus, the relative thermal constants of the four instars under various conditions can be estimated according to the 1:1:1:1.25 ratio.

Table 7.2 Duration of the instars of apterous \(H. lactucae\) reared on young leaves at 22°C and 12.5°C with 12:12h photoperiod; 50 aphids used under each experimental condition

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>First instar</th>
<th>Second instar</th>
<th>Third instar</th>
<th>Fourth instar</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>12.5</td>
<td>3.7±0.8</td>
<td>2-5</td>
<td>3.5±0.9</td>
<td>2-5</td>
</tr>
<tr>
<td>22.0</td>
<td>1.7±0.2</td>
<td>1-2</td>
<td>1.6±0.2</td>
<td>1-2</td>
</tr>
</tbody>
</table>

7.2.3 Life Span and Age-Specific Survival

The number of aphids alive each day is plotted as the proportion of the original 28 individuals (Figs. 7.2, 7.3 and 7.4). Table 7.1 shows that mean life span and time to 50% mortality increased with a decrease in temperatures. No mortality during the immature stages was detected, except
at the extremes of the temperature range. At a constant temperature of 28°C, all nymphs died as first instar. In every case, the average life span, i.e. the time elapsing between birth and death, is almost the same as that to 50% mortality. Except in the case of 12.5°C mentioned above, no significant differences were found between the mean life spans of aphids at each of the other two pairs of constant and the corresponding alternating temperatures (confirmed by t-test, in each case, P>0.05). The profound effect of temperature on the duration of life span is further illustrated in Fig. 7.5.

Table 7.3 shows the durations of different phases in the adult life of the aphid under different experimental conditions. The pre-reproductive period is relatively short. In fact, many aphids started to reproduce within 24 h of adult moult. Thus, the mean values for this period calculated from the records of daily observations are rather inaccurate. Both reproductive and post-reproductive periods increased as temperature decreased. However, the post-reproductive period is relatively long at lower temperatures compared with the reproductive period.

Table 7.3 Durations of different phases in adult life of *H. lactucae* in days reared on flowering shoots of *S. oleraceus* under various experimental conditions

<table>
<thead>
<tr>
<th>Temperature* (°C)</th>
<th>Prereproductive period Mean</th>
<th>Reproductive period Mean ± S.D.</th>
<th>Postreproductive period Mean ± S.D.</th>
<th>Mean adult life span Mean ± S.D.</th>
</tr>
</thead>
<tbody>
<tr>
<td>24</td>
<td>0.3</td>
<td>9.6 ± 3.2</td>
<td>1.5 ± 0.7</td>
<td>11.4 ± 3.5</td>
</tr>
<tr>
<td>22</td>
<td>0.4</td>
<td>12.2 ± 3.8</td>
<td>2.2 ± 0.8</td>
<td>14.8 ± 4.1</td>
</tr>
<tr>
<td>28-13.5</td>
<td>0.4</td>
<td>11.9 ± 4.5</td>
<td>3.3 ± 0.9</td>
<td>14.6 ± 4.6</td>
</tr>
<tr>
<td>17</td>
<td>0.6</td>
<td>15.1 ± 5.6</td>
<td>7.5 ± 2.9</td>
<td>23.2 ± 6.9</td>
</tr>
<tr>
<td>23.5-9.5</td>
<td>0.7</td>
<td>14.2 ± 4.5</td>
<td>5.1 ± 2.1</td>
<td>19.9 ± 5.6</td>
</tr>
<tr>
<td>20-5</td>
<td>0.8</td>
<td>22.2 ± 6.5</td>
<td>11.7 ± 4.5</td>
<td>34.7 ± 9.5</td>
</tr>
</tbody>
</table>

* For photoperiods and R.H., see Table 7.1.
$Y = 0.6965x - 1.3775$

**Fig. 7.1** Speed of development of apterous *H. lactucae* at alternating temperatures. The points plotted are observed values.

**Fig. 7.2** Age-specific survival and fertility rates of *H. lactucae* at constant temperatures of 24°C and 26°C.
Fig. 7.3 Age-specific survival and fertility rates of *H. lactucae* at constant and alternating temperatures with means of 22°C and 17°C.
Fig. 7.4 Age-specific survival and fertility rates of *H. lactucae* at alternating and constant temperatures of 20–5°C and 12.5°C.
Fig. 7.5 The effect of temperature on the duration of life span and fecundity of *H. lactucae*. The points depicted in the diagram are observed values with alternating temperatures except at 24°C where the data were obtained at constant temperature. The lines are fitted by eye.
7.2.4 Fecundity and Age-Schedule of Births

Within the temperature range tested, the mean number of young per female increased with a decrease in temperatures (Table 7.1; Fig. 7.5). The deleterious effect of 26°C constant temperature on reproduction was very apparent (Fig. 7.2). In fact, about half of the adults at this temperature died without producing any young. With the mean temperatures of 22°C and 17°C, the mean numbers of young produced under constant temperatures were very similar to those at alternating temperature regimes (confirmed by t-test, in each case, P>0.05).

Age-schedules of births (m_x) are illustrated in Figures 7.2, 7.3 and 7.4 as the mean number of young born per day per female alive during that day. The m_x curve at all temperatures reaches a peak early in the adult life, then fluctuates around the same level for a period, followed by a decline. At the mean temperatures of 22°C and 17°C, aphids showed very similar patterns of reproduction under constant and alternating temperatures.

7.2.5 Intrinsic Rate of Increase

Values of net reproductive rate (R_o), mean generation time (T) and intrinsic rate of increase (r_m) listed in Table 7.4 were computed on a daily basis from the l_x and m_x data presented in Figures 7.2, 7.3 and 7.4. Within the temperature range tested, r_m values increased with an increase in temperatures up to 24°C. The deleterious effects on survival and reproduction of the aphids at 26°C caused the value of r_m to drop to a very low level. In fact, the calculated intrinsic rate of increase can be regarded meaningless, as at this temperature the population vanished at the third generation (see Table 7.6).
Table 7.4  Net reproductive rate (R₀), mean generation time (T) and intrinsic rate of increase (rₘ) of apterous H. laotucae at various experimental conditions

<table>
<thead>
<tr>
<th>Temperature* (°C)</th>
<th>R₀</th>
<th>T</th>
<th>rₘ</th>
</tr>
</thead>
<tbody>
<tr>
<td>26</td>
<td>1.3</td>
<td>15.9</td>
<td>0.0017</td>
</tr>
<tr>
<td>24</td>
<td>40.1</td>
<td>11.1</td>
<td>0.3320</td>
</tr>
<tr>
<td>22</td>
<td>44.8</td>
<td>12.6</td>
<td>0.3017</td>
</tr>
<tr>
<td>28-13.5</td>
<td>48.3</td>
<td>12.3</td>
<td>0.3150</td>
</tr>
<tr>
<td>17</td>
<td>57.2</td>
<td>15.4</td>
<td>0.2631</td>
</tr>
<tr>
<td>23.5-9.5</td>
<td>58.0</td>
<td>15.6</td>
<td>0.2600</td>
</tr>
<tr>
<td>20-5</td>
<td>65.7</td>
<td>22.3</td>
<td>0.1880</td>
</tr>
</tbody>
</table>

* For photoperiods and R.H., see Table 7.1.

7.2.6 Performance at 12.5°C Constant Temperatures

As mentioned above the aphids reared at a constant temperature of 12.5°C with 12L:12D photoperiod showed different physiological characteristics from those reared at the corresponding alternating temperature. They took longer to develop, lived longer, and produced fewer young (Table 7.1, Fig. 7.4). Furthermore, out of the 1223 nymphs produced by the 28 aphids at this experimental condition, 354 were reddish. These reddish nymphs were produced through most of the reproductive life of the mothers (Fig. 7.4). No particular observation was made on the birth sequence of these coloured forms, but daily observations showed that it was common for a female to produce both greenish and reddish nymphs on the same day.

Rearing 40 reddish nymphs and 40 greenish ones from birth to maturity demonstrated that all reddish nymphs became males and their greenish siblings became virgino-parae (Table 7.5). Thus, it was clear that at 12.5°C constant temperature, a partial morph switch to sex-uparae had
occurred in the second generation and the aphids were not comparable to usual virginoparae.

It is of interest to note the differences between the first and second generation aphids at 12.5° constant temperature. The "male-producers" described above were individuals from the second generation (see 7.2.1), that is, they spent their embryonic and nymphal development under the same conditions. Observations on the reproduction of the first generation adults showed that very few (less than 1%) F$_2$ progeny were reddish nymphs. It is thus obvious that the conditions experienced during embryonic development were important in producing the observed physiological changes. However, with the limited data obtained, it is possible only to speculate on the timing and mechanisms involved.

By contrast, in the progeny of the second generation reared at the alternating temperature regime of 20-5°C with 12L:12D photoperiod, only very few reddish nymphs (approximately 1%) were observed. Experiments under the two temperature-light regimes were carried out using similar aphids at the same time (from March to June, 1981), so that the observed differences can not be attributed to different generation sequences. It appears clear therefore that in *H. lactucae* low constant temperatures are more conducive to the production of males than the corresponding fluctuating temperatures. Such an inference is supported by the samples taken from an aphid population subject to natural fluctuating temperatures in a field cage (see Chapter 8) from April to June, 1981. During this period, mean weekly temperatures fell gradually from above 15°C in April to lower than 10°C in late May and June. Photoperiod was also shortening from about 13 hours in April to shorter than 11 hours in June*. In these circumstances the proportion of males (recognized by the reddish colour of both nymphs and adults) in the population never exceeded 2%.

* The hours of photoperiod represent the time between sunrise and sunset plus that of both morning and evening civil twilights (see Beck 1980).
Table 7.5 Development of reddish nymphs and their greenish siblings reared on flowering shoots of *S. oleraceus* under different temperature-light regimes

<table>
<thead>
<tr>
<th>Body colour at birth</th>
<th>N</th>
<th>Rearing temp. (°C)</th>
<th>Photoperiod</th>
<th>% mortality immature stages</th>
<th>Aphid form when adult</th>
<th>Develop. time in days mean</th>
<th>Develop. time in days range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reddish</td>
<td>23</td>
<td>24</td>
<td>constant light</td>
<td>35</td>
<td>male</td>
<td>10.5</td>
<td>7-17</td>
</tr>
<tr>
<td>Reddish</td>
<td>17</td>
<td>12.5</td>
<td>12L:12D</td>
<td>0</td>
<td>male</td>
<td>19.7</td>
<td>14-24</td>
</tr>
<tr>
<td>Greenish</td>
<td>40</td>
<td>12.5</td>
<td>12L:12D</td>
<td>0</td>
<td>Apterous and alate virginoparae</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 7.6 Population parameters of apterous *H. lactucae* as affected by high constant temperatures in different generations

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Generation</th>
<th>N</th>
<th>% mortality in immature stages</th>
<th>Develop. time in days Mean</th>
<th>Develop. time in days Range</th>
<th>Av. life span (birth-death) in days</th>
<th>Time to 50% mortality in days</th>
<th>Av. young produced per adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>26</td>
<td>1</td>
<td>40</td>
<td>4.2</td>
<td>6.6</td>
<td>5-7</td>
<td>17.1</td>
<td>17.0</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>40</td>
<td>12.5</td>
<td>12.0</td>
<td>7-13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>20</td>
<td>95.0</td>
<td>12.5</td>
<td>12-13</td>
<td>7.5</td>
<td>8.1</td>
<td></td>
</tr>
<tr>
<td>28</td>
<td>1</td>
<td>54</td>
<td>4.0</td>
<td>6.1</td>
<td>5-8</td>
<td>14.6</td>
<td>15.3</td>
<td>14.5</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>100</td>
<td>100.0*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* All nymphs died as first instar
Fig. 7.6 Age-specific survival and fertility rates of *H. lactucae* reared at 28°C constant temperature in the first generation.
7.2.7 Deleterious Effects of High Temperatures

With the temperature-light regimes used, deleterious effects of constant temperatures of 26°C and 28°C on the development, survival and reproduction of the aphid were apparent (Table 7.1).

It is interesting to note the differences in the aphid performance between successive generations reared at high temperatures (Table 7.6). In the first generation, the developmental rate of the aphids was not greatly affected at either temperature, as the mean developmental time was still decreasing as temperature increased. Survival and reproduction were not seriously affected either, the aphids at 28°C living on average more than eight days after reaching maturity and producing young through most of their adult life (Fig. 7.6). However, from the second generation onwards, the temperatures exerted lethal effects on the aphid. At 26°C the aphid population became extinct in the third generation, while at 28°C all nymphs produced by the first generation died on the day when they were born.

7.3 INFLUENCE OF PHOTOPERIOD

7.3.1 Larviposition Rate in Relation to Light and Darkness

One hundred and sixty-two apterous adults obtained from the stock culture were divided randomly into three groups each consisting of 54 individuals. All were placed singly on young leaves set in vials and kept with the stock culture until the normal end of the photophase. Then all young produced were removed and each of the three groups was transferred into a different light regime, all held at a constant temperature of 24°C. Thereafter, the young produced were recorded and cleared at the end of each 12 h interval for four days.

The mean numbers of young produced each 12 h were plotted against
Fig. 7.7 Larviposition rate of apterous *H. lactucae* per 12 h in relation to light and darkness. Bars represent artificial light:dark cycles, and the vertical dotted line indicates the beginning of the experiments.
Table 7.7  Comparison between population parameters of apterous *H. lactucae* reared on flowering shoots or young leaves of *S. oleraceus* at 22°C with different photoperiods

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Photoperiod (light:dark,h)</th>
<th>Develop. time in days mean (n)</th>
<th>Av. life span (birth-death) in days ± S.D.</th>
<th>Time to 50% mortality in days</th>
<th>Av. young produced per adult ± S.D.</th>
<th>Intrinsic rate of increase (rm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flower heads</td>
<td>(14:10)</td>
<td>7.1 (47) a</td>
<td>21.2 ± 6.5 a</td>
<td>21.0</td>
<td>43.8 ± 21.7 a</td>
<td>0.3015</td>
</tr>
<tr>
<td>(12:12)</td>
<td></td>
<td>6.9 (46) a</td>
<td>20.8 ± 5.2 a</td>
<td>21.8</td>
<td>44.5 ± 15.9 a</td>
<td>0.3150</td>
</tr>
<tr>
<td>Young leaves</td>
<td>(16:8)</td>
<td>6.6 (57) a</td>
<td>26.5 ± 9.5 b</td>
<td>22.7</td>
<td>55.2 ± 14.8 b</td>
<td>0.3470</td>
</tr>
<tr>
<td>(12:12)</td>
<td></td>
<td>6.6 (49) a</td>
<td>27.8 ± 7.0 b</td>
<td>27.5</td>
<td>61.9 ± 15.9 b</td>
<td>0.3695</td>
</tr>
</tbody>
</table>

Note: Under each column, means followed by the same lower case letter are not significantly different at the 5% level (by Duncan's multiple range test)
Fig. 7.8 Age-specific survival and fertility rates of apterous *H. lactucae*

reared on flowering shoots and young leaves under 22°C with different
photoperiods.
time for the three groups (Fig. 7.7). When a dark:light cycle was continued, adults produced most of their young under light and few young in darkness (Group A). In Group B, experimental reversal of the photoperiod caused the larviposition activity to undergo a corresponding shift, so that most of the young were again born during the photophase. When constant light was provided (Group C), the diurnal pattern was largely lost after the first 24 hours. The results showed that larviposition rate in *H. lactucae* is strongly associated with the rhythm of illumination, and re-entrainment to different light:dark regimes can be completed in 1-2 days.

7.3.2 Effects of Photoperiod on Other Population Parameters

To examine the effects of photoperiod on the development, survival and reproduction of the aphid, four experimental populations were reared simultaneously under different photoperiods at 22°C constant temperature on either flower heads or young leaves (Table 7.7). The experimental procedures were identical with those described in 7.2.1. When young leaves were used, aphids were reared individually in the vials.

No significant difference was detected in developmental time, life span and fecundity between different photoperiods on either flower heads or young leaves (Table 7.7). However, comparison of life and fertility table data (Fig. 7.8) revealed consistent differences in survival and fertility rates between long and short photoperiods on both substrates. In particular, aphids in shorter photoperiods produced more young per day during early adult life, consequently they had much higher intrinsic rates of increase (*r*<sub>m</sub>) than the aphids reared on the same substrate in longer photoperiods (Table 7.7).
7.4 PRODUCTION AND PERFORMANCE OF ALATAE

7.4.1 Stages Sensitive to Crowding

Crowding has been established as a prime factor influencing the production of alatae in anholocyclic populations of *H. lactucae* (see 2.3.5). The limited data obtained in this study (Appendix 1) show that prenatal crowding of mothers and postnatal crowding of nymphs may both play important roles in the determination of wing development in this aphid.

7.4.2 Population Parameters of Alatae

To obtain data on the rates of development of alatae, nymphs produced by crowded apterous adults were reared at four different temperature-light regimes (Table 7.8) at a density of 20 nymphs per flowering shoot. The apterous mothers used were themselves born and reared under the respective experimental conditions. Daily observations were started when the nymphs reached the 4th instar and any alatae found were recorded and removed.

Table 7.8 shows that the mean developmental time of alatae increased with a decrease in temperature. In every case, alatae took longer to reach the adult stage than apterae (cf. Table 7.1). A linear regression of developmental rate (y) of alatae on mean daily temperature gave the equation

\[ y = 0.6495x - 1.0526 \quad (r^2 = 0.9989). \]

The notional development threshold (t) was estimated to be 1.62°C, which is almost identical to that estimated for

<table>
<thead>
<tr>
<th>Temperature* °C</th>
<th>Photoperiod (light:dark,h)</th>
<th>N</th>
<th>Mean develop. time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>28-13.5(22)</td>
<td>14:10 h</td>
<td>30</td>
<td>7.5</td>
</tr>
<tr>
<td>23.5-9.5(17)</td>
<td>13:11 h</td>
<td>44</td>
<td>10.1</td>
</tr>
<tr>
<td>20-5 (12.5)</td>
<td>12:12 h</td>
<td>20</td>
<td>14.4</td>
</tr>
<tr>
<td>16-1 (8.5)</td>
<td>12:12 h</td>
<td>13</td>
<td>21.8</td>
</tr>
</tbody>
</table>

* Figures in parentheses are corresponding mean daily temperatures.
Table 7.9  Comparison of population parameters of apterous and alate *H. Laeticae* reared on flowering shoots
at 17°C constant temperature, 13L:11D photoperiod

<table>
<thead>
<tr>
<th>Aphid form</th>
<th>Develop. time in days</th>
<th>Average pre-reproductive period (days)</th>
<th>Time to 50% mortality (days)</th>
<th>Av. life-span (from birth to death in days) ± S.D.</th>
<th>Mean generation time in days (T)</th>
<th>Net reproductive rate (<em>R₀</em>)</th>
<th>Intrinsic rate of increase (<em>rₘ</em>)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apteræ</td>
<td>9.5(80)</td>
<td>0.43</td>
<td>35.0</td>
<td>32.5 ± 9.6</td>
<td>15.4</td>
<td>57.2</td>
<td>0.2631</td>
</tr>
<tr>
<td>Alatae</td>
<td>10.1(44)</td>
<td>1.04</td>
<td>32.2</td>
<td>31.5 ± 7.4</td>
<td>16.8</td>
<td>45.8</td>
<td>0.2278</td>
</tr>
</tbody>
</table>

*Because no mortality was found during nymphal development, *R₀* is the average number of progeny per adult*. 


Fig. 7.9 Age-specific survival and fertility rates of both apterous and alate *H. lactucae* at 17°C, 13L:11D.
apterae (7.2.2). The thermal constant for the nymphal development of alatae was then calculated as $154.00^\circ\text{F}$.6 C.

Detailed data on the development, survival and reproduction of alatae obtained at 17°C constant temperature with 13L:11D photoperiod were compared with those of apterae reared at the same temperature-light regime (Table 7.9; Fig. 7.9). Life and fertility table data for alatae were based on 28 individuals which were reared at a density of 30 nymphs per flowering shoot until the 4th instar and thereafter individually until death. In comparison with apterae, alatae had a longer developmental time, experienced a longer pre-reproductive life, and produced fewer young per day through most of their reproductive life. Consequently, alatae had a longer generation time and lower intrinsic rate of increase.

7.5 ADDITIONAL OBSERVATIONS ON RATE OF NYMPHAL DEVELOPMENT

Purely for comparison, a separate experiment was carried out on the developmental rate of first-generation offspring of aphids collected from the field.

Fourth instar apteriform nymphs were collected from a large flowering plant of *S. oleraceus* near the Division of Entomology, CSIRO, Canberra on 15 October 1982. The mean daily temperatures in the period (1-15 October) during which these nymphs were developing were mostly around 10-15°C. These nymphs were then reared to adults on flowering shoots in the laboratory at 20°C, 14L:10D photoperiod. Cohorts of nymphs of uniform age were obtained by placing the reproducing apterae on young leaves set in plastic jars and collecting the newly born young every 2 h. The nymphs were transferred immediately into a caged pot, 10 nymphs per flowering shoot. Four groups of 60-80 nymphs each were reared throughout their development at four different alternating temperature regimes with a photoperiod of
12L:12D (Table 7.9). Daily observations were started when the nymphs reached the 4th instar, any adults found were recorded and cleared. From these data, the mean durations for nymphal development under the four temperature levels were calculated.

The mean developmental times of both apterae and alatae (Table 7.10) were very similar to those obtained in the previous year (see Tables 7.1 and 7.8). This is also shown by the similarity of the temperature coeffi-

Table 7.10 Developmental time of apterous and alate *H. lactucae* reared on flowering shoots of *S. oleraceus* under different temperature levels with 12h photoperiod

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Days from birth to adult</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Apterae Mean</td>
<td>N</td>
<td>Alatae Mean</td>
</tr>
<tr>
<td>28-16(22.0)*</td>
<td>6.9</td>
<td>38</td>
<td>7.5</td>
</tr>
<tr>
<td>25-10(17.5)</td>
<td>9.0</td>
<td>32</td>
<td>9.5</td>
</tr>
<tr>
<td>20-5(12.5)</td>
<td>13.6</td>
<td>34</td>
<td>14.1</td>
</tr>
<tr>
<td>16-1(8.5)</td>
<td>19.7</td>
<td>27</td>
<td>21.3</td>
</tr>
</tbody>
</table>

* higher temperatures during the photophase, figures in parentheses are corresponding mean daily temperatures

Table 7.11 Temperature coefficients of *H. lactucae* derived from laboratory experiments which were carried out under alternating temperature regimes with diurnal ranges of 14-15°C

<table>
<thead>
<tr>
<th>Aphid form</th>
<th>Aphid source of experiment</th>
<th>Linear regression equation*</th>
<th>Development threshold (°C)</th>
<th>Thermal constant of nymphal development D°</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apteræ</td>
<td>Stock culture</td>
<td>y = 0.6965x - 1.3775</td>
<td>2.0</td>
<td>143.4</td>
</tr>
<tr>
<td></td>
<td>Field</td>
<td>y = 0.7046x - 1.1493</td>
<td>1.6</td>
<td>141.9</td>
</tr>
<tr>
<td>Alataæ</td>
<td>Stock culture</td>
<td>y = 0.6495x - 1.0526</td>
<td>1.6</td>
<td>154.0</td>
</tr>
<tr>
<td></td>
<td>Field</td>
<td>y = 0.6459x - 0.8590</td>
<td>1.3</td>
<td>154.8</td>
</tr>
</tbody>
</table>

* Where y = percent development per day, x = mean daily temperature; in every case the coefficient of determination (r²) of the regression exceeds 0.99.
cients estimated from the two sets of data (Table 7.11). For subsequent calculations in the analyses of the results of field cage experiments (Chapters 8 and 9), the threshold temperature of development was rounded off to 2°C.

7.6 DISCUSSION

Within the favourable range, speed of development and reproductive rate increase as temperature rises, while both life span and total fecundity decline gradually at higher temperatures. Temperature, thus, affects virtually every aspect of the life history of the aphid. In terms of its influence on the potential for population increase, the effects of temperature are most appropriately summarized by the statistic $r_m$, the intrinsic rate of increase. Under the temperature-light regimes tested, the value of $r_m$ increases with an increase in temperatures until 24°C. The comparison between apterae and alatae shows that the latter has a lower reproductive potential.

The performance of the aphid at lower alternating temperatures demonstrates the innate ability of the original population of the stock culture to survive through relatively low temperatures without recourse to sexual reproduction. Indeed, at the lowest temperature regime tested, a daily 12 h exposure to a temperature as low as 1°C did not seem to have any obvious harmful effects on the development and reproduction of the aphid over two successive generations.

The estimated threshold temperatures were consistently lower than those estimated from the data reported previously (1.3.3). However, since the experimental methods in this study were different from those used by the other two authors and the threshold found by extrapolation of the linear regression line is often inaccurate (Campbell et al. 1974), meaningful
comparison between the estimates can not be made.

It is of interest to note the differences in aphid performance between the first and subsequent generations. The data show that expressions of final performance of an aphid are strongly influenced by the environment experienced during its embryonic development. As a result, the upper and lower limits of the tolerable temperature range may vary widely according to the thermal history of the test animals. Except under constant regimes, the range will vary further with the pattern and magnitude of temperature fluctuations (e.g. Messenger & Flitters 1959). It follows that the validity of temperature limits (e.g. favourable range, lethal high and low limits) estimated in laboratory studies may need careful qualification before they are extended to interpret field data.

The temperature coefficients derived from constant and alternating temperature data were very similar. In theory, if there is no developmental acceleration or deceleration resulting from temperature alternation, the two sets of temperature coefficients are unlikely to be similar unless the relationship between temperature and developmental rate over the whole temperature range under consideration is nearly linear. However, the data obtained under constant temperature in this study are insufficient for such a comparison to be made of the effects of constant and alternating temperatures (see Howe 1967 and also Chapter 13 of this thesis).

The patterns of the effects of temperatures in constant or alternating regimes appear rather complicated in *H. lactucae*. Within the middle temperature range, no measurable differences were detected in the population parameters investigated between constant and alternating temperatures with the same mean. The aphid developed differently, however, at lower constant temperatures so that direct comparison of the developmental rates of the aphid under lower constant and alternating temperatures was not possible. At
the higher temperature levels healthy development could proceed when the aphids were exposed regularly to extreme temperatures which would be harmful or even lethal if experienced continuously. It appears clear, therefore, that the thermal limits to normal development and reproduction of anholocyclic populations of H. lactucae are much wider under alternating than under constant temperatures and this widening of temperature-tolerance range is more noticeable at the lower thermal levels.

Although broad generalizations such as these are possible, it is important to remember the difference between the effects on successive generations. For example, general observations in the experiments and the results on the first generation at high temperatures show that normal development of the aphid under constant temperature can proceed over a much wider temperature range in the first generation than in the second generation. Detailed data covering the whole temperature range over two successive generations would therefore be necessary to analyze fully the effects of constant and alternating temperatures on the development and reproduction of this and possibly other aphids.

Data obtained on the influence of photoperiod are not extensive enough to reach any meaningful conclusion. The phenomenon was complicated by the fact that while aphids produced most of their young under light, they in fact gained greater population growth potential with shorter photoperiods mainly through their higher reproductive rates during early adult life. Although the effects of photoperiod on the developmental rate, survival and reproduction of aphids have not received extensive study, the available literature shows that increase in photoperiod up to 16L:8D usually results in an acceleration of nymphal development e.g. in Aphis craccivora Koch (Abdel-Malek et al. 1982; Radke, Benton & Yendol 1973), and an increase in total fecundity, e.g. in Acrthosiphon pisum (Kenten 1955; Sharma, Larrivée...
and Theriault 1973; Karlovic 1968) and *A. craccivora* (Radke, Benton & Yendol 1973). However, it has also been shown that light may affect aphids through its effects on the host plants (Banks & Macauley 1970).
8.1 INTRODUCTION

Large field cages have been used extensively in insect studies, especially in the evaluation of natural enemies (e.g. Hodek, Hagan and van Emden 1972) and more recently in the investigation of the dynamics of predator-prey systems (Frazer et al. 1981). With this technique, it becomes possible to manipulate the complexity of "a life system" (Clark et al. 1967) in the field to ascertain the main factors responsible for numerical changes and their relative importance. Provided that modifications to the environment caused by the cages are recognized, analyses of the results obtained can contribute considerably to the understanding of the factors under study (e.g. Frazer et al. 1981).

Four field cage experiments were carried out in this study, two with the aphid alone and the other two with both the aphid and the parasite. Their purpose was to examine the population dynamics of the aphid in the absence and presence of known numbers of its parasite. By applying laboratory data to the quantitative analyses of the field cage results, the validity of the studies carried out under closely controlled conditions can be further discussed. In this chapter, the two field cage experiments with the aphid alone are reported, together with the preliminary analysis of the results. Detailed analysis of the data was carried out by means of computer simulation modelling, which will be described in the next chapter.

8.2 THE FIELD CAGE

The cage consisted of a 4 m x 3 m x 1.5 m high wooden frame covered
with white terylene mesh (Fig. 8.1). The mesh was proved to be aphid- and parasite-proof in the insectary work, yet it provides about 75% open space mainly due to its small fibre size (0.05 mm). To prevent possible damage from strong wind, the net canopy was reinforced both inside and outside with plastic bird netting and battened along all the beams. The whole cage was held in position by four stakes driven into the ground inside the cage at each corner. The bottom of the cage was sealed with sand. Access to the cage was gained through a door on one side.

Despite the porosity and transparency of the mesh used, the cage inevitably changed the microclimate in various ways, such as a considerable reduction in light intensity and wind speed (see Woodford 1973). During the course of the four experiments, both temperature and humidity 1 m above the ground inside the cage were recorded continuously with a hygrothermograph (see Fig. 8.1). Comparison of the records with those outside the cage (from a weather station approximately 100 m away run by the CSIRO Division of Water and Land Resources) showed that temperatures inside the cage were very similar to outside temperatures except that in warm conditions cage maximum temperatures tended to be a few degrees higher, for example:

<table>
<thead>
<tr>
<th>Date (1981)</th>
<th>Maximum temperatures (°C)</th>
<th>Minimum temperatures (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Inside cage</td>
<td>Outside cage</td>
</tr>
<tr>
<td>April 6</td>
<td>25.2</td>
<td>22.9</td>
</tr>
<tr>
<td>7</td>
<td>25.2</td>
<td>23.0</td>
</tr>
<tr>
<td>8</td>
<td>27.2</td>
<td>25.2</td>
</tr>
<tr>
<td>9</td>
<td>28.2</td>
<td>25.0</td>
</tr>
<tr>
<td>May 18</td>
<td>9.0</td>
<td>9.6</td>
</tr>
<tr>
<td>19</td>
<td>11.2</td>
<td>11.0</td>
</tr>
<tr>
<td>20</td>
<td>11.2</td>
<td>11.3</td>
</tr>
<tr>
<td>21</td>
<td>10.5</td>
<td>11.2</td>
</tr>
</tbody>
</table>
Fig. 8.1 Field cage used in the experiments. Upper: outside, the Stevenson screen hung from the roof of the cage can be seen through the mesh. Lower: inside, the hoses are part of the drip irrigation system.
A generally higher level of humidity inside the cage was caused by the artificial watering for the plants and thus is not comparable with outside condition.

8.3 THE EXPERIMENTS

In each experiment the population was initiated with a given number of aphids of known ages. The population density was then estimated at regular intervals until the host plants collapsed.

The cage was placed in a paddock at the back of the Division of Entomology, CSIRO, Canberra. The two experiments were carried out during the seasons when the weather was favourable to the aphid, i.e. one from April to June (hereafter First cage experiment) and the other one from September to November (hereafter Second cage experiment). Fig. 8.2 shows the changing temperatures during the periods when the experiments were in progress.

To eliminate unwanted insects, one week before the host plants were transplanted the cage was sprayed thoroughly with 1% dieldrin and the soil inside was also treated with the same insecticide.

The host plants were first grown in 10 cm plastic pots containing compost soil in the glasshouse until each plant had about ten leaves and then transplanted into the cage. Twenty grams of osmocote (a slow-release fertilizer) was applied to the location of each plant. The initial numbers of plants were: 100 in the First cage experiment and 80 in the Second cage experiment. Although the cage admitted natural rain, the plants were watered with a drip irrigation system from time to time because of the dry weather.

The aphids used for the initial infestations were progeny produced by apterous adults taken from the aphid stock culture. The nymphs, collected
Fig. 8.2 Average weekly maximum, mean and minimum temperatures during the periods of the two field cage experiments in 1981.
within 24 h of birth, were reared on young seedlings in the insectary up to the desired ages. Infestation of the plants was started a few days after transplanting by transferring the specified number and types of aphids for each plant onto a young leaf in the laboratory and then placing one such leaf onto each plant.

The number and types of aphids used for the initial infestations in the two experiments were chosen rather arbitrarily, depending partially on technical convenience. In the First cage experiment, each plant was infested with two newly emerged apterous adults; while in the Second cage experiment each plant was infested with one 4th instar apteriform nymph and three newly emerged apterous adults.

After the introduced aphids had become established, samples of four to five plants (cut just above the soil) were taken weekly. The plants of each sample were brought back to the laboratory and the aphids were washed off with water at 70°C. Aphids from each plant were subsampled with sampling grids of different sizes until the number of aphids reduced to about 400 (see below). These remaining aphids (i.e. a known proportion of the total) were sorted into different instars and morphs and their numbers counted. The dry weight of each plant in the sample was also obtained and recorded.

**Subsampling with grids and its accuracy.** Sampling grids were marked on clear plastic petri dishes, each consisting of twelve equal-sized sectors (Fig. 8.3). Subsampling was carried out as follows. An aphid sample, in a small amount of alcohol, was spread out in the dish and thoroughly stirred. The excess alcohol was then sucked out with a small pipette. All aphids in at least three of the sectors were removed as a subsample, the remainder were discarded. This procedure was then repeated with the subsample until it contained about 400 aphids.
No experiments were performed to estimate the error of the subsampling procedure. Theoretically, the variance of a sample mean is negatively correlated with the ratio of sample size to population size (Gilbert 1973). Thus, the larger the sampling fraction, the more representative the sample will be. Since each time at least one quarter of all the aphids in a dish were taken as the "sample", the sampling error should be very small.

8.4 RESULTS AND PRELIMINARY ANALYSIS

The mean plant dry weight and the mean numbers of aphids in different instars and morphs per plant on each sampling occasion in the two experiments are presented in Table 8.1 and Table 8.2, respectively.

8.4.1 Growth of S. oleraceus

The plants in the cage grew quickly and appeared generally more succulent than plants observed in their natural environment, apparently due to the application of fertilizer and irrigation. As a result, aphids were found feeding all over the plants, except on a few old leaves and old stems. Despite the heavy load of aphids, most plants reached more than 1 m high at their peak growth and each produced about 30 flowering shoots. Since virtually all parts of these plants were utilized by the aphids, their capacity to support aphids throughout their growth seemed to be best described by their dry weight rather than numbers of suitable flower heads (see Martin 1979).

The values of plant dry weight were plotted against the accumulated day-degrees above 2°C - the threshold temperature of development for the aphid (Fig. 8.4). In both experiments, the plants grew exponentially until they had experienced about 500 D^°C. Thereafter they stopped growing, presumably due to both the natural maturing of the plants and the effect of heavy feeding by the aphids. Plants in both experiments died
Fig. 8.3  An aphid sampling grid

Fig. 8.4 Increases of plant dry weight of *S. oleraceus* in the field cage, arrows indicate the times when most plants collapsed.
Table 8.1 Growth of *S. oleracea*, population of *H. lactucae* in First cage experiment (April–June, 1981)

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Date</th>
<th>Accumulated D8C</th>
<th>Mean plant dry weight (g)</th>
<th>Number of aphids per plant</th>
<th>Proportion (%) of alatiform nymphs in $N_4$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>$N_1$</td>
<td>$N_2$</td>
<td>$N_3$</td>
</tr>
<tr>
<td>1</td>
<td>3 April</td>
<td>0.0</td>
<td>1.0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>17 April</td>
<td>214.5</td>
<td>4.0</td>
<td>157</td>
<td>56</td>
</tr>
<tr>
<td>3</td>
<td>24 April</td>
<td>309.3</td>
<td>10.5</td>
<td>596</td>
<td>309</td>
</tr>
<tr>
<td>4</td>
<td>1 May</td>
<td>378.5</td>
<td>15.1</td>
<td>1844</td>
<td>950</td>
</tr>
<tr>
<td>5</td>
<td>8 May</td>
<td>456.5</td>
<td>17.6</td>
<td>6949</td>
<td>4729</td>
</tr>
<tr>
<td>6</td>
<td>15 May</td>
<td>506.8</td>
<td>27.9</td>
<td>14996</td>
<td>8145</td>
</tr>
<tr>
<td>7</td>
<td>28 May</td>
<td>602.1</td>
<td>24.6</td>
<td>7639</td>
<td>11016</td>
</tr>
<tr>
<td>8</td>
<td>5 June</td>
<td>657.6</td>
<td>24.9</td>
<td>5378</td>
<td>9814</td>
</tr>
<tr>
<td>9</td>
<td>15 June</td>
<td>703.9</td>
<td>23.6</td>
<td>1258</td>
<td>2469</td>
</tr>
</tbody>
</table>
Table 8.2  Growth of *S. oleraceus*, population of *H. lactucae* in Second cage experiment

(September-November, 1981)

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Date</th>
<th>Accumulated D(^2)C</th>
<th>Mean plant dry weight (g)</th>
<th>Number of aphids per plant</th>
<th>Proportion (%) of alatiform nymphs in N(_4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>22 Sept</td>
<td>0.0</td>
<td>1.5</td>
<td>N(_1) 0 0 0 1 0 3 0 4</td>
<td>0.0</td>
</tr>
<tr>
<td>2</td>
<td>9 Oct</td>
<td>154.8</td>
<td>4.2</td>
<td>N(_2) 46 28 33 32 2 14 0 155</td>
<td>5.9</td>
</tr>
<tr>
<td>3</td>
<td>17 Oct</td>
<td>256.2</td>
<td>11.0</td>
<td>N(_3) 612 385 180 42 8 69 6 1302</td>
<td>16.0</td>
</tr>
<tr>
<td>4</td>
<td>24 Oct</td>
<td>327.2</td>
<td>13.3</td>
<td>N(_4)apt 1430 824 684 313 243 173 28 3695</td>
<td>43.7</td>
</tr>
<tr>
<td>5</td>
<td>31 Oct</td>
<td>438.6</td>
<td>23.9</td>
<td>N(_4)al 15502 8991 5609 820 2380 1245 596 35143</td>
<td>74.4</td>
</tr>
<tr>
<td>6</td>
<td>7 Nov</td>
<td>526.7</td>
<td>32.3</td>
<td>Aapt 36329 16227 14585 1162 13612 1944 5126 89035</td>
<td>92.1</td>
</tr>
<tr>
<td>7</td>
<td>13 Nov</td>
<td>605.1</td>
<td>34.4</td>
<td>Aal 24537 11115 8748 585 8908 495 6951 61370</td>
<td>93.8</td>
</tr>
<tr>
<td>8</td>
<td>22 Nov</td>
<td>712.3</td>
<td>31.5</td>
<td>Total 11364 12204 10237 1059 4825 706 422 40817</td>
<td>82.0</td>
</tr>
</tbody>
</table>
at about 800 $D^\circ C$.

The relation between the increase of plant dry weight and effective temperatures during the first 500 $D^\circ C$ in the two experiments can be described satisfactorily by exponential curves:

$y = 1.071342e^{0.006558x} (r^2 = 0.98, \text{d.f.} = 5, P < 0.001)$

for First cage experiment, and

$y = 1.617651e^{0.006445x} (r^2 = 0.98, \text{d.f.} = 4, P < 0.001)$

for Second cage experiment, where $y$ is the dry weight of a plant in grams and $x$ the accumulated $D^\circ C$. The curves could be transformed to straight lines by plotting $\log_{10}y$ against $x$ (Fig. 8.4). The slopes of the two lines were almost identical.

The above analysis showed that the plants in the two experiments increased their dry weight at a similar rate on a physiological time scale. This is understandable, since the basic methods of culturing the plants were standardized. The higher initial dry weight in the Second cage experiment was due to bigger size of the plants at the time of transplanting because they were kept longer in the glasshouse. The higher peak weight in the same experiment was the result of a reduced plant density (80 rather than 100).

8.4.2 Changes in Aphid Numbers

The introduced aphids established themselves successfully in both experiments. Luckily, no unwanted insects occurred in the cage. The established populations increased their numbers more or less exponentially until 500 $D^\circ C$ then levelled off, and then declined rapidly as the host plants died (Fig. 8.5).

In both experiments, some adults (mostly alatae) appeared on the mesh inside the cage when the number of aphids on each plant exceeded 4000. The number of adults on the mesh increased rapidly as the total
Fig. 8.5 Changes of aphid numbers in two field cage experiments; arrows indicate the times when the populations crashed as the host plants died.

Fig. 8.6 Relationship between aphid density and proportion of 4th instar alatiform nymphs.
numbers of aphids on each plant continued to increase. After the host plants stopped growing, the adults found on the mesh were so numerous that a few panels of the cage were virtually covered with aphids and appeared black.

During the course of the two experiments, the open space inside the cage was gradually reduced as the plants were growing. In both cases, the plants began to touch one another only 350 $D^2C$ after the experiments were started. The dense plant populations created high humidity inside the cage. As a result, aphids infested with fungus disease were observed at the time of the 6th sample (500 $D^2C$) in each experiment. In subsequent samples the aphids were heavily infected. However, the plants continued to deteriorate and then collapsed despite the great mortality of the aphids caused by the fungus disease. The aphid populations eventually crashed as the host plants died out.

Thus, the reduction of the exponential increase of the aphid populations and their eventual decline were caused mainly by three factors: (1) deterioration of the quality of food available, (2) overcrowding, and (3) infection by fungus disease, each of which was exacerbated by the cage conditions.

8.4.3 Occurrence of Apterous and Alate Forms

Tables 8.1 and 8.2 show for successive samples the proportions of alatiform nymphs in the fourth instar. In *H. lactucae*, the proportion of alatae increases with increase of population density (Martin 1979) and the effects of crowding operate prenatally and postnatally (7.4.1). In the two experiments, the proportion of alatiform nymphs in the fourth instar ($y$) in each sample was found to be closely correlated in a non-linear way with the aphid density in the previous sample ($x$):

$$y = \exp (-29.9847/x^{0.7456})$$
$r^2 = 0.90$, d.f. $=12$, $P < 0.001$, aphid density being measured as the number of aphids per gram dry weight of plant material. It can be seen from Fig. 8.6 that the relationship between the two variables was rather similar in the two experiments, though the two populations were developing in two different seasons (see Fig. 8.2). Thus, promotion of the effects of crowding by low temperatures, as reported by Martín (1979), was not apparent in the results obtained.
9.1 INTRODUCTION

This chapter describes the development of a deterministic simulation model and analysis of data obtained in the field cage experiments (Chapter 8) with the model. The model integrates available knowledge on various components of the biology of the aphid, and then uses them to reproduce the observed population changes in the field cage. The main objective is to obtain a qualitatively correct and quantitatively reasonable picture of the interactions of the biological processes which determine the aphid population changes in the absence of its parasite.

In both field cage experiments, fungal infections killed substantial proportions of the aphid populations after 600 D\textdegree C (8.4.2). Since little is known about the relations between the aphid and the fungus diseases, detailed analyses of the two sets of data were restricted to the periods when no fungus was present, i.e. from the start to 600 D\textdegree C.

9.2 FORMULATION OF THE BASIC MODEL

This section shows how pieces of data on the aphid were transformed into various numerical or algebraic components of the model and then assembled together to make a "variable life-table" for the aphid.

9.2.1 Physiological Time Scale

The rates of various physiological processes in an aphid and its associated organisms vary directly with temperature. Consequently, it is possible to describe, synthesize and then analyze those processes on physiological time-scales, thereby eliminating much of the variation caused directly by changes in temperatures (Hughes & Gilbert 1968;
Gilbert et al. (1976). In this model, a physiological time-unit was used as the basic scale of time, which was 8.5 D^2C, equivalent to one quarter of the time required to complete the development of each of the first three instars of the aphid (a quip, i.e. a quarter of an instar period). New population values were then calculated to every 8.5 D^2C. Time in the model is thus expressed in quips, T = 1, 2, 3...70.

The choice of this time unit as the step length in the model was based on the experience of other aphid modellers. Since the model approximates continuous biological processes by a step-by-step computation, the necessary length of step depends on the rates at which variables change in value. Thus the faster the population changes in size, the shorter the required step length. Compared with the aphids whose populations have been modelled so far, e.g. Brevicoryne brassicae (Hughes & Gilbert 1968), Aphis craccivora (Gutierrez et al. 1974) and Acrhythosiphon pisum (Frazer & Gilbert 1976), H. lactucae shows no greater innate competence for population increase (Chapter 7). The time unit, one quip, which has been shown to be appropriate in the modelling of the above aphid systems, was therefore adopted in this model.

Day-degrees for field cage temperatures were calculated using a computer program which integrates the area under sine curves through daily maximum and minimum temperatures and above the developmental threshold (2°C) for the aphid (Allen 1976). The accumulated day-degrees were then divided by 8.5 to convert to quips.

9.2.2 Rate of Nymphal Development

The temperature coefficients for nymphal development of the aphid are presented in Table 7.11. For the analysis of the field cage data, the threshold temperature was rounded off to 2°C, which could be done without
affecting the accuracy of the physiological time scale (see Campbell et al. 1974). Thus, the numbers of day-degrees for complete development of apterae and alatae were taken as 144.5 D°C (17 quips) and 153.0 D°C (18 quips), respectively.

Table 7.2 shows that in apterous *H. lactucae* the first three nymphal instars are of approximately equal duration, while the fourth instar has 1.25 times the duration of the earlier instars. In the model, it is assumed that the first three nymphal instars of both apterae and alatae each require an average of 34 D°C (4 quips) to complete development, and apteriform and alatiform fourth instar nymphs require 42.5 D°C (5 quips) and 51 D°C (6 quips) respectively.

### 9.2.3 Survival and Fecundity Rates

The survival and fecundity rates of the aphid were studied in the laboratory under a range of temperature-light regimes (Chapter 7). For the modelling of survival and fecundity rates of apterae, data obtained from the three alternating temperature regimes were used.

If development of adults and reproduction were solely a function of effective temperature, the durations of different phases in adult life should be very similar on a physiological time scale and the total fecundity should be independent of temperature (cf. Frazer & Gilbert 1976; Gutierrez *et al.* 1974). Such is not the case in *H. lactucae*. Most obviously, the mean number of young produced per female increased at lower temperatures (see Fig. 7.5). Although the durations of reproductive periods were rather similar when expressed in D°C, the adult life span also increased at lower temperatures:

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>Reproductive period days</th>
<th>Adult life span D°C</th>
<th>D°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>28 - 13.5</td>
<td>11.9</td>
<td>14.6</td>
<td>292</td>
</tr>
<tr>
<td>23.5 - 9.5</td>
<td>14.2</td>
<td>19.9</td>
<td>299</td>
</tr>
<tr>
<td>20 - 5</td>
<td>22.2</td>
<td>34.7</td>
<td>364</td>
</tr>
</tbody>
</table>
Since the durations of reproductive periods remained the same on a physiological time scale and the general time patterns of reproduction (i.e. $m_x$ curves in Figs. 7.2, 7.3 & 7.4) were also similar, the higher total fecundity of the aphid at lower temperatures must result in corresponding higher fecundity rates, thereby showing a higher potential for population increase on this time scale. This is shown clearly by the following examples:

<table>
<thead>
<tr>
<th>Temperature ($^\circ$C)</th>
<th>Intrinsic rate of increase, $r_m$</th>
<th>Number of aphids after 420 D$^\circ$C$^\dagger$</th>
</tr>
</thead>
<tbody>
<tr>
<td>28 - 13.5 (22)*</td>
<td>0.3150</td>
<td>746</td>
</tr>
<tr>
<td>20 - 5 (12.5)</td>
<td>0.1880</td>
<td>1845</td>
</tr>
</tbody>
</table>

* Figures in parentheses are corresponding daily mean temperatures.  
† Calculation started with one female at time zero.

From these considerations, it is obvious that the modelling of survival and especially fecundity rates must take into account the effects of different daily mean temperatures.

(i) Survival rates

Figure 9.1 shows the relationship between daily mean temperature and the reciprocals of both adult life span and reproductive period of the aphid under the three alternating temperature regimes. The temperature coefficients estimated from the relationships were:

<table>
<thead>
<tr>
<th>Phases of aphid life</th>
<th>Linear regression</th>
<th>r$^2$</th>
<th>t($^\circ$C)</th>
<th>K(D$^\circ$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult life span $Y_1$</td>
<td>100/$Y_1$= 0.4169X-2.2368</td>
<td>0.99</td>
<td>5.4</td>
<td>240.5</td>
</tr>
<tr>
<td>Reproductive period $Y_2$</td>
<td>100/$Y_2$= 0.4080X-0.3568</td>
<td>0.96</td>
<td>0.9</td>
<td>243.2</td>
</tr>
</tbody>
</table>

The threshold temperature for reproductive period is similar to that for nymphal development, while that for adult life span is somewhat higher. If the survival rates of the aphid at the higher temperature
Fig. 9.1. Relationship between daily mean temperature and percent adult life span and reproductive period in apterous *H. lactucae*.

Fig. 9.2. Survival and fecundity rates of *H. lactucae* in laboratory studies. Each unit of time on the abscissa equals 8.5 D°C.
(28-13.5°C) are converted to D° equivalent and used in the model, the length of reproductive period is effectively independent of daily mean temperature, but the total adult life span will be underestimated when the daily mean temperatures are relatively low. Since the prereproductive period is very short at all temperature levels (Table 7.3), the underestimation at lower temperatures is mainly a reduction of post-reproductive life and thus will have little impact on the overall picture of the population except causing a slight reduction of total number of adults. So, for simplicity, the complexity of the effect of temperature on postreproductive period was ignored in the model. The survival rates of the aphids reared at 28-13.5°C were then converted to rates per 8.5 D°C (i.e. per quip) and given in the model (Fig. 9.2). Since apterae and alatae reared at the same temperature (17°C) showed similar time patterns of survival (see Fig. 7.9), the survival rates shown in Fig. 9.2 are also applied to alatae.

(ii) Fecundity rates

Modelling of fecundity rates for apterae was also based on the data for aphids reared at the three alternating temperature regimes. Since the pattern of reproduction was similar at the different temperatures, the fecundity rates of the aphids reared at 28-13.5°C were converted to the physiological time scale, i.e. rate per quip (Fig. 9.2) and used as the basis for fecundity rates in the model.

The correction for the effect of lower temperatures to increase fecundity rates is specified in the model according to the linear regression equation (Fig. 9.3) derived from the data obtained under the three alternating temperature regimes (see Fig. 7.5). Duffus (1963) reported that the total fecundity of this aphid was highest somewhere between 5°C and
15°C. In the model, fecundity rates were assumed to increase until the daily mean temperature drops to 10°C, and then remain constant (Fig. 9.3).

In the laboratory experiments aphids were reared from birth to death under the respective temperature regime. Presumably, the temperatures experienced by an aphid during both its nymphal development and early adult life may all affect its reproductive rates. In the model the effects of temperature on the fecundity rates of the aphid was assumed to act through nymphal development and early adult life, i.e. through the first 33 quips after birth. To implement the calculations of fecundity rates in the model, the daily mean temperatures applying at the time of each quip after the start of each population are stored in an array. The overall daily mean temperature experienced in the first 33 quips after birth by the aphids becoming adult at each quip is calculated and their fecundity rates are corrected throughout their reproductive life by a factor estimated from the relationship depicted in Fig. 9.3.

$$Y = 1.820756 - 0.036937x$$

Fig. 9.3. The relationship between daily mean temperature and aphid fecundity rates where the fecundity at 22°C is taken as unity. Y is assumed to remain unchanged at temperature lower than 10°C as indicated by the dotted line.
At the one temperature tested (17°C), the fecundity rates of alatae were lower than those of apterae through most of their reproductive life (Fig. 7.9). Since data are not available on the reproduction of alatae at different temperature levels, the correction for the effect of temperature on fecundity rates was assumed to be the same as that for apterae (Fig. 9.3). To calculate the basic fecundity rates of alatae for use in the model, the \( m_x \) data of alatae at 17°C were first converted to the physiological time scale and to bring them to the same standard temperature for apterae (22°C), the values in each quip were then multiplied by a factor of 0.84 (Fig. 9.2). With the basic fecundity rates derived this way, the same correction equation for fecundity rates at different temperature levels could be applied to both apterae and alatae.

9.2.4 Crowding and the Production of Alatae

Modelling of crowding and the production of alatae is based on the preliminary analysis of the occurrence of apterous and alate forms in the two field cage experiments (8.4.1; 8.4.3). Aphid density is defined as the number of aphids per gram dry weight of plant material. In the two field cage experiments, plant dry weight was found to increase exponentially on a physiological time scale and the growth rates were similar in the two seasons. In the model, the increase of dry weight per plant (\( Y \)) is calculated as a function of effective temperature (\( X \) D^°C) according to the equation:

\[
Y = 1.071342e^{0.006558X}
\]

The different initial dry weight is simulated by adding the appropriate number of day degrees to the time scale for the plant. Plants in the field cage grew exponentially until about 500 D^°C after they were transplanted and then stopped growing. In the model, the dry weight of plant is assumed to
be constant after 500 D\textdegree C.

In the two field cage experiments, the proportion of alatiform nymphs in the fourth instar (\(y\)) was found to be closely correlated with the aphid density when the nymphs were in the first instar (\(x\)) according to the equation (Fig. 8.6):

\[
y = \exp\left(-29.9847/x^{0.7456}\right)
\]

This equation is adopted directly in the model to calculate the proportions of apterous and alate forms. In the model, morph determination is assumed to occur towards the end of the first instar as a function of the aphid density at that time. The relationship is then used to estimate the proportion of the first instar nymphs which will ultimately become alatae. Since in the cage experiments there were always a few alatae even if the aphid densities were very low, the lower limit of \(y\) in the above equation was set arbitrarily as 0.10 in the model.

9.2.5 Synopsis of the Basic Model

The various biological processes described above were assembled together into a Fortran program to make a "variable life-table" for the aphid (see Appendix 2). Fig. 9.4 illustrates the sequences of events which occur in the model.

The model has been formulated to simulate the aphid numbers on one plant. However, it will apply equally well to ten or 100 plants if a multiplying factor is applied appropriately throughout.

The model is driven by the increment of effective temperatures. To simulate the aphid numbers in one season, the model is first primed with data particular to that season: a number of aphids in different age classes equal to those used for the initial infestation are entered into the specified array and the array for storing the daily mean temperatures applying at the
Fig. 9.4  Computer algorithm for populations of H. lactucae in a field cage.
time of each quip is filled with the temperature recordings of that season. The number of day-degrees to be run can be varied at will. After the required number of day-degrees is entered, the model then predicts the population changes during the season. The model prints out the values of the numbers of aphids in all instars/morphs (i.e. $N_1$, $N_2$, $N_3$, $N_4$ apt., $N_4$ al., $A$ apt., and $A$ al. and also the total number of aphids) which occur at the end of each quip after the start of the population. The output can then be compared with values observed in the field cage experiments.

9.3 SIMULATION EXPERIMENTS AND RESULTS

In the simulation experiments, the performance of the model was always judged by comparing the simulations of the changes of aphid numbers in all instars/morphs with actual numbers counted.

9.3.1 Initial Application of the Basic Model to the Field Cage Data

The first version of the model as described above gave answers widely different from the two sets of data. The numbers of aphids in each instar/morph were obviously too high and the differences were larger for adults than for nymphs. Also, the differences became larger and larger in all instars/morphs as the time units increased. This was expected, since no mortality during the nymphal stages had yet been imposed and dead nymphs of all instars were frequently encountered in the samples. Moreover, the massive losses of adults due to emigration, i.e. the large number of adults found on the mesh inside the field cage (8.4.2), had not yet been incorporated into the model. To incorporate these observed events into the model, simulation experiments were then carried out using the data of the First cage experiment.
9.3.2 Simulation Experiments with the Data of First Cage Experiment

Because the observed numbers of aphids were lower than those predicted by the model right from the beginning and large numbers of emigrating adults were not observed until the number of aphids on each plant exceeded 4000, it appeared clear that the tuning of the model should proceed accordingly in two steps:

(a) Manipulate the parameters of the model within acceptable limits to give the right answers for the population during the early stage of the experiment when no apparent losses of adults due to emigration were observed; and

(b) Incorporate the observed losses of adults and test the performance of the model against all data points.

(i) Adding overall mortality to the basic model

The presence of dead nymphs of all instars in the samples indicated that mortality during nymphal stages occurred in the cage population.

![Graph](image)

Fig. 9.5. Modification of survival rates curve: solid line - survival rates in laboratory; dotted line - survival rates in laboratory multiplied by a factor of 0.997 through all age classes.
Since it is unlikely that any mortality factor would operate only during the nymphal stages, a constant correction factor was applied to the survival rates of all age classes. By trial-and-error, a reasonable fit of the simulations to the data points up to time 40 was obtained when a correction factor of 0.997 was applied. Fig. 9.5 shows the effect of the application of the factor on the overall survival rates of the aphid as a statistical artifact.

(ii) Incorporating losses of adults due to emigration

In the experiment, many emigrating adults were first observed between time 40 and time 45, and thereafter the number increased rapidly. When the model was run up to time 54, there were obviously too many adults. Comparison of the 4th instar:adult ratio in the model and in the data at time 54 revealed a deficiency of 6% in apterae and 55% in alatae. Since there was some discrepancy between the simulations and the data before time 40, the calculated deficiency provided only a rough estimate. The ages of adults lost were unknown, presumably they were young adults migrating to find fresh host plants, as work on other aphids showed that heavy losses of adults, especially alatae occur before they start to breed, e.g. in Aphis fabae (Way & Banks 1967; Shaw 1970b) and Brevicoryne brassicae (Hughes & Gilbert 1968). Undoubtedly, the observed emigration in the experiment was largely caused by population pressure. Inspection of data showed that at the time when large number of adults were first found on the cage screens the aphid density had reached more than 150 per gram dry weight of host plant. Losses of various proportions of newly moulted apterae and alatae above the defined density (i.e. 150 aphids per gram dry weight of plant material) were then incorporated into the model to test its performance. The best fit of the simulated results to the
data was found when 10% losses of newly moulted apterae and 50% losses of newly moulted alatae were applied.

(iii) Simulating the data of First cage experiment

The performance of the model, after the observed mortality and losses due to emigration have been incorporated, in simulating the data of the First cage experiment is shown in Fig. 9.6. Bearing in mind the various approximations made during the simulation experiments and the likely sampling errors in the data, the results of simulation are considered very reasonable.

9.3.3 Application of the Model to Second Cage Experiment

The results of applying the model (with parameters appropriate for the First cage experiment; see Appendix 2) to the data of the Second cage experiment are shown in Fig. 9.7. Again, the simulated and observed population trends are very similar.

9.4 DISCUSSION

Notwithstanding the assumptions made when quantitative experimental data were not available, the tuned model was able to give reasonable simulations to an independent set of population data. Although it does not follow that the components assembled in the model necessarily reproduce the biological details correctly (for example, the estimate of losses of newly-moulted adults, specified in the model as a constant proportion above a given population density, is too simple to be realistic), a partial evaluation of the simulation results may still be made.

The validity of the laboratory data on the speed of development and fecundity rates of the aphid shown in the model probably reflects the similarity of the host plant material used in laboratory experiments and that in the field cage. Although the effect of temperature on fecundity rates of the aphid (Fig. 9.3) can not be tested rigorously with the data
Fig. 9.6. Comparison for First cage experiment of the observed and simulated population trends. The dots are actual data points, while the solid lines are those predicted by the final version of the model.
Fig. 9.7. Comparison for Second cage experiment of the observed and simulated population trends. The dots are actual data points, while the solid lines are those predicted by the final version of the model.
obtained. (This is because: (1) in both experiments the aphids used to start the populations were reared at 22°C, i.e. at the temperature where the correction factor is 1.0, and (2) the differences in temperatures between the two experiments were not substantial (see Fig. 8.2)). Results of some further simulation experiments (not figured here) indicated that the performance of the model was not as good when the relationship between temperature and fecundity rates was omitted: while the simulations still resembled the data of the First cage experiment well, the model generally underestimated the numbers of aphids for the Second cage experiment. This situation occurred apparently because of the different mean temperatures during the initial periods of the two experiments. For the Second cage experiment, omission of the relationship resulted in an apparently substantial decrease of the aphid numbers generated at the beginning, while such a decrease was very small for the First cage experiment. This suggests that a similar relationship between temperature and fecundity rates as that demonstrated in laboratory studies probably indeed exists under field conditions. Thus, on its own physiological time scale, the aphid can multiply more rapidly at relatively low temperatures.

The simulation results showed that as the population density increases, large proportions of alatae and small proportions of apterae are lost from the population. It is probable that the actual losses of adults from each plant were reduced in the field cage, as the enclosure could have forced some of the emigrants to settle on other plants inside the cage. Nevertheless, the simulation results indicate clearly that the control of population through density-related emigration operates very early in the population cycle.

According to the model, reproduction of the aphid is little affected by population density when the plants are actively growing. When the
ratio of first instar:adults in the two experiments was plotted against population density (Fig. 9.8), there is no sign that the fecundity of adults was reduced at higher densities. (If the populations had not been infected by fungus diseases after the host plants matured, analysis of population changes of the whole seasonal cycle would probably gain more insight into the relationship between density and reproduction.) Thus, these results seem to lend support to the earlier contention (2.3.4) that in *H. lactucae* the effect of population density on reproductive rate *per se* is probably insignificant over much of a population cycle, the principal control being the density-related emigration shown above.

The peak numbers of aphids per plant in the field cage are not unrealistically high in view of the population density of *H. lactucae* observed in the field, which may reach more than 2000 per flowering shoot (Martin 1979, pp. 101-102 & pp. 130-131). Direct observations in the field showed that large solitary plants of *S. oleraceus* can bear 20-30 young flowering shoots at their peak growth. Thus, in cases where all the young flowering shoots are heavily infested with aphids, one plant may bear a total number of more than 60,000 aphids. However, the growth and eventual size (thus the number of young flowering shoots at their peak growth) of sowthistle plants vary greatly with soil condition (4.3.2), plant density (8.4.1) and other environmental factors such as light intensity and photoperiod (Lewin 1948; Martin 1979). Generally, most plants in the field grow in soil less fertile than that in the field cage (and also sometimes in more crowded conditions created usually by plants of other species), they are smaller and less succulent. Thus, the average potential capacity per plant to support aphids in field conditions is usually much lower than that seen in the field cage. As *H. lactucae* is a typical "flush" feeder and emigrates when the flower heads start to mature,
Fig. 9.8. Ratio of first instar:adults v. aphid density in the two field cage experiments.
the density-related rate of emigration (and possibly other density-related mechanisms) will adjust the numbers of aphids in accordance with the supporting capacity of the colonized plants. Furthermore, the possible peak number of aphids on any one particular plant depends also on the time within the favourable season when the plant is first infested by either flying alatae or crawling apterae. As sowthistle plants are normally scattered in the field, it is inevitable that many plants are not infested until late in the season.

Although the model simulates only part of the population cycle in the field cage, the simulation results showed that it is now possible to describe, quantitatively, population changes of the aphid in field cage conditions. Based on the model, it is now also possible to assess the impact of the aphid's natural enemies on its population dynamics in field cage conditions, e.g. the association of natural enemy activity with changes in age structure of the aphid populations.
PART IV

STUDIES ON *APHIDIUS SONCHI* AND

THE HOST-PARASITE INTERRELATIONSHIPS
10.1 INTRODUCTION

Any ecological studies of insects require, in the first place, a thorough knowledge of the life history and behaviour of the subject species. As no information was available on the biology of *A. sonchi* (see Chapter 3), observations were made on each phase of its life history with *H. lactucae* as its host.

10.2 DEVELOPMENT OF IMMATURE STAGES

The following is a simplified account of the development of *Aphidius*, based on the generalized descriptions given by Stary (1970). Members of this genus are obligatory, solitary internal parasites. The female lays an egg into the body of the host aphid. After eclosion from the egg, the larva lives unattached inside the body cavity of the aphid and passes through four instars. During the first three instars, the larva feeds on the body fluids of the aphid. On reaching the fourth instar, it begins to feed on the vital organs and gradually consumes all the contents of the aphid. After the aphid is killed, the fully grown larva cuts a hole in the ventral surface of the intact aphid skin and, working from inside, glues it to the substratum with a silken secretion from its salivary glands. The larva lines the internal surface of the aphid skin with its silken secretion, voids the meconium and then pupates. The dead aphid skin is bloated, parchment-like, whitish or brownish and called a "mummy". The pupa develops gradually into an adult wasp which cuts a circular hole usually through the dorsum of the mummy and emerges.

Observations on *A. sonchi* showed that the whole cycle from egg to adult
in this species took about two weeks under 20°C. When more than one egg were laid in an aphid either by the same female or by different females, only one of them developed to adulthood. When eggs were deposited at approximately the same time, all of them would hatch successfully (checked by dissection, also see 10.6.1). However, dissection of large numbers (more than 5000) of superparasitized aphids showed that all supernumerary larvae always disappeared in the first or second instar. Their disappearance was unlikely to be caused by cannibalism, because only twice were the mouthparts of one larva found attached to another larva. The elimination of supernumerary ones therefore was more likely brought about through physiological suppression by the survivor (see Stary 1970, p. 234).

10.3 EMERGENCE OF ADULTS

An emerging adult of *A. sonchi* first cut a circular lid in the mummy with its mandibles, and then pushed itself out with its head. Emergence holes were almost invariably cut in the posterodorsal portion of the mummified aphid. At 20°C, the whole emergence process required usually 20 to 30 minutes. Once out of the emergence hole, the adult parasite ran round, stopping frequently to clean itself or to feed if food was available.

10.4 REPRODUCTION AND REPRODUCTIVE CAPACITY

*A. sonchi* is a biparental species, and unmated females produce only male progeny. In an experiment conducted at 22°C and 14L:10D, ten virgin females were caged with unparasitized *H. lactucae* reared on flowering shoots. All the resultant 240 adult parasites were males. The potential reproductive capacity of *A. sonchi* was largely determined by the number of eggs present in the ovaries on emergence. The number of eggs produced during adult life constituted only about 20% of the total complement. The phenomenon was examined in the following experiment: Forty 12-24 h post-
emergent, mated female parasites were obtained from the parasite stock culture. Thirty of the females were dissected between 24-36 h after emergence and the numbers of eggs contained were counted (Methods for dissecting are described in detail in 11.3.1). These females had on average 179 eggs and over 80% of the eggs appeared to be mature (see Fig. 11.5). The remaining ten females were each caged with 50 second and third instar aphid nymphs for 24 h at 22°C, 14L:10D and 70-90% R.H. and transferred daily to a new caged pot with a fresh supply of aphids until the parasite died. All the aphids exposed were reared for a further 60-70 h under the experimental conditions and then dissected to determine the number of eggs laid by counting the number of first instar parasite larvae present at that time (see 10.2). These females laid on average 215 eggs, i.e. they had developed a further 36 eggs during adulthood -17% of the total complement in comparison with the females dissected.

10.5 MATING

In order to observe the mating behaviour of *A. eonchi*, mummies from the stock culture containing near-emergent parasites were kept at 20 ± 2°C and 50-60% R.H. and monitored continuously. Pairs of newly emerged adults were then transferred to a caged pot containing an aphid-free flowering shoot and honey drops as food. Observations were made under fluorescent lighting.

The time interval between emergence and mating varied widely among both male and female individuals. Some males were observed to chase females and successfully copulate within a few minutes of emergence, while others showed no signs of arousal in the presence of virgin females until two to three hours after emergence. Usually, however, the pre-mating period lasted about 10 to 30 minutes in males. The pre-mating period was
longer in females. Most females rejected all copulatory attempts until at least one hour after emergence. But if females were confined together with males for periods of twelve hours, they were always found to have been mated.

Virgin females did not actively seek out males. When confined with males, most females stayed in the shade under a leaf, while the males were attracted to light. The males seemed to detect virgin females by odour and not by sight, since an aroused male would run around, waving his antennae from side to side and frequently raising the wings vertically above the thorax. On making physical contact, the male would vibrate his wings and run his antennae over the female. If the female rejected the advances, and walked away, the male usually followed her in a persistent manner. Once the female accepted the advances, antennal tapping was usually exchanged between the male and the female, followed by the attempts of the male to mount the female. The female then sat quietly with her wings folded, while the male bent his abdomen downwards to meet the sex organs of the female. During copulation, the male continued to vibrate his wings and tap the female with his antennae. Copulation usually lasted from 30 to 60 seconds.

Females were never observed to mate more than once in their lifetime, although on several occasions mated females were caged with males. When the males attempted to copulate, the mated females inevitably pushed them away or bent their abdomen downwards, thus preventing copulation.

Virgin female *A. sonchi* which have commenced oviposition can still mate successfully (cf. Stary 1970, p. 68). In one experiment, ten virgin females were caged with unparasitized aphids at 22°C and 12L:12D for 24 h. They were then caged with ten males for 12 h and one female was observed to mate successfully within 10 minutes. The females were then caged individually
with unparasitized aphids for a further period of 24 h. By rearing the aphids attacked by the virgin females it was found that 180 had been parasitized and the resultant parasites were all males. After the females had spent 12 h with males, in the next 24 h they parasitized on average of 30 aphids each, and 8 out of the 10 produced both male and female offspring (sex ratio: male:female=1:4), indicating that mating had occurred.

Males were observed to be capable of mating more than once. For example, one male was observed to copulate successfully with five different virgin females within four hours of emergence.

10.6 OVIPOSITION

Observations on oviposition of the parasite were made at 20°C, 50-60% R.H., using newly emerged adults from the parasite stock culture and caged pots as experimental units, unless stated otherwise.

10.6.1 Oviposition Behaviour and Reaction of the Aphid

Newly emerged females contained large numbers of mature eggs (see 10.4), but even in the presence of host aphids, the period between emergence and the onset of oviposition by both virgin and mated females was usually between one to two hours.

On being introduced into a colony of aphids, the female walked around with her antennae directed towards tapping the plant surface. Once an aphid was located, apparently by odour as well as sight, she waved her antennae over the aphid without touching it, and immediately adopted the attack posture, that is, the female bent her abdomen forward beneath and anterior to her head and thorax, and balanced on her extended legs. Then, by moving her abdomen forward quickly, the female attempted to lay an egg in the aphid with her ovipositor.

The female generally did not orient herself to sting any particular
part of the aphid body, but struck the aphid from whatever angle she happened to approach. However, observations suggested that the ventral part of the thorax of the aphid was stung more frequently than any other part of the aphid body, especially if the aphids were in the first or second instar.

A successful oviposition act usually lasted less than a second and was characterized by a strong and jerky withdrawal of the ovipositor. In older females, the oviposition act could last up to two seconds. Once an egg was laid, the female usually moved on in the search for another aphid. If an aphid escaped during an attempt of oviposition, the parasite would usually chase the aphid, whilst still remaining in the oviposition posture until successful oviposition had occurred. If an oviposition attempt failed and the aphid did not move away, the parasite usually moved back and changed her position before making another attempt with or without cleaning her ovipositor in between times. Less frequently, the female continued striking in the same position. However, an aphid often reacted to the presence of ovipositing females, especially after being struck or walked over, by shaking its body from side to side. Furthermore, large aphids sometimes kicked or knocked the ovipositing females away with their legs and/or wings. A female usually left an aphid after repeated unsuccessful oviposition attempts.

That *A. sonchi* females lay only one egg per successful oviposition act was shown in the following experiment: Sixty third instar aphid nymphs were exposed individually to 15 ovipositing females. When oviposition (identified by the sight of attack and the strong and jerky withdrawal of the parasite's ovipositor as described) was considered to have occurred, the aphid was immediately withdrawn. Since the parasite eggs are very small (Fig. 11.5) and difficult to detect, the exposed aphids were
reared for 60-70 h and then dissected. Each of the 60 aphids contained one first instar parasite larva.

10.6.2 Oviposition Activity

When first caged with a group of aphids, the female parasite deposited five to eight eggs in rapid succession. She then walked away to a shaded area and stood still cleaning herself occasionally. Ten to 15 minutes later, the female engaged in a similar cycle of oviposition before resting again. After a few such activity-rest sequences, oviposition then became irregular and mostly occurred singly.

10.6.3 Superparasitization

Although the parasite female usually moved on in search of another aphid after an egg was inserted, she was unable to distinguish between parasitized and unparasitized aphids, whether the aphid had been parasitized by herself previously or by another female. Close observations in which unparasitized aphids, parasitized aphids containing parasites of different developmental stages (i.e. from egg to fourth instar larva) and dead aphids (killed by wounding their head with a pair of sharp forceps one hour before exposure) were exposed simultaneously to attack, showed that the ovipositing female attempted oviposition in any live aphids she encountered (also see Chapter 11) but generally ignored the dead ones. It should be noted that the female parasites used in these tests had previously been kept with non-test aphids, i.e. their oviposition urge would have been normal.

10.6.4 Oviposition in Relation to Light and Darkness

It is generally believed that females of aphidiiids do not oviposit in darkness (Stary 1970). Preliminary experiments showed that female
A. sonchi laid some eggs during the scotophase of each 24 h period, but the proportion of eggs laid differed widely according to whether the substratum on which the aphids were exposed was simple or complex. Further experiments were therefore carried out to investigate the oviposition activity of this parasite in relation to light and darkness, and how the phenomenon is influenced by the type of substratum.

Second and third instar aphid nymphs from the aphid stock culture were reared, either on young leaves set flat in a jar or on flowering shoots in a caged pot at 20°C, 70-90% R.H., 12L:12D. The parasites used were 12-24 h post-emergent, mated females obtained from the parasite stock culture. In the experiments where the aphids were reared on young leaves, each female parasite was provided with 20 unparasitized aphids each 12 h period until all the females died. Where the aphids were reared on flowering shoots, each female parasite was provided with either 20 or 200 unparasitized aphids each 12 h period. All the test aphids were reared for a further 70-80 h and then dissected. The number of larvae in each aphid was recorded. Since it had already been determined that there was virtually no mortality of the parasite during its embryonic development under the experimental conditions studied (10.2; 10.6.1), the data were then used to calculate the numbers of eggs laid and numbers of aphids parasitized.

The results of the experiments are summarized in Table 10.1 and depicted in detail in Figs. 10.1 and 10.2. Female A. sonchi laid some eggs in darkness. A higher proportion of eggs was deposited in darkness with higher aphid density on the same substratum (flowering shoots), and when aphids were exposed on young leaves rather than on flowering shoots. A higher proportion of eggs was also laid in darkness by the females starting oviposition in a 12 h dark period than those starting oviposition
Table 10.1  Oviposition activity of *A. sonehi* in relation to light and darkness
with host aphids reared on two different substrata

<table>
<thead>
<tr>
<th>Substratum*</th>
<th>No. aphids provided each 12 h</th>
<th>N</th>
<th>Mean no. eggs laid per female</th>
<th>Eggs laid in light</th>
<th>Eggs laid in darkness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young leaves L</td>
<td>20</td>
<td>6</td>
<td>229.7</td>
<td>186.1</td>
<td>43.6</td>
</tr>
<tr>
<td>Young leaves D</td>
<td>20</td>
<td>6</td>
<td>207.0</td>
<td>134.3</td>
<td>72.7</td>
</tr>
<tr>
<td>Flowering shoots D</td>
<td>20</td>
<td>12</td>
<td>105.3</td>
<td>99.1</td>
<td>6.2</td>
</tr>
<tr>
<td>Flowering shoots D</td>
<td>200</td>
<td>6</td>
<td>248.7</td>
<td>204.9</td>
<td>43.8</td>
</tr>
</tbody>
</table>

* L = females starting oviposition in 12 h light period; D = females starting oviposition in 12 h dark period.
Fig. 10.1 Oviposition activity of A. sonchi in relation to light and darkness with host aphids reared on young leaves.
Fig. 10.2 Oviposition activity of *A. sonchi* in relation to light and darkness with host aphids reared on flowering shoots.
with a 12 h light period when equal numbers of aphids were provided on the same substratum (young leaves in Table 10.1).

Since it is impractical to make observations in total darkness, one can only speculate on the oviposition activity of the female parasite under such conditions. The positive correlation between the proportion of eggs laid in darkness and the availability of hosts (varied by number or complexity of substratum) suggests that host seeking in the dark is minimal, but the female parasite can still oviposit during the limited searching periods.

*A. sonchi* is not the first aphid parasite reported to oviposit in darkness. Singh & Sinha (1982) reported that female *Trioxys indicus* can parasitize nearly half as many aphids in the dark as they do in the light during the same length of time.

10.7 ADULT LIFE SPAN

Adult life span in the aphidiids is affected by many factors, such as temperature, humidity, food, presence or absence of hosts, etc. (Stary 1970).

No attempt was made to study all the factors which may affect adult life span in *A. sonchi*. Experiments described below were carried out to examine: (1) whether adult life span differs between males and females in the absence of hosts, (2) whether adult life span in the female is affected by the presence of hosts; and (3) whether, in the presence of hosts, the ovipositing female needs extra water supply. The effect of host density, and the effect of temperature will be reported in Chapters 12 and 13.

The following experiments were conducted at 22°C, 14L:10D, and 70–90% R.H. using adult parasites and second and third instar aphid nymphs taken from the respective stock cultures.

In the first experiment, 117 adult parasites, collected within 24 h
of emergence, were kept in a 10 x 20 cm clear plastic gauze-ended container and provided with honey and water. The container was examined daily and any dead adults (male or female) were recorded and removed until all the adults died. The results were as follows:

<table>
<thead>
<tr>
<th>Sex</th>
<th>N</th>
<th>Adult life span in days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean ± S.E.</td>
</tr>
<tr>
<td>Male</td>
<td>42</td>
<td>8.4 ± 0.4</td>
</tr>
<tr>
<td>Female</td>
<td>75</td>
<td>10.5 ± 0.3</td>
</tr>
</tbody>
</table>

On average, the females lived longer than males (t = 4.37, d.f. = 115, P < 0.001).

In the second experiment, 20 12-24 h post-emergent, mated females were reared individually until dead in a caged pot containing a flowering shoot and each provided with a fresh supply of 100 unparasitized second and third instar aphid nymphs each 24 h. Tap water was supplied to ten of the females by placing a small piece of water-soaked sponge on the gauze top of the cage. The sponge was soaked in water every 12 h to ensure continuous water supply. The other ten females were not provided with water. All the test aphids were reared for a further six days. The resultant mummies were then counted and taken as the number of aphids parasitized per female per 24 h period.

Although the females were occasionally observed to feed on the water supplied, there were no significant differences between the two groups in either adult life span or the number of aphids parasitized (Table 10.2). As it is well known that honeydew, which is the excreta of aphids, has a high carbohydrate/sugar content and is a source of food for many hymenopterous wasps, the results of the experiment suggest that, under the experimental conditions, the female parasites can obtain enough water from the aphid's honeydew and also probably from the plant material. However, on
Table 10.2 Life span of and numbers of aphids parasitized by females of A. sonchi either provided with extra water supply or not. Each female in both cases was supplied with 100 second and third instar aphid nymphs reared on one flowering shoot each 24 h period at 22°C, 14L:12D and 70-90% R.H.

<table>
<thead>
<tr>
<th>Water</th>
<th>Adult age in days</th>
<th>Mean adult life span</th>
<th>Mean no. aphids parasitized per female†</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>I. No. females surviving to the beginning of each day</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplied</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Not supplied</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>II. Mean no. aphids parasitised per original female*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Supplied</td>
<td>54.1±3.7</td>
<td>51.6±5.5</td>
<td>55.7±4.1</td>
</tr>
<tr>
<td>Not supplied</td>
<td>48.2±2.4</td>
<td>48.2±6.1</td>
<td>49.8±3.8</td>
</tr>
</tbody>
</table>

* Mean ± S.E. where applicable.
† The differences between the two means are not significant at the 5% level (t = 0.98, d.f. = 18, P>0.20).
average, the adult females in this experiment lived only half as long as did the females in the first experiment where no host aphids were provided. Since the females in the second experiment were each provided with 100 aphids daily throughout their adult life, i.e. plenty of honeydew was always available, the difference in adult life span can perhaps be attributed to the difference in energy usage (e.g. host-seeking, oviposition) in the two groups of females.

10.8 ADULT INTEGUMENTAL COLORATION IN RELATION TO TEMPERATURE

Striking, consistent differences in coloration were observed between adult parasites subjected to different temperatures during development. When *A. sonchi* was reared (from egg to adult) at low temperatures the resultant adults were darker than those reared at high temperatures, the greatest difference in coloration being in the face and thorax as the following table shows:

<table>
<thead>
<tr>
<th>Body parts of female*</th>
<th>Rearing temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>28°C</td>
</tr>
<tr>
<td>Face</td>
<td>Orange</td>
</tr>
<tr>
<td>Mesothorax (except mesoscutum), meta-</td>
<td>Orange or</td>
</tr>
<tr>
<td>thorax and propodeum</td>
<td>orange-brown</td>
</tr>
<tr>
<td>Predominant colour facies</td>
<td>Orange and</td>
</tr>
<tr>
<td></td>
<td>orange-brown</td>
</tr>
</tbody>
</table>

* First generation progeny of (light-coloured) adult parasites from the parasite stock culture.

Males were usually slightly darker than the females under the same rearing conditions.

Temperature-responsive colour lability has been demonstrated in other members of the Aphidiidae (Mackauer & Finlayson 1967, Liu & Carver 1982). Liu and Carver (1982) further showed that in *Aphidius smithi* the mid to late pupal stage is the only period in the life of the parasite
during which the adult integumental coloration is temperature-responsive. Colour variability to a varying degree and depending on the species has been demonstrated in the following aphidiids by rearing them from their early pupal stage at low temperature (12°C) and high temperature (28°C): *Aphidius colemani* Viereck, *A. pisivorus* Smith, *A. ervi* Haliday, *Praon volucre* (Haliday), *Lysiphlebus confusus* Tremblay and Eady, *L. fabarum* (Marshall), *L. testaceipes* (Cresson) (M. Carver, unpublished data). Since, like in *A. smithi*, the colour variation in *A. sonchi* is fully expressible within one generation, it is believed that the adult integumental coloration in this parasite is also affected mainly by the temperature experienced during the pupal stage.

10.9 DIAPAUSE

Laboratory and field investigations showed that facultative diapause occurs in *A. sonchi*.

The parasite spent the diapause period as a mature larva inside the mummy. Generally, a mummy housing a diapausing larva appeared dark brown instead of being white or white and brownish as in mummies containing non-diapausing individuals. The cocoon was much tougher and the slit in the venter of the aphid body was sealed with dark brown silk so that the parasite larva inside was not visible, whereas a non-diapause larva was usually visible through the translucent ventral surface of the mummy (when removed from the substratum).

Diapausing individuals occurred all year round in the stock culture. The proportion of diapausing individuals remained fairly constant, being usually about 6%. For example:

<table>
<thead>
<tr>
<th>Date of sampling</th>
<th>N</th>
<th>Parasites in diapause</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Number</td>
</tr>
<tr>
<td>11 September, 1981</td>
<td>148</td>
<td>8</td>
</tr>
<tr>
<td>1 October, 1981</td>
<td>131</td>
<td>8</td>
</tr>
<tr>
<td>3 March, 1982</td>
<td>240</td>
<td>18</td>
</tr>
</tbody>
</table>
In each of the samples, diapause was confirmed by maintaining the dark brown mummies in the insectary for a further two weeks after the non-diapause adults had emerged and then dissecting the mummies to see the live larva inside.

Diapausing individuals have also been found in field samples taken from a few sites in both New South Wales and Victoria during 1982 (L.T. Woolcock, unpublished data). However, the limited field data do not provide enough information on the seasonal occurrence of diapause in the parasite.

No detailed diapause studies were attempted. However, the results of some preliminary experiments (Appendix 3) suggest that food, temperature and photoperiod may all affect the induction of diapause in this parasite, and that, prior to the inception of diapause, individuals which are going to enter diapause develop at a similar rate as non-diapause ones.

10.10 Hyperparasites

Two species of hyperparasites have been reared from field recovery samples of *A. sonchi* taken from various sites in New South Wales and Victoria during 1982. They were *Alloxysta ancylocera* (Cameron) (Cynipoidea) and *Pachyneurion aphidis* (Bouche) (Chalcidoidea) (L.T. Woolcock, unpublished data, identified by M. Carver). The incidence of hyperparasitization was low (usually about 0-10%) in most of the samples, though on occasion it was substantial. For example, from a sample taken from Irymple, Victoria on the 27th April, 1982, out of 13 mummies obtained, seven produced *P. aphidis*.

10.11 Host Specificity

*A. sonchi* is known as a specific parasite of *Hyperomyzus* species (Chapter 3). However, preliminary observations showed that *A. sonchi*
also oviposits in *Macrosiphum euphorbiae* (Thomas), an aphid occurring commonly on *Sonchus* with *H. lactucae*. As a result, close observations were made on the relationship between *A. sonchi* and *M. euphorbiae*.

The parasites used were 1-2 days post-emergent, mated females obtained from the parasite stock culture. The females were always kept with *H. lactucae* before being introduced to the test aphids, so that their oviposition activity would not be affected by any intensified oviposition urge caused by lack of hosts. *H. lactucae* used were taken from the aphid stock culture, while *M. euphorbiae* were obtained from a temporary culture of this aphid maintained on *S. oleraceus* in the same insectary. The observations were made at 20°C and 50-60% R.H.

When ovipositing females of *A. sonchi* were provided with both *H. lactucae* and *M. euphorbiae*, the parasites did not seem to show any preference for *H. lactucae* but tried to oviposit in any aphids encountered. The adult females were also observed to oviposit readily in *M. euphorbiae* when aphids of this species were presented alone. Dissection of some *M. euphorbiae* immediately after exposure to the parasites revealed the presence of parasite eggs. However, no parasite larvae were ever found, indicating that development of the parasite in *M. euphorbiae* was arrested during the egg stage.

As *A. sonchi* oviposits in *M. euphorbiae* so readily in the laboratory, it is very likely that it also does so in the field.
11.1 INTRODUCTION

Natural populations of aphids on their secondary host plants are characterized by a broad overlap of generations, resulting in several or all instars being available simultaneously to attack by their natural enemies, such as the aphid parasite concerned here. However, experimental evidence has repeatedly shown that while aphids of different instars/morphs can be utilized as hosts they are usually not attacked with equal frequency (Stary 1970). Since the consequences of parasitization on both the host and the parasite within it vary with the instars/morphs attacked (Campbell and Mackauer 1975; Stary 1970), host developmental stage is therefore an important ecological variable in an aphid–parasite system, and the potential of the parasite to select a specific type of host needs investigation.

This chapter describes laboratory experiments in which the following three aspects of the interrelationships between *H. lactucae* and *A. sonchi* were examined:

(i) Effects of parasitization of different instars/morphs on the aphid's development, survival and reproduction;
(ii) Effects of parasitization of different instars/morphs of the host on the parasite; and
(iii) Host instar selection by and searching behaviour of the parasite.

11.2 EFFECTS OF PARASITIZATION ON THE APHID

11.2.1 Effects of parasitization on development, survival, and reproduction

11.2.1.1 Materials and Methods

The experimental aphid cohorts were started either with first instar nymphs produced by apterae taken from the aphid stock culture or with aphids
drawn directly from the stock culture. The parasites used were 1-2 days post-emergent, mated adult females taken from the parasite stock culture. All the experimental aphid and parasite cultures for different host instars/morphs were set up separately and maintained in environmental cabinets under the experimental conditions.

For the treatments with apterous aphids, first instar nymphs were obtained by placing apterous adults from the stock culture on young leaves at 20°C to reproduce. All nymphs were collected within 2 hours of birth and transferred onto young leaves placed in the vials where they were reared individually both before and after oviposition by the parasite.

For the treatments with fourth instar alatiform nymphs and alatae, large numbers of third instar nymphs and fourth instar alatiform nymphs taken from the aphid stock culture were kept separately on young leaves at 20°C. Newly moulted fourth instar alatiform nymphs and alatae were then collected within 6 hours of moulting and exposed to oviposition by the parasite. Thereafter they were also reared individually on young leaves in the vials.

For oviposition, female parasites were placed in 8 x 4 cm clear plastic vials where they were provided with aphids of a particular instar/morph, one individual at a time. Each aphid was withdrawn immediately after it had been parasitized by a female, i.e. after an egg had been inserted (see 10.6).

The experiments were carried out under two different temperature-light regimes: 22°C, 14L:10D, and 17°C, 13L:11D. Such a replicate was designed to investigate whether, and then how, the effects of parasitization change under different rearing conditions. Eight cohorts of aphids at 22°C and six cohorts of aphids at 17°C were exposed to oviposition by the parasite at different times during their development (see Tables 11.1 and 11.2 for ages and sample size). In addition, at each of the two experimental conditions there was also a control treatment where the aphids were not
exposed to attack by the parasite.

Aphids in all treatments were examined daily to record their development, mortality and fecundity. The young produced were removed from the vials at each observation. The time when mummification occurred was also recorded. From these data, life and fertility tables were constructed for each aphid cohort to evaluate the effects of parasitization.

11.2.1.2 Results and Analysis

(i) Development and Survival

The age at which an aphid became parasitized influenced its subsequent performance and the stage at which mummification occurred (Tables 11.1 and 11.2). Nymphs that were parasitized in the first or early second instar developed at a normal rate into the fourth instar and then were mummified in that instar, although some of them remained alive until one or two days after they would normally have moulted into the adult stage. Nymphs that became parasitized in late second instar or after developed at a normal rate into adults and then mummified at various ages depending on the age attacked.

The survival rates of the parasitized apterous aphids are shown in detail in Figs. 11.1 and 11.2, together with those of unparasitized ones. The survival rates of parasitized aphids in every instance were not affected until about five days at 22°C, and seven days at 17°C after the beginning of parasitization. Thereafter the survival rates dropped to zero in two or three days except in instar 1 at 22°C, and in instars 1, 2 and 3 at 17°C where a few aphids remained alive as fourth instar nymphs for three to five times the normal durations of that stadium and then died as fourth instar nymphs without becoming mummified. In such cases, both the aphid and parasite within it failed to develop to maturity.
<table>
<thead>
<tr>
<th>Stage attacked</th>
<th>N</th>
<th>Mean development from birth to the end of 3rd instar</th>
<th>Mean development from birth to adult</th>
<th>No. individuals mummified as 4th instar</th>
<th>No. individuals mummified as adult</th>
<th>Mean number of young produced before death</th>
<th>Average life span from birth to death in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (in h) &amp; instar</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 - 6 N₁</td>
<td>43</td>
<td>4.6</td>
<td></td>
<td>39</td>
<td>0</td>
<td>0.0</td>
<td>6.8</td>
</tr>
<tr>
<td>22 - 26 N₁</td>
<td>38</td>
<td>4.9</td>
<td></td>
<td>36</td>
<td>0</td>
<td>0.0</td>
<td>7.5</td>
</tr>
<tr>
<td>42 - 46 N₂</td>
<td>42</td>
<td>4.8</td>
<td></td>
<td>42</td>
<td>0</td>
<td>0.0</td>
<td>7.8</td>
</tr>
<tr>
<td>60 - 64 N₂</td>
<td>36</td>
<td>4.6</td>
<td></td>
<td>21</td>
<td>15</td>
<td>1.6</td>
<td>8.6</td>
</tr>
<tr>
<td>83 - 87 N₃</td>
<td>32</td>
<td>4.6</td>
<td></td>
<td>0</td>
<td>32</td>
<td>7.6</td>
<td>10.3</td>
</tr>
<tr>
<td>120 - 124 N₄apt.</td>
<td>35</td>
<td>4.7</td>
<td></td>
<td>0</td>
<td>33</td>
<td>14.5</td>
<td>11.3</td>
</tr>
<tr>
<td>- N₄al.</td>
<td>46</td>
<td>-</td>
<td></td>
<td>0</td>
<td>42</td>
<td>6.6</td>
<td>-</td>
</tr>
<tr>
<td>170 - 174* Aapt.</td>
<td>38</td>
<td>4.6</td>
<td></td>
<td>32</td>
<td>22.2</td>
<td>13.3</td>
<td></td>
</tr>
<tr>
<td>Unparasitized apterae</td>
<td>30</td>
<td>4.7</td>
<td></td>
<td>6.6</td>
<td></td>
<td>61.6</td>
<td>25.3</td>
</tr>
</tbody>
</table>

* Apterous adults were not exposed to oviposition at the same time, instead each of them was exposed on the day of the final moult (i.e. on the 6th, 7th or 8th day). The age in h is the calculated mean time of the beginning of parasitization.
Table 11.2 The consequences of parasitization of different instars/morphs of *H. laotuae* by *A. sonchi* at 17°C, 13L:11D and 60-80% R.H. The host aphids were reared on detached young leaves

<table>
<thead>
<tr>
<th>Stage attacked</th>
<th>N</th>
<th>Mean development from birth to the end of 3rd instar (days)</th>
<th>Time in days from birth to adult (days)</th>
<th>No. individuals mummified</th>
<th>Mean number of young produced before death</th>
<th>Average life span from birth to death in days</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (in h) &amp; instar</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>36 - 40</td>
<td>36</td>
<td>6.5</td>
<td>35</td>
<td>0</td>
<td>0</td>
<td>11.6</td>
</tr>
<tr>
<td>84 - 88</td>
<td>34</td>
<td>6.6</td>
<td>11</td>
<td>19</td>
<td>2.7</td>
<td>14.8</td>
</tr>
<tr>
<td>132 - 136</td>
<td>31</td>
<td>6.7</td>
<td>29</td>
<td>10.1</td>
<td>15.0</td>
<td></td>
</tr>
<tr>
<td>180 - 184</td>
<td>30</td>
<td>6.4</td>
<td>27</td>
<td>17.7</td>
<td>16.1</td>
<td></td>
</tr>
<tr>
<td>228 - 232*</td>
<td>31</td>
<td>6.5</td>
<td>26</td>
<td>27.6</td>
<td>20.2</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>33</td>
<td>-</td>
<td>25</td>
<td>15.8</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Unparasitized apterae</td>
<td>30</td>
<td>6.6</td>
<td>73.2</td>
<td>34.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Apterous adults were not exposed to oviposition at the same time, instead, each of them was exposed on the day of the final moult (i.e. on the 8th, 9th, 10th or 11th day). The age in h is the calculated mean time of the beginning of parasitization.
Fig. 11.1. The effect of parasitization of apterous *H. lactucae* of different instars by *A. sonchi* at 22°C, 14L:10D, showing the daily survival and fertility rates of unparasitized aphids and aphids parasitized at various stages (ages in hours are shown in the parentheses). Arrows in the graph indicate the beginning of parasitization, i.e. oviposition. The vertical dotted line indicates the mean time of final moult of unparasitized aphids.
Fig. 11.2. The effect of parasitization of apterous *H. lactucae* of different instars by *A. sonchi* at 17°C, 13L:11D, showing the daily survival and fertility rates of unparasitized aphids and aphids parasitized at various stages (ages in hours are shown in the parentheses). Arrows in the graph indicate the beginning of parasitization, i.e. oviposition. The vertical dotted line indicates the mean time of final moult of unparasitized aphids.
The survival rates of parasitized alatiform nymphs and alatae (not figured here) also were not affected until mummification began to occur.

(ii) Reproduction

Parasitization by the parasite had a significant impact on the reproductive rates of and the total number of progeny produced by the aphid. Progeny production started to decline from normal three days after attack at 22°C, and five days after attack at 17°C, and then ended in one or two days (Figs. 11.1 and 11.2). Consequently, aphids which became parasitized in the first or early second instar failed to produce any young. Thereafter, the mean number of young produced per aphid increased with an increase in the age of the aphids at the time of parasite attack (Tables 11.1 and 11.2).

(iii) Effects of parasitization in relation to the development of the parasite and modelling of the effects of parasitization on the population increase potential of the aphid

Under each of the two temperature-light regimes the mean time from oviposition by the parasite to the end of reproduction and mummification of the aphid remained relatively constant irrespective of the aphid age at the beginning of parasitization (Tables 11.3 and 11.4). Further analysis showed that the length of the time from oviposition to the occurrence of various lethal effects on the aphid is a function of the relative proportions of the parasite developmental time (Table 11.5).

The fecundity rates of the parasitized aphids remained normal until the parasites inside had completed 30% of their development and then declined to zero in one or two days. The analysis of the effect of parasitization on the aphid population increase potential can thus be made on the assumption that an aphid reproduces normally till the parasite within it has completed
Table 11.3 The effect of parasitization of different instars/morphs of *H. lactucae* by *A. sonchi* at 22°C, 14L:10D

<table>
<thead>
<tr>
<th>Aphid instar attacked</th>
<th>N</th>
<th>Mean time in days from being attacked to the end of reproduction</th>
<th>Mean time in days to becoming mummified</th>
</tr>
</thead>
<tbody>
<tr>
<td>N₁</td>
<td>81</td>
<td>6.6</td>
<td></td>
</tr>
<tr>
<td>N₂</td>
<td>78</td>
<td>6.2</td>
<td></td>
</tr>
<tr>
<td>N₃</td>
<td>32</td>
<td>6.5</td>
<td></td>
</tr>
<tr>
<td>N₄ apt.</td>
<td>35</td>
<td>6.3</td>
<td></td>
</tr>
<tr>
<td>N₄ al.</td>
<td>46</td>
<td>5.9</td>
<td></td>
</tr>
<tr>
<td>A apt.</td>
<td>38</td>
<td>6.3</td>
<td></td>
</tr>
</tbody>
</table>

Table 11.4 The effect of parasitization of different instars/morphs of *H. lactucae* by *A. sonchi* at 17°C, 13L:11D

<table>
<thead>
<tr>
<th>Aphid instar attacked</th>
<th>N</th>
<th>Mean time in days from being attacked to the end of reproduction</th>
<th>Mean time in days to becoming mummified</th>
</tr>
</thead>
<tbody>
<tr>
<td>N₁</td>
<td>36</td>
<td>10.0</td>
<td></td>
</tr>
<tr>
<td>N₂</td>
<td>34</td>
<td>9.9</td>
<td></td>
</tr>
<tr>
<td>N₃</td>
<td>31</td>
<td>9.5</td>
<td></td>
</tr>
<tr>
<td>N₄ apt.</td>
<td>30</td>
<td>9.6</td>
<td></td>
</tr>
<tr>
<td>A apt.</td>
<td>31</td>
<td>9.5</td>
<td></td>
</tr>
<tr>
<td>A al.</td>
<td>33</td>
<td>9.7</td>
<td></td>
</tr>
</tbody>
</table>

Table 11.5 The times when *A. sonchi* exerts lethal effects on its host, *H. lactucae*, and their proportions to the whole duration of development of the parasite itself

<table>
<thead>
<tr>
<th>Rearing condition</th>
<th>Mean time in days from oviposition to cessation of reproduction of the aphid</th>
<th>Death of the aphid</th>
<th>Mean time in days from oviposition to emergence of adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>22°C, 14L:10D</td>
<td>3.6 ± 0.2 (32%)</td>
<td>6.3 ± 0.2 (57%)</td>
<td>11.1 ± 0.3 (100%)</td>
</tr>
<tr>
<td>17°C, 13L:11D</td>
<td>5.9 ± 0.2 (34%)</td>
<td>9.7 ± 0.2 (55%)</td>
<td>17.5 ± 0.3 (100%)</td>
</tr>
</tbody>
</table>

* Mean ± S.E. throughout the table, and the figure in the parentheses is the proportion of that time to the whole duration of development of the parasite.
Fig. 11.3. The relationship between the achieved intrinsic rate of increase of apterous *H. lactucae* and the aphid age at the beginning of parasitization by *A. sonchi* at 22°C, 14L:10D. The solid circles are observed values and the vertical dotted lines indicate mean durations of the nymphal stages of unparasitized aphids.
33% of its development and then stops reproducing. Based on this time scale, the intrinsic rate of increase, $r_m$, can be calculated for aphids which become parasitized at various stages throughout their lifetime under different conditions. Figure 11.3 shows the results of such calculations for the aphids reared on detached young leaves at 22°C and 14L:10D, together with the observed values in the experiment. Aphids that become parasitized in the first or second instar do not, or only insignificantly, contribute to population increase. The intrinsic rate of increase then increases rapidly as the aphid age at the beginning of parasitization increases until about two days after the final moult. Aphids which are parasitized three days after the final moult or later show similar potential for population increase to that of unparasitized aphids.

11.2.2 Effects of Parasitization on Wing Development

11.2.2.1 Materials and Methods

Cohorts of nymphs with high proportions of presumptive alatiform individuals were exposed to parasite attack at various ages, and the wing development of parasitized aphids and that of unparasitized ones within each cohort were compared.

To obtain cohorts of nymphs with high proportions of presumptive alatiform individuals, apterae were collected from a crowded cage population and placed on detached young leaves at 20°C to reproduce (see Appendix 1). First instar nymphs were then collected within 4 hours of birth and transferred onto young leaves set flat in the plastic jars, 30 aphids per jar, where they were reared before and after exposure to parasite attack at the desired ages.

Parasitization of the aphids was achieved by introducing one 1-2 days post-emergent, mated female parasite taken from the parasite stock culture
into each jar for 2 h.

The experimental aphid and parasite cultures were maintained in an environmental cabinet at 15°C, 12L:12D and 70-90% R.H. Mummies began to appear 10 days after oviposition by the parasite. Aphids that did not show any evidence of parasitization 14 days after exposure to parasite attack were considered as unparasitized. These unparasitized aphids in each jar were used as "controls" in subsequent morph comparison.

11.2.2.2 Experiments and Results

(i) Parasitization of first instar alatiform nymphs

One hundred and twenty aphids reared in four jars were exposed to parasite attack between 48 to 50 h after birth when they were in the mid of the first instar. All the parasitized aphids were killed as fourth instar nymphs. At the time of death only few of them had visible wingpads, while the "control" aphids consisted of 41% alatae as shown by the following table:

<table>
<thead>
<tr>
<th></th>
<th>Unparasitized</th>
<th>Parasitized</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of aphids</td>
<td>64</td>
<td>56</td>
</tr>
<tr>
<td>Normal apteriform</td>
<td>38 (59%)</td>
<td>52 (93%)</td>
</tr>
<tr>
<td>Normal alatiform</td>
<td>26 (41%)</td>
<td>0</td>
</tr>
<tr>
<td>Nymphs with short wingpads</td>
<td></td>
<td>4 (7%)</td>
</tr>
<tr>
<td>as shown in Fig. 11.4A</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(ii) Parasitization of second instar alatiform nymphs

One hundred and twenty aphids reared in four jars were exposed to parasite attack between 96 and 98 h after birth when they were in the mid of the second instar. Most of the parasitized aphids were mummified during the fourth instar and the rest were mummified as adults. The results are summarized as follows:
Fig. 11.4. Mummies of fourth instar alatiform nymphs and alate which became parasitized in the second instar (A & B) or in the third instar (C & D). Notice the varying degree of wing differentiation in each instance.
### (iii) Parasitization of Third Instar Alatiform Nymphs

One hundred and twenty third instar alatiform nymphs collected from ten jars were placed in four new jars, 30 aphids each jar, and exposed to parasite attack between 144 to 146 h after birth when they were in the mid of the third instar. Of the 120 aphids, 61 became parasitized and there was much variation in wing differentiation among them as the following table shows:

<table>
<thead>
<tr>
<th></th>
<th>Unparasitized</th>
<th>Parasitized</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of aphids</td>
<td>59</td>
<td>61</td>
</tr>
<tr>
<td>Normal alatiform</td>
<td>59 (100%)</td>
<td>18 (30%)</td>
</tr>
<tr>
<td>Aphids mummified in fourth instar with short wingpads as shown in Fig. 11.4C</td>
<td>11 (18%)</td>
<td>32 (52%)</td>
</tr>
</tbody>
</table>
the fourth instar invariably developed into normal alatae no matter how early in the instar they were parasitized.

11.3 EFFECTS OF PARASITIZATION OF DIFFERENT INSTARS/MORPHS OF THE HOST ON THE PARASITE

11.3.1 Materials and Methods

All test aphids were obtained directly from the aphid stock culture. Seven instars/morphs were recognized: N₁, N₂, N₃, N₄ apt., N₄ al., A apt., and A al. The parent parasites used were 1-2 days post-emergent, mated adult females from the parasite stock culture. The experiment was carried out in the insectary at 22-25°C, 14L:10D and 50-60% R.H.

Thirty aphids of a given instar/morph were placed onto young leaves set flat in an inverted plastic jar and allowed to settle down for 1 h. A single female parasite was then introduced and allowed to oviposit for a 3 h period. There were four jars for each of the three younger instars: N₁, N₂ and N₃, and six jars for each of the remaining four instars/morphs.

Immediately after the female parasite was removed, aphids in each jar were transferred into a caged pot containing one flowering shoot where they were reared until all the parasitized aphids had been mummified. All mummies of a given instar/morph were collected from the flowering shoots and kept in a 8 x 4 cm clear plastic vial except for N₁ and N₃ where the mummies were kept individually in 4 x 1 cm glass tubes. The vials and tubes were examined daily and any adults found were recorded and removed. Unproductive mummies were dissected at a later date to determine mortality during the pupal stage (About 5% of the parasites entered diapause, these individuals were not considered in subsequent analyses).

To determine the body size and the number of eggs of newly emerged female parasites, 30 adult females reared from each of the seven
instars/morphs were killed in ethanol, measured and dissected on the day they emerged. Measurements of body size were restricted to the maximum head width (to the outer edges of eyes) seen through a stereomicroscope equipped with an ocular micrometer, thus allowing precision to the nearest 0.01 mm. To count the number of eggs, females were first dissected in Ringer's solution to remove their ovaries which were further dissected in 1% acid fuchsin (Fig. 11.5). As most eggs appeared to be mature (spindle-shaped) and it seemed difficult to distinguish between mature and immature eggs, all eggs found were counted. For N₁ and N₃, the abdominal width of the mummy was also measured for each adult female dissected.

11.3.2 Results and Analysis

Developmental time, mortality during immature stages, head width and number of eggs on the day of emergence of the parasites reared from different instars/morphs are presented in Table 11.6.

(i) Sex Ratio and Developmental Time

The proportion of female parasites obtained from different instars/morphs varied from 67% to 75%. However, since no attempt was made to standardize the mating of the parents used to start the experimental cultures (e.g. the supply of sperm is gradually reduced with successive matings of males, see Stary 1970, p. 74), the observed differences in sex ratio were not compared. The mean developmental times of both male and female produced from different host instars/morphs were not significantly different (in male, F = 1.34, d.f. = 6/119, P > 0.05; in female, F = 1.66, d.f. = 6/325, P > 0.05).

(ii) Mortality During Immature stages

The data on mortality during egg-larval stages presented in Table 11.6
Fig. 11.5. Eggs in the ovaries (x 90) of adult female of *A. sonchi* dissected in 1% acid fuchsin.
Table 11.6 Development time, mortality in immature stages, head width and number of eggs on the day of adult emergence of *A. sonchi* in relation to host instars/morphs attacked

<table>
<thead>
<tr>
<th>Host instar/morph attacked</th>
<th>Mean development time in days ± S.D. (N)</th>
<th>% mortality in immature stages</th>
<th>Attributes of adult female</th>
<th>Mean head #</th>
<th>Mean no. of eggs ± S.E.</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td>egg-larva (N)* pupa (N)</td>
<td>total</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N₁</td>
<td>11.2 ± 0.78 (24)</td>
<td>11.5 ± 0.97 (52)</td>
<td>6.0 (117)</td>
<td>3.8 (78)</td>
<td>9.8</td>
<td>22.6 ± 0.2 d 168.3 ± 9.5</td>
</tr>
<tr>
<td>N₂</td>
<td>11.0 ± 0.65 (28)</td>
<td>11.2 ± 0.82 (57)</td>
<td>3.6 (112)</td>
<td>2.3 (87)</td>
<td>5.9</td>
<td>24.4 ± 0.2 c 189.5 ± 10.2</td>
</tr>
<tr>
<td>N₃</td>
<td>10.9 ± 0.76 (20)</td>
<td>11.1 ± 0.78 (62)</td>
<td>3.2 (63)</td>
<td>2.4 (84)</td>
<td>5.6</td>
<td>25.2 ± 0.2 ab 198.1 ± 10.4</td>
</tr>
<tr>
<td>N₄apt.</td>
<td>11.1 ± 0.79 (14)</td>
<td>11.4 ± 0.84 (48)</td>
<td>6.7 (75)</td>
<td>3.1 (64)</td>
<td>9.8</td>
<td>25.5 ± 0.2 a 179.1 ± 9.7</td>
</tr>
<tr>
<td>N₄al.</td>
<td>11.0 ± 0.62 (13)</td>
<td>11.3 ± 0.69 (41)</td>
<td>8.7 (46)</td>
<td>3.6 (56)</td>
<td>12.3</td>
<td>24.8 ± 0.2 bc 172.1 ± 9.8</td>
</tr>
<tr>
<td>Aapt.</td>
<td>10.9 ± 0.74 (15)</td>
<td>11.1 ± 0.75 (37)</td>
<td>15.9 (69)</td>
<td>3.7 (54)</td>
<td>19.6</td>
<td>24.9 ± 0.2 abc 178.0 ± 11.7</td>
</tr>
<tr>
<td>Aal.</td>
<td>11.2 ± 0.84 (12)</td>
<td>11.4 ± 0.89 (35)</td>
<td>24.2 (33)</td>
<td>4.1 (49)</td>
<td>28.3</td>
<td>24.4 ± 0.3 c 165.1 ± 9.1</td>
</tr>
</tbody>
</table>

* Data on mortality during egg-larval stages were derived from the experiment described in 11.2.1.

# Head widths are presented in units, 50 units = 1.00 mm. Figures followed by the same letter are not significantly different at the 5% level according to Duncan's multiple range test.
were derived from the experiments on the effects of parasitization on the aphid (12.2.1) where parasitized aphids were reared individually under two temperature-light regimes. The incorporation of the data into the results of the present experiment seems reasonable, as the two temperature-light regimes are close to the experimental conditions used here and well within the favourable range (see Chapter 13). The percent mortality presented takes into account any parasitized aphid which failed to yield a mummy. The mortality was consistently low when parasitization began before the aphids reached the fourth instar, but increased steadily thereafter with the age of the aphid attacked. Such an increase was largely due to the increasing proportion of natural deaths of the aphids which occurred before mummification could take place. Thus the mortality during egg-larval stages will increase further if aged adults are parasitized.

The mortality during the pupal stage presented in Table 11.6 includes all dead individuals found in the aphid mummy, either a dead mature larva, a pupa, or an adult which failed to emerge. There was no apparent difference in this attribute between the parasites reared from different instars/morphs.

Overall it can be inferred that mortality during the immature stages of the parasite was the lowest when parasitization began with instars 2 and 3, increased slightly with instars 1 and 4, and became substantial when adults were parasitized.

(iii) Body Size and Number of Eggs in the Ovaries of Adult Females

The head widths of adult females produced from different aphid instars/morphs were significantly different (F = 18.57, d.f. = 6/203, P < 0.01). Assuming that head width is a good indicator of the body size (see Southard et al. 1982), the females produced from *N* 4 apt. were the largest among the seven cohorts, and those produced from *N* 1 were the smallest (Table 11.6).
Fig. 11.6. Relationship between abdominal width of mummy and the head width of the resultant adult female of *A. sonchi*; measurements are presented in units, 50 units = 1.00 mm; open circle, host instar 1 and solid circle, instar 3.

Fig. 11.7. Comparison of host instar "preference" for oviposition in *A. sonchi* and the mean number of eggs of adult female parasites produced from different instars/morphs.
Fig. 11.8 Relationship between head width and number of eggs on the day of emergence in adult females of A. sonchi produced from different host instars/morphs.
As the head widths of the parasites were highly positively correlated with the abdominal widths of the mummies in the two instars investigated ($r^2 = 0.91$, d.f. = 59, $P < 0.001$; Fig. 11.6), the differences in parasite head width between host instars/morphs were presumably due largely to the different aphid size at the time when the parasite was in its fourth larval instar.

The number of eggs per female varied widely within each cohort, ranging from 100 to 300. Consequently no significant differences were revealed among the means by analyses of variance ($F = 1.66$, d.f. = 6/203, $P > 0.05$). However, subsequent analyses showed that there is a positive correlation between the host instar "preference" of the parasite (11.4, Fig. 11.9) and the mean number of eggs per female produced from different instars/morphs (Fig. 11.7). In fact, the mean number of eggs in $N_3$ (the instar with the highest probability to be attacked) is significantly higher than the mean number of eggs in Aal. (the instar with the lowest probability to be attacked, $t = 2.18$, d.f. = 58, $P < 0.05$) and that in $N_1$ ($t = 1.94$, d.f. = 58, $P < 0.05$), as judged by t-test.

The correlation between head width and the number of eggs was rather poor in every host instar/morph (Fig. 11.8), though there appeared to be a general tendency for larger females to have more eggs. When the relationship between the two attributes of the adult female was examined over the whole range of host instars/morphs, head width was indeed very poorly correlated with the number of eggs (Table 11.6). For example, the mean head widths between the female parasites from $N_1$ and those from Aal. differed significantly, yet the mean numbers of eggs in the two cohorts of parasites were very similar.
11.4 HOST INSTAR SELECTION BY AND SEARCHING BEHAVIOUR OF THE PARASITE

11.4.1 Introduction

In studies of aphids and their parasites, experiments are often performed to find out the host instar "preference" of the parasite. Generally, instars 2 and 3 (less often instar 4) have been found to be parasitized more frequently than other instars (e.g. Singh and Sinha 1982; see review by Stary 1970). Stary (1970) tries to relate such observed "preference" to fitness* of the parasite. Little attempt has been made, however, to associate such "preference" with other aspects of the behaviour of a parasite in relation to its hosts. With the exception of Hafez (1961) working on Diaeretiella rapae and its host aphid Brevicoryne brassicae, most workers go little further than to show that the distribution of attacks among aphids of different instars/morphs is non-random. However, Rogers (1972) has pointed out that while a Poisson distribution is unlikely to occur if the search is non-random, other types of egg distributions do not rule out random searching as the basic behaviour.

Experiments carried out here were aimed to investigate the host instar selection of A. sonchi. At the same time, the frequency distributions of parasite eggs among different instars/morphs were used to examine the searching behaviour of the parasite. The results of the searching behaviour analysis, together with the results of direct observations on the behavioural interaction between the aphid and the parasite (10.6.1) were then used to explore explanations for the observed differential attack on different host instars/morphs.

11.4.2 Materials and Methods

The test aphids used were collected from the aphid stock culture. Again,

* In the sense used here, fitness is defined as the short-term capability of an individual or population to survive and leave viable progeny.
seven instars/morphs were recognised (see 11.3.1). For Aapt. and Aal., care was taken to use newly moulted individuals (obtained by inspecting large number of fourth instar nymphs placed on detached young leaves and collecting new adults at 2 h intervals), so that very few or no young were produced during the exposure period.

Female parasites used were obtained in the following way. Mummified aphids were collected from the parasite stock culture prior to each test and held in glass tubes in the test environment until the adult parasites emerged. Both males and females were then kept in 10 x 20 cm clear plastic guaze-ended containers for an additional 24 h (12L:12D). During this time the parasites were provided with water, honey and some aphids and the females were mated and had started oviposition. All the females used were taken without bias from the container towards the end of the 12 h dark period. This procedure reduced the chance that any intensified ovipositional urge would override the preference of the parasite, yet intensive oviposition activity could be expected during the test exposure as oviposition in this parasite was most frequent during the early part of the light period of each day (see 10.6.2).

**Exposure techniques.** Aphids of the seven instars/morphs were exposed either separately or together (see below) in inverted clear plastic jars each with two or three young leaves set flat onto the surface (about 28 cm²) of nutrient agar. After being transferred to the jar, the aphids were allowed to settle for 30 minutes before a parasite was introduced. Each test exposure lasted 3 h under constant illumination in the temperature-controlled room held at 22°C, 60-70% R.H.

**Assessment techniques.** After 3 h the parasite was removed and the aphids were held under the experimental conditions for a further 72-80 h (in
cases where aphids of the seven instars/morphs were exposed together, they were separated into seven similar jars immediately after the removal of the parasite). The aphids were then dissected and the presence and number of parasite larvae were recorded. Preliminary observations showed that in cases where superparasitization took place on the same day, all eggs hatched and although only one larva finally matured, the relics of the other larvae remained up to about the end of the second instar of the survivor, i.e. about 90 h after oviposition (see 10.2). The numbers of eggs laid in each aphid in the experiments were therefore assumed to be equal to the numbers of larvae seen in the dissections.

Experimental design and replication. Two series of tests were carried out. In the first, groups of 28 individuals of each of the seven instars/morphs were exposed to parasites. There were five replicates for each instar/morph. This series was designed to estimate the intrinsic mean number of eggs laid in each instar/morph, and the nature of the distribution of eggs between individual aphids in a jar. This series is referred to as Experiment 1.

In the second series of tests, groups of 28 aphids made up of four individuals of each of the seven instars/morphs were exposed to parasites. There were sixteen replicates in this series of tests. This series was designed to estimate any modifications of the mean numbers of eggs laid in individuals of each instar/morph when they were presented together, and the nature of the distributions of eggs between individuals in each instar/morph. This series is referred to as Experiment 2.

It was impossible to carry out all the replicates of both experiments at the same time, so replicates were split into two blocks a week apart.
11.4.3 Results and Analysis

The frequency distributions of parasite eggs recorded in Experiment 1 and Experiment 2 are presented in Tables 11.7 and 11.8 respectively. In both experiments, most aphids received 0, 1, or 2 eggs, with a few aphids having large numbers (up to 8 and 11).

A low level of mortality (about 4%, shown by the unequal sample sizes in Tables 11.7 and 11.8) occurred among the test aphids. In subsequent statistic analysis, the individuals which died before dissection were assumed to have the same probability of being attacked by the parasite as the remaining aphids in the same replicate.

(1) Analysis for Instar Preference

The mean numbers of eggs received per aphid among different instars/morphs in the two experiments are presented in Table 11.9 and Fig. 11.9. In both experiments, differences between instars/morphs were obvious. For example, in Experiment 2, aphids of instar 3 received on average 2.310 eggs, while the alate adults had only 0.118 eggs per individual. From the results, it can be inferred that female *A. sonchi* oviposit in third, second, first and fourth instar apteriform nymphs in preference to fourth instar alatiform nymphs and adults. Liu, Morton and Hughes (in preparation) further show that instar differences are not the same between the two experiments: in Experiment 2, there was a higher probability that N3, N4apt., N4al. and Aapt. would be parasitized, while the probability for N1, N2 and Aal. was reduced.
Table 11.7  Distribution of eggs of *A. sonchi* among host aphids (*H. lactucae*) of different instars/morphs in Experiment 1

<table>
<thead>
<tr>
<th>Aphid instar</th>
<th>No. aphids tested</th>
<th>0 egg</th>
<th>1 egg</th>
<th>2 eggs</th>
<th>3 eggs</th>
<th>4 eggs</th>
<th>5 eggs</th>
<th>6 eggs</th>
<th>7 eggs</th>
<th>8 eggs</th>
<th>df</th>
<th>X²</th>
<th>P#</th>
</tr>
</thead>
<tbody>
<tr>
<td>N₁</td>
<td>127</td>
<td>32</td>
<td>41</td>
<td>29</td>
<td>11</td>
<td>9</td>
<td>3</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td>122</td>
<td>138.30</td>
</tr>
<tr>
<td>N₂</td>
<td>135</td>
<td>26</td>
<td>37</td>
<td>34</td>
<td>19</td>
<td>7</td>
<td>5</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td></td>
<td>130</td>
<td>186.04</td>
</tr>
<tr>
<td>N₃</td>
<td>139</td>
<td>36</td>
<td>50</td>
<td>25</td>
<td>11</td>
<td>7</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td></td>
<td></td>
<td>134</td>
<td>202.99</td>
</tr>
<tr>
<td>N₄apt.</td>
<td>140</td>
<td>59</td>
<td>54</td>
<td>21</td>
<td>4</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>135</td>
<td>129.53</td>
</tr>
<tr>
<td>N₄al.</td>
<td>136</td>
<td>68</td>
<td>51</td>
<td>12</td>
<td>4</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>131</td>
<td>130.47</td>
</tr>
<tr>
<td>Aapt.</td>
<td>130</td>
<td>59</td>
<td>42</td>
<td>22</td>
<td>6</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>125</td>
<td>129.39</td>
</tr>
<tr>
<td>Aal.</td>
<td>138</td>
<td>83</td>
<td>43</td>
<td>9</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>133</td>
<td>135.50</td>
</tr>
</tbody>
</table>

# Values of one-tail probability: small P means underdispersed, i.e. contagious; large P means overdispersed. Thus values of P less than 0.05 or larger than 0.95 can be taken as evidence of departure from random distribution (indicated by **).
Table 11.8  Distribution of eggs of *A. sonchi* among host aphids (*H. lactuca*) of different instars/morphs in Experiment 2

<table>
<thead>
<tr>
<th>Aphid instar</th>
<th>No. aphids tested</th>
<th>No. aphids with</th>
<th>X²-test*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 egg</td>
<td>1 egg</td>
<td>2 eggs</td>
</tr>
<tr>
<td>N₁</td>
<td>60</td>
<td>14</td>
<td>23</td>
</tr>
<tr>
<td>N₂</td>
<td>60</td>
<td>11</td>
<td>22</td>
</tr>
<tr>
<td>N₃</td>
<td>59</td>
<td>10</td>
<td>16</td>
</tr>
<tr>
<td>N₄ apt.</td>
<td>61</td>
<td>17</td>
<td>22</td>
</tr>
<tr>
<td>N₄ al.</td>
<td>60</td>
<td>25</td>
<td>21</td>
</tr>
<tr>
<td>A apt.</td>
<td>51</td>
<td>24</td>
<td>13</td>
</tr>
<tr>
<td>A al.</td>
<td>48</td>
<td>40</td>
<td>7</td>
</tr>
</tbody>
</table>

* Since there are only 4 individuals of each instar in each replicate, the X²-test excludes those replicates in which either no eggs were found or more than one aphid died before dissection. For instar 3, the three replicates in which aphids received excessively high number of eggs were also excluded from the test.

# Values of one-tail probability, for explanation, see Table 11.7.
Table 11.9  Mean number of eggs laid per aphid by *A. sonchi* in relation to different instars/morphs of its host, *H. lactucae*, in two experiments.

<table>
<thead>
<tr>
<th>Aphid instar</th>
<th>Expt 1</th>
<th>Expt 2</th>
<th>Expt 2 – Expt 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>N₁</td>
<td>1.535</td>
<td>1.283</td>
<td>-0.252</td>
</tr>
<tr>
<td>N₂</td>
<td>1.948</td>
<td>1.767</td>
<td>-0.181</td>
</tr>
<tr>
<td>N₃</td>
<td>1.583</td>
<td>2.310</td>
<td>+0.727</td>
</tr>
<tr>
<td>N₄apt.</td>
<td>0.821</td>
<td>1.475</td>
<td>+0.654</td>
</tr>
<tr>
<td>N₄al.</td>
<td>0.669</td>
<td>0.850</td>
<td>+0.181</td>
</tr>
<tr>
<td>Aapt.</td>
<td>0.831</td>
<td>0.941</td>
<td>+0.110</td>
</tr>
<tr>
<td>Aal.</td>
<td>0.514</td>
<td>0.188</td>
<td>-0.326</td>
</tr>
<tr>
<td>All instars combined</td>
<td>1.139</td>
<td>1.294</td>
<td>+0.155</td>
</tr>
</tbody>
</table>

Fig. 11.9. Mean number of eggs laid per host aphid by adult females of *A. sonchi* in relation to different instars/morphs in two experiments: Experiment 1 – without choice; Experiment 2 – with choice.
(ii) Analysis of Searching Behaviour as Reflected by the Frequency Distributions of Parasite Eggs

In the simple experimental setup used, there are potentially three ways in which the eggs can be distributed by a searching parasite:

(a) If the parasite places each egg independently of the placement of the other eggs, each aphid is then equally likely to receive a particular egg and the distribution of eggs in the population will have a Poisson expectation, i.e. be random;

(b) If the parasite is more likely to place each egg in aphids which have received one or more eggs, i.e. some aphids are favoured by the parasite, the distribution of eggs will be contagious;

(c) If the parasite oviposits in a systematic way, thus avoiding aphids in which there is an egg already, the distribution of eggs will be overdispersed.

It can be seen that the Poisson distribution lies between the other two. Thus, the analyses should be based on the sample variance:

$$s^2 = \frac{1}{n-1} \sum_{j=1}^{n} (x_j - \bar{x})^2$$

If the distribution of eggs is random (a), the variance $s^2$ has an expectation equal to the mean $\bar{x}$, while the other two distributions will give either a larger (b) or a smaller (c) variance. Therefore, the actual test can be based on the chi-square statistic for each replicate (Liu, Morton and Hughes, in preparation):

$$\chi^2 = \frac{n}{\bar{x}} \sum_{j=1}^{n} (x_j - \bar{x})^2 / \bar{x}$$

Summing over the replicates, the total of the chi-square statistic
\[ x^2 = \sum_{i=1}^{k} x^2_{(n-1)} \]

can be used in a two-tailed test for positive (b) and negative (c) departure from the Poisson expectation.

For the data of Experiment 1, \( x^2_{(n-1)} \) is calculated separately for each of the five replicates of a particular instar/morph. The sum of the chi-square statistic for each instar/morph and the test results are shown at the right-hand side of Table 11.7. For five of the seven cases, the female parasites distributed their eggs in ways indistinguishable from random. The exceptions were for N2 and N3, where the numbers of eggs laid in a small proportion of the hosts were rather large.

For the data of Experiment 2, \( x^2_{(n-1)} \) is calculated separately for each instar/morph group (4 individuals) within each of the 16 replicates and the values for a particular instar/morph were summed over all replicates. The results are shown at the right-hand side of Table 11.8. In all cases the distribution of eggs within aphids of the same instar/morph could not be distinguished from a random distribution.

With Rogers' (1972) comments in mind, it seems reasonable to conclude that:

(a) The parasites searched for hosts at random;

(b) As a result of (a), the parasites allocated their eggs randomly when each individual within the area being searched has a similar susceptibility of being attacked; and

(c) In an environment with aphids showing different susceptibility, the parasites laid their eggs without bias among similar hosts.
11.5 DISCUSSION

11.5.1 Effects of parasitization of different instars/morphs on the relative fitness of the aphid and the parasite

Parasitization of aphids by the aphidiids results in the host's organs and tissues being gradually affected, destroyed and finally consumed by the parasite larva. The various biochemical and physiological effects produced by the developing parasite appear gradually, and the parasitized aphid continues to feed, grow and reproduce more or less normally until the parasite larva inside reaches its destructive feeding phase, commonly at the beginning of the third or fourth instar (Cloutier and Mackauer 1979; Couchman and King 1979; Soldan and Stary 1981; Stary 1970). Thus, there is a time lag between the beginning of parasitization and the times at which effects of parasitization on development and reproduction of the host become evident. The results obtained in this study showed that when *H. lactucae* was parasitized by *A. sonchi*, reproduction of the aphid was not affected until the parasite inside had completed 30% of its development (presumably at the beginning of the third instar), while developmental rate of the host, as indicated by the process of moulting, was not affected until the parasite had completed about 40% of its development (presumably at the beginning of the fourth instar). However, the wing differentiation of the host was affected and inhibited by the parasite very early during the development of the parasite, apparently beginning in the egg stage, as almost all alatiform aphid nymphs parasitized in the first instar had no wingpads when they reached the third instar (*cf.* Johnson 1959).

The data obtained on the consequences of parasitization of different instars/morphs on the parasite showed that although *A. sonchi* could develop successfully into the adult stage in all development stages of *H. lactucae*,
host age at the time of oviposition as well as host morph affected the probability of survival, final size and potential fecundity of the parasite. From the results obtained, it appeared clear that both survival and body size of the parasite were largely determined by the same attributes of the host. However, the effects of host on the potential fecundity of the parasite seemed rather subtle: while the number of eggs in the ovaries of the parasites upon emergence was poorly correlated with their own body size, the same attribute was found to be positively correlated with the observed host instar "preference" of the parasite. With the data obtained, it seems very difficult to speculate on the mechanisms involved.

The host instar-dependent effects of parasitization on the relative fitness of both the aphid and the parasite has a consequence that the degree of impact of *A. sonehi* on the population dynamics of *H. lactucae* is effectively influenced by the host instar preference of the parasite. Since the times when various lethal effects on the host occur are largely a function of the durations of the developmental stages of the parasite and aphids of first instar seem to endow greater fitness to the parasite than adults, any relative shift of preference to younger instars for oviposition will increase the impact of the parasite on the aphid population growth. Indeed, the analysis on the relationship between host instar attacked and the achieved intrinsic rate of increase (Fig. 11.3) shows that the host stage at the beginning of parasitization is crucial in determining the consequence of parasitization. Thus, any simple comparison of the potential for population increase, e.g. a comparison of the values of intrinsic rate of increase *r_m*, between the aphid and the parasite will offer very little knowledge about the potential impact of the parasite on the growth of aphid population (*cf.* Messenger 1964a).
11.5.2 Evidence for host instar preference of the parasite in relation to searching behaviour

In the experiments carried out in this study, more eggs were laid by *A. sonchi* in aphids of instars 2 and 3 than in aphids of (particularly) later stages. This fits in with the general pattern of parasite/aphid interactions and since these two instars were found to be the most favourable for the survival and fecundity of *A. sonchi* the data seem to lend support to Stary's (1970) contention of the condition of preference.

However, the analyses on the frequency distributions of parasite eggs show that the parasite searches for hosts randomly. In that case the larger the host the more likely it is to be found. This is probably why more eggs were laid in the second instar than in the first. However, in aphids of later instars, the mechanical defence of the aphid (10.6.1) becomes effective in preventing oviposition by the parasite. The effectiveness of such reactions is apparently correlated with the size of the potential host, and thus could account at least in part for the decline in the number of eggs laid in later (larger) instars. Thus, the frequency distributions of eggs alone do not reflect the preference of the parasite. However, the behaviour of random search suggests that *A. sonchi* appears to have evolved a preference for relatively large hosts. Since this tendency is countered by the aphid response, the overall interaction results in more eggs being laid in instars which endow the parasite with greater fitness (cf. Hafez 1961).

The argument presented above suggests that in *A. sonchi* host acceptance is more flexible than optimality for the development of the immature stages might suggest (cf. Mackauer 1973). Such behavioural flexibility was further reflected by the evidence summarized in Table 11.9 and Fig. 11.9: relatively
more eggs were laid in less suitable instars/morphs when there was no choice. Furthermore, the observations made on the interaction between *A. sonchi* and *M. euphorbiae* (10.11) showed that an aphid's lack of suitability for development does not prevent oviposition.

Such host instar tolerance and errors of host selection in *A. sonchi* may be advantageous to the parasite in the context of "spreading of risk" of the species' extinction (den Boer 1968). Relaxation of instar preference may be an important attribute for the parasite's success as the age structure of the host populations in natural environment changes continuously. Parasitization of late instar alatiform nymphs and alatae may help the parasite to disperse in the field. As Mackauer (1973) suggests, flexibility in host acceptance by the female parasite may provide a further advantage "in so far as it ensures that species or strains that (in the course of their evolution) become suitable as hosts will be explored".

### 11.5.3 Production of random distributions of parasite eggs

Rogers (1972) limits the production of random egg distributions to parasites searching at random and depositing one egg at each and every encounter with a host individual. As mentioned in Chapter 10 and above, ovipositing females of *A. sonchi* are frequently kicked or knocked away by aphids of advanced instars. Undoubtedly, such reactions from the aphid will result in lower numbers of eggs laid than the number of encounters. This was reflected by the variations in the mean numbers of eggs laid in different instars/morphs in the present experiment when aphids of different instars/morphs were exposed separately. However, the distributions of parasite eggs among aphids of later instars were, in every case, indistinguishable from random (Table 11.7). The results therefore indicate that the distribution of parasite eggs among hosts will be random if:
(1) The parasite searches at random;
(2) The parasite lays her eggs one at a time; and
(3) Each host within the area being searched has a similar susceptibility to be attacked.
CHAPTER 12
EFFECT OF HOST DENSITY ON FECUNDITY, REPRODUCTIVE RATE AND ADULT LIFE SPAN OF APHIDIUS SONCHI, WITH AN ADDITIONAL ANALYSIS OF THE FUNCTIONAL RESPONSE OF THE PARASITE TO HOST DENSITY

12.1 INTRODUCTION

Experimental evidence has shown that a number of basic attributes of adult female parasites, such as life span, fecundity, progeny sex ratio, searching behaviour, etc., may vary widely with different host densities (e.g. Cook & Hubbard 1980; Force & Messenger 1964b; Mackauer & van den Bosch 1973). This chapter describes experiments on the effect of host density upon fecundity, reproductive rates and adult life span of A. sonchi. Attention will also be directed to the phenomenon that the relationship between host density and the average number of hosts parasitized per unit time by an individual parasite, i.e. the functional response of the parasite to host density, may vary with adult age.

12.2 MATERIALS AND METHODS

Aphids used in the experiments were second and third instar nymphs drawn directly from the aphid stock culture.

The adult female parasites used were obtained and standardized in the following way. Twelve hours before the female parasites were to be introduced to the test aphids, large numbers of mummies containing near-emergent parasites were collected from the parasite stock culture. These mummies were kept under the experimental conditions (22°C, see below) in 10 x 20 cm clear plastic gauze-ended containers and provided with honey and water. Each female used was taken without bias from the containers 0-12 h after emergence and was accompanied by a male parasite during the first 24 h period of the oviposition test.
The oviposition tests were carried out in environmental cabinets under 22°C, 14L:10D and 70-90% R.H., using the caged pots each containing one flowering shoot as the experimental unit. The aphid densities used were 5, 10, 25, 50, 100 and 200, with five replicates at each density (Hereafter, all the figures referring to host density are used in the sense of the number of aphids per pot). The aphids were placed into each caged pot 2-6 h before the introduction of the female parasites.

Experiments with the six aphid densities were started on the same day. Each female parasite was introduced into a caged pot with a predetermined number of aphid nymphs. Twenty-four hours later the female parasite was withdrawn from the first caged pot and transferred to another with a fresh batch of hosts at the same density. This was repeated each day until the female parasite died. Each day's batch of aphids was reared in the caged pots under the experimental conditions for a further 60-72 h period, after which time the aphids were dissected and number of parasite larvae in each aphid was recorded. Since the numbers of parasite larvae recorded this way approximate very closely to the actual numbers of eggs laid (10.2), the records were used to calculate the number of eggs laid and the number of hosts parasitized in each case.

12.3 RESULTS AND ANALYSIS

12.3.1 Fecundity

In this host-parasite system, only one parasite can develop successfully to the adult stage in each aphid, the supernumerary ones die in the first or second larval instar (10.2). Thus, the number of eggs laid and that of aphids parasitized represent two different measurements of fecundity. In effect, only the number of aphids parasitized constitutes the true potential fecundity at each host density. The number of eggs laid is of
value, however, in providing an estimate of the maximal oviposition of the parasite in each situation. Therefore, the effects of host density on both the number of eggs laid and the number of aphids parasitized have been analyzed, and the relationship between the two measurements shown whenever appropriate.

For both the eggs laid and the aphids parasitized the mean total numbers per female parasite increased with host density (Table 12.1, Fig. 12.1). The patterns of increase decelerated towards a limit apparently imposed by the parasite's egg supply. The numbers of eggs laid per female were very similar at host densities of 50, 100 and 200 per day. However, since *A. sonchi* females search for hosts at random (Chapter 11), an increase of host density will always decrease the extent of superparasitization. This was shown by the lower mean number of eggs laid per aphid parasitized at higher host densities in the present experiment (Fig. 12.1). However, because of the nature of random egg allocation, the decrease became negligible at high host densities and the mean numbers of aphids parasitized by the females at the host densities of 100 and 200 per day were very similar.

Table 12.1  Effect of host density on oviposition activity and life span of *A. sonchi* at 22°C, 14L:10D and 70-90% R.H.; figures shown in the table are mean values per female parasite

<table>
<thead>
<tr>
<th>Events</th>
<th>Number of aphid nymphs provided each 24 h</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5</td>
</tr>
<tr>
<td>Total number of nymphs exposed</td>
<td>22</td>
</tr>
<tr>
<td>Percentage of exposed nymphs parasitized</td>
<td>70.5</td>
</tr>
<tr>
<td>Total number of eggs laid</td>
<td>54.9</td>
</tr>
<tr>
<td>Total number of nymphs parasitized</td>
<td>15.5</td>
</tr>
<tr>
<td>Mean number of eggs received per parasitized aphid</td>
<td>3.5</td>
</tr>
<tr>
<td>Adult life span in days</td>
<td>4.0</td>
</tr>
</tbody>
</table>
Fig. 12.1  Mean adult life span of, mean numbers of eggs laid and aphids parasitized by *A. sonahi* with various host densities at 22°C, 14L:10D, together with the mean number of eggs received per parasitized aphid. All filled and unfilled circles are observed values, and the curves are fitted by eye.
Table 12.2  Survival of, number of eggs laid and aphids parasitized by *A. sonchi* with different aphid density at 22°C, 14L:10D and 70-90% R.H.

<table>
<thead>
<tr>
<th>Host density</th>
<th>Adult age in days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td>(1) Number of ovipositing females surviving to the end of each day</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td>25</td>
<td>5</td>
</tr>
<tr>
<td>50</td>
<td>5</td>
</tr>
<tr>
<td>100</td>
<td>5</td>
</tr>
<tr>
<td>200</td>
<td>5</td>
</tr>
<tr>
<td>(2) Mean number of eggs laid per female ± S.E.*</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>14.0±1.1</td>
</tr>
<tr>
<td>10</td>
<td>21.4±1.5</td>
</tr>
<tr>
<td>25</td>
<td>39.2±6.8</td>
</tr>
<tr>
<td>50</td>
<td>56.2±5.2</td>
</tr>
<tr>
<td>100</td>
<td>71.8±5.2</td>
</tr>
<tr>
<td>200</td>
<td>97.8±5.5</td>
</tr>
<tr>
<td>(3) Mean number of aphids parasitized per female ± S.E.*</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>4.3±1.1</td>
</tr>
<tr>
<td>10</td>
<td>8.0±1.5</td>
</tr>
<tr>
<td>25</td>
<td>16.2±1.8</td>
</tr>
<tr>
<td>50</td>
<td>30.4±5.5</td>
</tr>
<tr>
<td>100</td>
<td>48.2±2.4</td>
</tr>
<tr>
<td>200</td>
<td>72.5±3.0</td>
</tr>
</tbody>
</table>

* Figures are mean values of the females which oviposited in each day and also survived to the end of that day, i.e. the numbers of females shown under (1).
Fig. 12.2 Mean numbers of eggs laid and aphids parasitized by *A. sonchi* at different host densities at 22°C, 14L:10D.
12.3.2 Reproductive Rate

The distributions between days of both the numbers of eggs laid and the numbers of aphids parasitized by the female parasites are shown in Table 12.2 and Fig. 12.2. Here, the two different measurements give two different estimates of reproductive rates, i.e. the apparent maximal oviposition rate and the true reproductive rate. As in the case of fecundity, reproductive rates increased with host density. At the three highest host densities (i.e. 50, 100 and 200), where the total numbers of eggs laid per female were similar, both the numbers of eggs laid and the numbers of aphids parasitized on the first day of adult life were higher at higher host densities.

12.3.3 Adult Life Span

In contrast to changes in fecundity and reproductive rates, adult life span of the female parasites was more or less independent of host density (Table 12.1, Fig. 12.1).

12.3.4 Functional Response

Preliminary plotting of the mean number of eggs laid and the mean number of aphids parasitized per female per day calculated from the lifetime totals of each female parasite against host density indicated that, overall, *A. sonchi* shows a typical type 2 functional response proposed by Holling (Holling 1959a), i.e. the response rises at a continually decreasing rate (see Fig. 12.3). This type of response is usually described by the familiar "disc equation" of Holling (1959b), namely:

\[ N_a = \frac{a'T_h N_0}{1+a'T_h N_0} \]

where \( N_a \) = number of hosts attacked; \( N_0 \) = number of hosts available; \( T_t \) = total time that host and parasite(s) are exposed to each other;
a' = a constant, the "rate of parasite search"; $T_h$ = a constant, the "handling time" per host.

The assumptions implicit in this equation are discussed by Royama (1971) and Rogers (1972). As these authors point out, since this equation does not allow for the effect of the exploitation of the host population during the experimental period, it will not apply to situations where the hosts available for attack decrease with time, e.g. where the parasites avoid superparasitization. It will apply, however, if the hosts are continually replenished as they are exploited. In other words, the disc equation will yield accurate estimates of the instantaneous coefficients, $a'$ and $T_h$, of a function response from experimental data if the actual encounters of the parasite with a constant host density are scored (see Hassell 1978, pp. 32-33).

In this experiment, female parasites were each provided with a given number of the second and third instar aphid nymphs each 24 h period. Direct observations showed that aphid nymphs of these two instars are almost always attacked successfully by the parasite (i.e. the aphid receives a parasite egg) when encountered. Since the parasite lays only one egg during each oviposition act (10.6.1) and places each egg independently of the placement of any other eggs (11.4.3), the disc equation provides a good model for analyzing the functional response of the parasite in this simple experimental setup if the number of eggs laid ($N_e$) is substituted for the number of aphids attacked in the equation, that is,

$$N_e = \frac{a'T_hN_o}{1+a'T_hN_o}$$

As is evident from the upper curve of Fig. 12.3, the equation fits the data well ($X^2_5 = 1.61$, $P = 0.90$). From the fitted equation the rate of search may be calculated as 3.4264 and the handling time as 0.017686. However, since *A. sonchi* is essentially day-active (10.6.4), the above
values were corrected for the photoperiod of 14 h (0.58 days), which gave 
\( a' = 5.9076 \text{ cage}^{-1} \text{ day}^{-1} \) and \( T_h = 0.01026 \text{ days (or 14.77 minutes)} \). And, once 
again, as the parasite oviposits at random, the number of hosts parasitized 
can be predicted by Thompson's (1939) random oviposition equation when the 
number of eggs laid is known. The random oviposition equation has the form:

\[
N_p = N_0 (1 - \exp(-N_e/N_0))
\]

the terms involved being the same as in the disc equation. When the disc 
equation for predicting \( N_e \) is incorporated, the equation becomes:

\[
N_p = N_0(1-\exp(Ta'/(1+a'ThN_0)))
\]

This is the familiar "random parasite equation" proposed by Messenger (1968) 
and Rogers (1972). When the estimated functional response coefficients are 
substituted into the equation, predictions of the numbers of aphids parasi-
tized agree closely with the observed values (Fig. 12.3, lower curve; 
\( X^2_5 = 1.45, P = 0.92 \)).

Whereas the disc equation and random parasite equation fit the data 
well, it does not follow that the search rate and the handling time are 
invariant throughout the parasite's adult life. When the mean numbers of 
eggs laid per female at the six different host densities during each day of 
the adult life of the parasite were plotted against host density (Fig. 
12.4), it became clear that, from the start, the relationship between the 
number of eggs laid and host density changed through time. Since mortality 
of the female parasites reduced the sample size considerably from the 
fourth day onwards (Table 12.2). detailed analysis could be carried out 
only on the data of the first three days.

The functional response of the parasite to host density on each succes-
sive day was compared using the disc equation. The equation fits the data 
well for the first day and also the second day but not for the third day
Fig. 12.3 Functional response curves of *A. sonchi* parasitizing *H. lactucae*. Unfilled and filled circles represent the overall means of eggs laid and of aphids parasitized calculated from the lifetime totals of each female parasite, bars show the standard errors. Upper curve for $N_e$ was fitted from Holling's disc equation, while the lower curve for $N_p$ was fitted from Messenger's (1967) random parasite equation.
Fig. 12.4 Mean number of eggs laid by *A. sonchi* at various host density during its adult life at 22°C, 14L:10D
Fig. 12.5 Mean numbers of eggs laid by female *A. sonchi* at different host densities during the first three days of adult life at 22°C, 14L:10D. Solid circles represent data, bars show standard errors and continuous lines were fitted from Holling's disc equation.
during which the functional response became more clearly dome-shaped (Fig. 12.5; Table 12.3). With the good fit of the data for the first two days, it is possible to estimate the search rate and the handling time for the parasite in each case. The estimates show that the rate of search increased by 34% and the handling time nearly doubled on the second day (Table 12.3).

Table 12.3 Comparison of functional response parameters of *A. sonchi* during the first three days of adult life at 22°C, 14L:10D

<table>
<thead>
<tr>
<th>Adult age in days</th>
<th>$r^2$#</th>
<th>Rate of search (cage$^{-1}\text{day}^{-1}$)</th>
<th>Handling time $T_h$ (minutes)</th>
<th>Test of goodness of fit† (d.f. = 5) $X^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.91</td>
<td>4.86</td>
<td>7.99</td>
<td>2.14</td>
<td>0.83</td>
</tr>
<tr>
<td>2</td>
<td>0.78</td>
<td>6.53</td>
<td>13.49</td>
<td>4.26</td>
<td>0.52</td>
</tr>
<tr>
<td>3</td>
<td>0.54*</td>
<td>—</td>
<td>—</td>
<td>13.53</td>
<td>0.02</td>
</tr>
</tbody>
</table>

# This is the $r^2$ value for the linear regression of $N_e/N_o$ on $N_e$, an asterisk indicates that the correlation is not significant at the 5% level.

† Goodness of fit test between the numbers of actual eggs laid and those predicted from Holling's disc equation.

12.4 DISCUSSION

12.4.1 Effect of Host Density on Fecundity, Reproductive Rate and Life Span

Both the fecundity and reproductive rates of *A. sonchi* are strongly influenced by host density. At host densities of less than 50 aphids per day oviposition constraints resulting from lack of hosts reduced the number of eggs laid per day. Since adult life span was more or less unaffected by host density, the daily reduction of oviposition at sub-optimal host densities effectively limited the total number of eggs deposited during the lifetime of the parasite. As female *A. sonchi* search and oviposit at random, a decrease of the number of eggs laid at a given host density will always result in a reduction of the number of aphids parasitized. At host
densities higher than 50 aphids per day, although the total number of eggs laid was no longer affected, the number of aphids parasitized was still positively correlated with host density.

No ready explanation can be found for the adult life span of the female parasites being little affected by host density in this experiment, as elsewhere female *A. sonchi* in the absence of hosts lived twice as long as they did in the presence of a large number of hosts (10.7). Although the mechanisms involved in that experiment were not ascertained, the results suggest strongly that the different lengths of adult life were attributed, at least in part, to the different energy usage, i.e. the females provided with hosts spent part of their energy seeking for hosts and ovipositing. Thus, intuitively, one would expect that female *A. sonchi* would live longer at lower host densities where they lay fewer eggs per day.

A possible mechanism involved in producing the pattern of adult longevity of the parasite in this experiment is the difference in food (i.e. honeydew) available to the females at different host densities. The females at densities of less than 50 hosts each day could have had difficulty in finding honeydew on which to feed. This point can not be clarified without further experimentation.

A similar situation has been reported by Mackauer (1983) for the parasite *Aphidius smithi* reared on the pea aphid, *Acyrthosiphon pisum*. The number of eggs laid per female per day was greatly reduced when each female was provided with less than 40 hosts each day, while adult life span of the parasite was not evidently affected by host density.

12.4.2 Functional Response of the Parasite to Host Density

The two fundamental components in this relationship are the rate at which each predator, or parasite, searches, and the handling time taken to
cope with each prey, or host, encountered. Both components have been shown to vary with developmental stage (or size) of predators (see review by Hassell, Lawton & Beddington 1976). There has also been ample experimental evidence that the two components may also vary through time within one developmental stage (also see Hassell, Lawton & Beddington 1976; Mackauer 1983). These variations can be readily envisaged when their subcomponents are examined (Holling 1965, 1966):

(1) Rate of search \( (a') \):
   (a) speed of movement of the predator or parasite relative to that of the prey or host;
   (b) the predator's or parasite's reactive field; and
   (c) the proportion of attacks that are successful.

(2) Handling time \( (T_h) \):
   (a) the time spent pursuing and subduing a prey or host;
   (b) the time spent eating each prey, or parasitizing each host; and
   (c) any time spent resting or cleaning as a result of feeding by predators, or ovipositing by parasites.

The overall values of \( a' \) and \( T_h \) (hence the functional response) are determined by the behaviour of each of the above subcomponents and their interactions. In \( A. sonchi \), direct observations showed that all the subcomponents listed above are likely to change as the female ages (10.6). For example:

(a) The speed of movement of the parasite becomes slower (as a result the relative proportion of successful oviposition attempts will be reduced);

(b) The time spent pursuing, subduing and then parasitizing each host becomes longer; and

(c) More time is spent resting or cleaning.

Among the three aspects of behaviour, the increase of the relative length
of time spent resting was most obvious. This is probably why the analysis of the functional response of the parasite in the first two days revealed a significant increase in handling time, but not a decrease in the rate of search. During the experiment direct observations were not made on the behaviour of the ovipositing females at different host densities. However, as oviposition frequency was strongly positively correlated with host density at the initial period of adult life of the parasite, it was very likely that the relative proportion of time spent resting would increase more at higher host densities. If this is so, the "turn-down" seen in the functional response at higher densities beginning on the second day was probably caused mainly by longer resting periods at these densities.

The overall increase of resting periods in *A. sonchi* is more likely to be a function of the fatigue resulting from host searching and ovipositing rather than a function of the supply of mature eggs. Females of this parasite emerge with the bulk of their eggs mature and the number of eggs produced in adult life is relatively small (10.4). It has also been shown that when females of this parasite were provided with 20 second and third instar aphid nymphs on detached young leaves in the jar (where aphids are fully exposed to attack on one surface, thus host searching is minimal) each 12 h period under similar temperature-light regime, they were able to lay the whole complement of eggs within three days after emergence (Table 10.1, Fig. 10.1).

In host-parasite systems, the functional response of the parasite within each age interval influences not only the number of hosts attacked during that age interval but also the age specific fecundity. Thus, the significance of its variations through adult life is obvious. For instance, it is impossible to build a simulation model for any host-parasite system incorporating detailed age-structure without this information.
Hassell, Lawton & Beddington (1976) suggested that the functional response of aphid parasites will vary with host instar (or size) provided. While this was not investigated quantitatively in this study, direct observations on the oviposition behaviour of the parasite (10.6.1) provided evidence that most of the components of $a'$ and $T_h$ may vary with host instar. Further evidence was provided by the variation in the numbers of eggs laid in different instars/morphs in the experiment on host instar selection (11.4) where host density and exposure time were constant.
CHAPTER 13

BIOCLIMATIC AND LIFE-FERTILITY TABLE STUDIES OF APHIDIUS SONCHI

13.1 INTRODUCTION

Climate exerts important and often limiting influences on the distribution and abundance of insects (Andrewartha and Birch 1954). This chapter describes laboratory experiments in which the development, survival and reproduction of A. sonchi were examined under various temperature-light regimes. The data obtained here, together with the data on the relationship between host density and reproduction of the parasite previously reported (Chapter 12), are then used to estimate the potential for population increase of the parasite at different temperature levels. Finally, the implications of the different responses to temperatures of the aphid and the parasite in the numerical relationship between them will be discussed.

13.2 DEVELOPMENT, BODY SIZE AND NUMBER OF EGGS IN THE OVARIES UNDER VARIOUS TEMPERATURE-LIGHT REGIMES

13.2.1 Materials and Methods

Sources of test aphids and parent parasites. Host aphids used were second and third instar nymphs drawn directly from the aphid stock culture. Parasites used to start the cultures were 1-2 days post-emergent, mated females obtained from the parasite stock culture. These female parasites were not allowed access to aphids until they were introduced to the test aphids.

Establishment of experimental populations of parasite. Experimental parasite populations under various temperature-light regimes (see Table 13.1) were initiated in the following standardized way: groups of thirty aphids each were placed onto young leaves set flat in inverted plastic jars (see Fig. 4.2). After being transferred to the jars, the aphids were allowed to settle for 1-2 h and two female parasites were introduced into
each jar for a 2 h period to oviposit under conditions of 20°C, 60-70% R.H. and constant illumination. The exposed aphids were then transferred onto flowering shoots in caged pots and placed in environmental cabinets under the appropriate experimental conditions.

**Experimental design and observations.** The development of the parasite was observed under seven constant- and five alternating-temperature regimes (Table 13.1). All the experiments were carried out from October 1981 to February 1982.

For estimation of the developmental rate of the parasite, only the total time from oviposition to emergence of adults was recorded. Emergence under each temperature-light regime was checked at 24 h intervals from the start of the experiment and any adults found were recorded and removed. All unproductive mummies were dissected at a later date. From these data the mean time-to-adult, the percentage of mortality during pupal stage and the proportion of diapause individuals at each temperature-light regime were calculated.

To examine the effect of temperature and photoperiod on the body size and potential fecundity of the parasite, 30 females from each of three different temperature-light regimes (see Table 13.4) were measured and dissected on the day they emerged. The methods of measuring and dissecting were identical with those described in 11.3.1.

13.2.2 Results and Analysis

(i) Rate of development

Time from oviposition to emergence of adults increased with decreased temperatures, either constant or alternating (Table 13.1). In every case, males reached the adult stage earlier than females. However, since the developmental differences between sexes were consistently small, the
analysis of developmental rate was carried out on the pooled data of both males and females.

When the mean developmental times at the four lower constant temperatures were compared with those at the corresponding alternating temperatures, the parasites under the latter conditions reached the adult stage earlier at the lower temperatures but took longer to develop at the higher temperatures. Under the three temperature regimes with a daily mean of 12.5°C, the developmental time decreased as the amplitude of temperature alternation increased.

It is well-known that, because of the non-linear relationship between temperature and speed of development in insects, valid evidence for developmental acceleration or deceleration between constant and fluctuating temperatures can be shown only by comparison based on real temperature effects rather than on temperature means (Howe 1967; Messenger & Flitters 1959). This requires that the curve for the constant temperature equivalent of the variable regimes has been determined as precisely as possible. The comparison can then be made on the fraction of development per unit time at various temperatures. The data obtained under constant temperature for *A. sonchi* were found to be described satisfactorily by the empirical Pearl-Verhulst logistic curve (Fig. 13.1, see Davidson 1944). The data obtained at 28°C were excluded from the curve fitting as the reversal in trend of developmental rate at this temperature was obvious.

The substantial mortality at 28°C and the high incidence of diapause at 12.5°C suggest that in this parasite it is not practical to examine experimentally the average rate of development outside the temperature range covered in this study. Thus, according to the principles outlined above, the comparison between effects of constant and alternating temperatures on the rate of development in *A. sonchi* can be made only
### Table 13.1 Mortality during pupal stage, developmental time and proportions of diapause individuals of *A. sonchi* under various temperature-light regimes

<table>
<thead>
<tr>
<th>Rearing condition*</th>
<th>N</th>
<th>No. died during pupal stage</th>
<th>Mean time in days from oviposition to emergence of adults</th>
<th>No. diapause</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Male (N) Female (N) Male + female Mean Range</td>
<td></td>
</tr>
<tr>
<td>28°C 14L:10D 50-80% RH</td>
<td>277</td>
<td>105(13.9%)</td>
<td>10.1(37) 10.2(135) 10.2 9-12 0</td>
<td></td>
</tr>
<tr>
<td>26°C 14L:10D 50-80% RH</td>
<td>192</td>
<td>32(19.2%)</td>
<td>9.2(35) 9.6(106) 9.5 9-12 9(5.0%)</td>
<td></td>
</tr>
<tr>
<td>24°C 14L:10D 50-79% RH</td>
<td>158</td>
<td>12(7.1%)</td>
<td>9.7(23) 10.1(112) 10.1 8-12 11(7.0%)</td>
<td></td>
</tr>
<tr>
<td>28-13.5°C 14L:10D 40-80% RH</td>
<td>131</td>
<td>7(5.9%)</td>
<td>12.5(19) 12.7(99) 12.7 11-16 6(4.6%)</td>
<td></td>
</tr>
<tr>
<td>22°C 14L:10D 70-90% RH</td>
<td>264</td>
<td>8(3.0%)</td>
<td>11.0(90) 11.3(161) 11.2 10-14 5(1.9%)</td>
<td></td>
</tr>
<tr>
<td>26-11.5°C 14L:10D 70-90% RH</td>
<td>279</td>
<td>10(3.6%)</td>
<td>13.4(64) 13.5(203) 13.5 12-18 3(0.7%)</td>
<td></td>
</tr>
<tr>
<td>20°C 14L:10D 60-90% RH</td>
<td>133</td>
<td>2(1.5%)</td>
<td>12.2(23) 12.6(106) 12.5 11-16 2(1.5%)</td>
<td></td>
</tr>
<tr>
<td>23.5-9.5°C 13L:11D 60-80% RH</td>
<td>210</td>
<td>7(3.4%)</td>
<td>15.5(27) 15.7(175) 15.7 14-19 1(0.5%)</td>
<td></td>
</tr>
<tr>
<td>17°C 13L:11D 70-90% RH</td>
<td>83</td>
<td>3(3.5%)</td>
<td>17.2(26) 18.0(52) 17.7 15-21 2(2.4%)</td>
<td></td>
</tr>
<tr>
<td>20-5°C 12L:12D 70-85% RH</td>
<td>135</td>
<td>1(0.8%)</td>
<td>22.2(24) 22.9(110) 22.7 20-27 0</td>
<td></td>
</tr>
<tr>
<td>17.5-7.5°C 12L:12D 70-85% RH</td>
<td>370</td>
<td>3(0.8%)</td>
<td>26.0(79) 26.3(286) 26.2 23-30 2(2.4%)</td>
<td></td>
</tr>
<tr>
<td>12.5°C 12L:12D 70-80% RH</td>
<td>230</td>
<td>3(1.3%)</td>
<td>31.0(34) 31.3(107) 31.2 27-37 86(37.4%)</td>
<td></td>
</tr>
</tbody>
</table>

* In case of alternating temperature regimes, the higher temperature coincides with the light period each 24 h, and data of each alternating temperature regime and those of the corresponding constant temperature are grouped more closely by extra horizontal space.
within the temperature range 11.5-27°C (with the extrapolation of 1°C at both ends from the data). When the observed rate of development at 26-11.5°C was compared with that calculated from the curve for constant temperature data (Fig. 13.1), there is no evidence for developmental acceleration or deceleration as the following table shows:

<table>
<thead>
<tr>
<th>Temperature-light regime</th>
<th>Percent development per day</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>26-11.5°C, 14L:10D</td>
<td>7.40</td>
<td>267</td>
</tr>
</tbody>
</table>

* The calculation assumes that the parasite spent 14 h at 26°C and 10 h at 11.5°C each day. In fact, it usually took 1 h to change gradually from one temperature to the other. However, since the maintenance of constant temperature was not precise (+0.5°C), there is little point to take the temperature fluctuations during these two hours into account in the calculation. The same consideration applies in other similar comparisons described in this chapter.

The results of this comparison suggest that within the mid temperature range temperature alternation neither stimulates nor retards the rate of development. If it can be assumed that when a temperature within this range is alternated with a temperature outside its effect on the rate of development still follows that specified by the curve for constant temperature data, the amount of development experienced at the latter temperature can then be estimated. For example, at 17.5-7.5°C and 12L:12D, the percent development per day was 3.80%. Therefore, it can be argued that the parasite completed 3.05% of its total development during the 12 h at 17.5°C and the remaining 0.75% was completed during the 12 h at 7.5°C. From this it is then possible to estimate the rate of development at the latter temperature. Such calculations were performed for the remaining four alternating temperature regimes. Although the methods of calculation tend to shift all the experimental errors to the temperatures outside the middle temperature range.
range, the estimated rates of development generally agreed very closely with those extrapolated from the curve for the constant temperature (Table 13.2).

Table 13.2 Comparison between the estimated developmental rates of *A. sonchi* under some extreme temperatures which were each alternated with a favourable temperature and the developmental rates under these temperatures as extrapolated from the constant-temperature curve

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Percent development per day</th>
<th>Estimated*</th>
<th>Extrapolated</th>
<th>Difference† (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.0</td>
<td>0.97</td>
<td>0.98</td>
<td></td>
<td>-1.00</td>
</tr>
<tr>
<td>7.5</td>
<td>1.51</td>
<td>1.51</td>
<td></td>
<td>-0.04</td>
</tr>
<tr>
<td>9.5</td>
<td>2.58</td>
<td>2.09</td>
<td></td>
<td>+18.92</td>
</tr>
<tr>
<td>28.0</td>
<td>10.84</td>
<td>11.40</td>
<td></td>
<td>-5.13</td>
</tr>
</tbody>
</table>

* See text for methods of estimation  
† Differences expressed as the percent increase of the estimated value in comparison with the extrapolated.

The results of the above analysis show that the relationship between temperature and the rate of development in *A. sonchi* is of the pattern shown in Fig. 13.1 (or at least very close to it). Such a shallow sigmoid curvilinear relationship between the two variables has a corollary that if the varying temperature is represented by a mean, the parasite will reach the adult stage as expected only when the temperature fluctuations do not exceed the linear zone of the sigmoid curve; at lower temperatures the parasite will reach the adult stage sooner than expected, at higher temperatures the parasite will reach the adult stage later than expected. Moreover, such differences will increase in magnitude with the diurnal range of temperature fluctuations. All this was confirmed by the earlier direct comparison of developmental times based on temperature means. It follows that if the reciprocals of developmental times (or the reciprocals of developmental times multiplied by 100) are plotted against mean temperatures and a linear regression is used to estimate the developmental
Fig. 13.1 Developmental rate of *A. sonchi* at constant temperatures. The circles on the graph are observed values.

\[ y = \frac{13.2317}{1 + e^{3.468736 - 0.189123x}} \]

Fig. 13.2 Rate of development of *A. sonchi* at constant temperatures and that at alternating temperatures with an alternating amplitude of 14-15°C. The filled and unfilled circles are observed values and the lines are drawn according to the linear regression equations shown in Table 13.3.
threshold and thermal constant (see Campbell et al. 1974), different values will be obtained with data collected under temperatures with different patterns of fluctuations. Generally, a wider range of temperature fluctuations will result in a lower developmental threshold and also a higher thermal constant. The calculations with the data shown in Table 13.1 (within the appropriate range) show that in A. sonchi the threshold temperature estimated from data obtained under alternating temperature regimes with a diurnal range of 14-15°C was 7°C lower than that estimated from constant temperature data (Table 13.3; Fig. 13.2). It is not difficult to

<table>
<thead>
<tr>
<th>Temperature regime</th>
<th>Development threshold, $t$ (°C)</th>
<th>Thermal Constant, $K$ (D°C)</th>
<th>Linear regression Equation*</th>
<th>$r^2$</th>
<th>d.f.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>7.47</td>
<td>161.14</td>
<td>$100/Y = 0.6189X - 4.6229$</td>
<td>0.9932</td>
<td>4</td>
</tr>
<tr>
<td>Alternating†</td>
<td>0.37</td>
<td>268.36</td>
<td>$100/Y = 0.3726X - 0.1373$</td>
<td>0.9882</td>
<td>3</td>
</tr>
</tbody>
</table>

† Alternating with an amplitude of 14-15°C.
* In the equations, $Y$ is the number of days required to develop from egg to adult under the daily mean temperature $X$.

see that the two sets of temperature coefficients will give quite different predictions of the development of the parasite in the field, especially when temperatures below the middle range may account for an appreciable part of any summation of day-degrees. As an example, the expected numbers of generations of the parasite were estimated using each of the two sets of temperature coefficients for the two seasons in 1982 when the two field cage experiments were carried out (see Fig. 14.1). The results are shown below:

<table>
<thead>
<tr>
<th>Time (1982)</th>
<th>Day-degrees accumulated</th>
<th>No. generations expected</th>
<th>Day-degrees accumulated</th>
<th>No. generations expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>25 Mar-26 Apr</td>
<td>223.7</td>
<td>1.39</td>
<td>422.5</td>
<td>1.57</td>
</tr>
<tr>
<td>16 Sept-28 Oct</td>
<td>202.1</td>
<td>1.25</td>
<td>431.1</td>
<td>1.61</td>
</tr>
</tbody>
</table>

Note: The method for summation of day-degrees above a threshold was described in Chapter 9.
As expected, the two sets of predictions differ considerably. It is obvious that the numbers of generations predicted by the first set of temperature coefficients are too low because the amount of development that may occur below 7.5°C is ignored. The predictions made by the second set of coefficients are probably very close to the real situations in this particular case, as the diurnal ranges of temperature fluctuations in the field during these periods were around 14-16°C, similar to the range of temperature alternations used in the laboratory experiments. However, it is important to remember that the temperature coefficients tend to overestimate the rate of development at low temperatures, the error created may become substantial when the prediction covers many generations.

(ii) Mortality during pupal stage

The percent mortality during pupal stage was consistently low within the range of daily mean temperatures 12.5 to 24°C, either constant or alternating (Table 13.1). Under constant temperatures above 24°C, the mortality during pupal stage increased rapidly as temperature increased. The rapid increase in mortality under these rearing conditions and the substantial mortality shown by the parasites at 28°C suggest that the upper lethal constant temperature for complete development was being approached.

(iii) Diapause

The proportion of diapause individuals was consistently low at all temperature-light regimes tested except at 12.5°C, 12L:12D where 37.4% of the parasites entered diapause (Table 13.1). The results probably suggest that low constant temperature with a 12L:12D photoperiod favours the induction of diapause.

(iv) Body size and number of eggs in the ovaries

The mean head widths and the mean numbers of eggs in the ovaries of
the parasites reared under three different temperature-light regimes are shown in Table 13.4. Analysis of variance showed that there were no significant differences in the two attributes between the three cohorts of parasites (for head widths, $F = 1.66$, d.f. = $2/87$, $P > 0.05$; for numbers of eggs, $F = 1.15$, d.f. = $2/87$, $P > 0.05$).

Table 13.4  Head width and number of eggs on the day of emergence of adult females of *A. sonchi* reared at three different temperature-light regimes

<table>
<thead>
<tr>
<th>Rearing condition</th>
<th>N</th>
<th>Head width*</th>
<th>No. eggs on the day of emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean ± S.E.</td>
<td>Mean ± S.E.</td>
</tr>
<tr>
<td>28-13.5°C, 14L:10D</td>
<td>30</td>
<td>25.05 ± 0.20</td>
<td>170.13 ± 6.85</td>
</tr>
<tr>
<td>23.5-9.5°C, 13L:11D</td>
<td>30</td>
<td>25.20 ± 0.21</td>
<td>184.17 ± 10.26</td>
</tr>
<tr>
<td>20-5°C, 12L:12D</td>
<td>30</td>
<td>24.88 ± 0.23</td>
<td>167.70 ± 6.51</td>
</tr>
</tbody>
</table>

* Head width is presented in units, 50 units = 1.00 mm.

13.3 LOWER TEMPERATURE THRESHOLD FOR OVIPOSITION

13.3.1 Materials and Methods

Aphids used were second and third instar nymphs from the aphid stock culture and reared on flowering shoots held in the caged pots. The parasites used were mated females obtained from an experimental cohort which was reared from egg to adult at 12.5°C, 12L:12D in an environmental cabinet.

Two groups of parasites, each consisting of ten females of similar age, were tested. Parasites in the first group were introduced to test aphids 12-24 h after emergence, and those in the second group were introduced to test aphids 36-48 h after emergence. None of the females were allowed access to aphids until they were used in the tests.

The test exposures were carried out in an environmental cabinet at 10°C, 12L:12D and 70-80% R.H. Each female was provided with 50 aphids for
a 24 h period and then discarded. The exposed aphids were reared at 22°C, 14L:10D for a further 72-80 h and then dissected to determine the number of eggs laid by each female parasite.

13.3.2 Results

The results of the experiment were summarized in the following table:

<table>
<thead>
<tr>
<th>Parasite age after emergence</th>
<th>N</th>
<th>No. females which did not oviposit</th>
<th>Females that oviposited</th>
<th>Number</th>
<th>Mean no. of eggs laid</th>
</tr>
</thead>
<tbody>
<tr>
<td>12-24 h</td>
<td>10</td>
<td>3</td>
<td>7</td>
<td>12.5</td>
<td></td>
</tr>
<tr>
<td>36-48 h</td>
<td>10</td>
<td>0</td>
<td>10</td>
<td>21.3</td>
<td></td>
</tr>
</tbody>
</table>

The data show that the lower temperature threshold for oviposition in *A. sonchi* is lower than 10°C. The higher number of eggs laid by the parasites in the second group suggest that the threshold temperature may be much lower for female parasites which have not had access to aphids for long periods.

13.4 OVIPOSITION RATE UNDER VARIOUS TEMPERATURE-LIGHT REGIMES

13.4.1 Materials and Methods

Aphids used were second and third instar nymphs from the aphiod stock culture and reared on flowering shoots held in the caged pots.

The adult female parasites used at each temperature-light regime were reared from egg to the adult stage under the same conditions. All females used were introduced to the first batch of their host aphids within 12 h of emergence and were each accompanied by a male parasite during the first 24 h period of the oviposition test.

The experiments were carried out in environmental cabinets under four different temperature-light regimes (Table 13.5), and under each temperature-light regime 15 female parasites were used. Each female parasite was
provided with a fresh batch of 50 aphids on one flowering shoot in a caged pot daily until the parasite died. All the exposed aphids were left on the plant material for an additional 72-80 h at 22°C, 14L:10D and then dissected to determine both the number of eggs laid and the number of aphids parasitized (see 11.4.2).

13.4.2 Results

The percent survivors at the beginning of each day and mean numbers of eggs laid and aphids parasitized per female per day are shown in Fig. 13.3. Both age specific survival of the adult females and their fecundity rates throughout adult life were very similar at 22°C, 23.5-9.5°C and 20-5°C. At 28-13.5°C, although the fecundity rates were not affected during the first two days, the parasites suffered heavy mortality from the second day onwards and all died within five days. The obvious difference in survival between the parasites at 28-13.5°C and those at the other three temperature-light regimes suggest that 14 h per day at 28°C was harmful to the adult females.

<table>
<thead>
<tr>
<th>Experimental conditions</th>
<th>N</th>
<th>Mean adult life span in days</th>
<th>Mean number of eggs laid ± S.E.</th>
<th>Mean number of aphids parasitized ± S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>28-13.5°C 14L:10D 40-90% R.H.</td>
<td>15</td>
<td>2.3</td>
<td>142.0 ± 10.1</td>
<td>89.6 ± 5.7</td>
</tr>
<tr>
<td>22°C 14L:10D 70-90% R.H.</td>
<td>15</td>
<td>4.7</td>
<td>224.9 ± 18.3</td>
<td>146.8 ± 10.2</td>
</tr>
<tr>
<td>23.5-9.5°C 13L:11D 70-90% R.H.</td>
<td>15</td>
<td>4.9</td>
<td>219.7 ± 17.8</td>
<td>156.6 ± 11.1</td>
</tr>
<tr>
<td>20-5°C 12L:12D 70-90% R.H.</td>
<td>15</td>
<td>4.3</td>
<td>206.9 ± 15.5</td>
<td>153.2 ± 12.8</td>
</tr>
</tbody>
</table>

Mean adult life span and mean lifetime fecundity indicated either by the number of eggs laid or by the number of aphids parasitized, were
Fig. 13.3 Survival of eggs laid and aphids parasitized by *A. sonchi* under different temperature-light regimes; each adult female was provided with 50 second and third instar aphid nymphs reared on one flowering shoot each 24 h period. The mean number of eggs laid and that of aphids parasitized take into account any female which survived to the beginning of that day irrespective of success or failure of oviposition.
significantly reduced at 28-13.5°C in comparison with those at the other three temperature-light regimes (Table 13.5). Under the remaining three temperature-light regimes, the parasites survived for a similar length of time and achieved very similar lifetime fecundities (for both the mean number of eggs laid and the mean number of aphids parasitized per female, $F < 0.23$, d.f. = 2/42, $P > 0.05$).

13.5 REALIZED FECUNDITY AND PROGENY SEX RATIO UNDER TWO DIFFERENT TEMPERATURE-LIGHT REGIMES

13.5.1 Materials and Methods

The temperature-light regimes used were: 22°C, 14L:10D and 20-5°C, 12L:12D.

The aphids and parasites used, and the experimental procedures were the same as described under 13.4.1 except that the aphids exposed each day were held under their respective temperature-light regime until the parasite progeny had become adults. All the resultant adult parasites in each caged pot were sexed and counted to determine daily progeny production and sex ratio. All the unproductive mummies were dissected at a later date to find out the percent mortality during the pupal stage and the proportion of diapausing individuals.

13.5.2 Results

The mean numbers of mummies produced per female parasite under each of the two temperature-light regimes were very similar to the number of aphids parasitized as determined previously by host dissection (Table 13.6, see Table 13.5), indicating that little mortality occurred in the egg and larval stages under these conditions. The low mortality during pupal stage and low proportions of diapause individuals agreed closely with those obtained previously under the same temperature-light regimes (see Table 13.1).
Table 13.6 Adult life span, realized fecundity and progeny sex ratio of *A. sonchi* under two different temperature-light regimes. Each adult female was provided with 50 second and third instar aphid nymphs reared on one flowering shoot each 24 h period.

<table>
<thead>
<tr>
<th>Rearing conditions</th>
<th>N</th>
<th>Mean adult span in days</th>
<th>Mean no. mummies produced per female $\pm$ S.E.</th>
<th>Mean number of progeny</th>
<th>Mortality in pupal stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>22°C 14L:10D 80-90% R.H.</td>
<td>10</td>
<td>4.7</td>
<td>151.8 $\pm$ 13.2</td>
<td>38.3(26.5%) 106.9(73.5%) 144.3</td>
<td>4.0(2.6%) 3.5(2.3%)</td>
</tr>
<tr>
<td>20-5°C 12L:12D 70-90% R.H.</td>
<td>10</td>
<td>5.0</td>
<td>146.0 $\pm$ 11.5</td>
<td>43.1(31.1%) 95.6(68.9%) 138.7</td>
<td>3.6(2.5%) 3.7(2.5%)</td>
</tr>
</tbody>
</table>
Fig. 13.4 Survival, realized fecundity and progeny sex ratio of *A. sonchi* reared under two different temperature-light regimes. Each adult female was provided with 50 second and third instar aphid nymphs reared on one flowering shoot each 24 h period.
Figure 13.4 shows the average progeny per female per day under each of the two temperature-light regimes. Throughout the reproductive life of the parasites, their progeny were composed of about 70% females.

13.6 LIFE AND FERTILITY TABLES AND INTRINSIC RATE OF INCREASE

13.6.1 Methods

The techniques for life and fertility table studies have been discussed in Chapter 5. To collect data for the construction of a complete age-specific life and fertility table, it is necessary to follow a cohort through successive short time intervals from birth to death and record the number still alive and the young produced since the previous observation.

The endoparasitic life of aphid parasites precludes any direct observations of their egg and larval stages. Thus, it is often impossible to follow a given sample of newly born individuals throughout their life until all have died. This means that both the age-distribution of the mortality during egg and pupal stages and the sex ratio of progeny must be estimated from data of additional experiments. However, for the determination of the intrinsic rate of increase $r_m$, the actual age distribution of the mortality during immature stages becomes unimportant as all deaths that occur before the commencement of reproduction have an equal influence on the value of $r_m$ to be calculated (see 5.3).

The intrinsic rate of increase was estimated for *A. sonchi* reared under four different temperature-light regimes: 28-13.5°C, 14L:10D; 22°C, 14L:10D; 23.5-9.5°C, 13L:11D and 20-5°C, 12L:12D. The results were compared with those on the aphid reported previously (Chapter 7).

Life and fertility table data (on a daily basis) for the parasite were derived in the following manner:

(1) *Developmental time.* Time in days from egg to adult under the four
temperature-light regimes were shown in Fig. 13.1. These data are used
directly to specify the period from egg to adult under each regime.

(2) Mortality during immature stages. Mortality during the pupal stage
under the four temperature-light regimes was shown in Table 13.1. The
values are used directly to specify the percentage of mortality during the
pupal stage and the age when the mortality occurs is assumed to be the
mid point of the pupal stage.

Comparison between the data on oviposition rate and those on realized
fecundity of the parasite (13.5.2) suggested that within the temperature
range considered here the mortality during the egg and larval stages is
insignificant (except perhaps under 28-13.5°C). In the construction of
life tables, the percent mortality during the egg and larval stages under
each temperature-light regime is assumed to be equal to that during the
pupal stage and the mortality is assumed to occur towards the end of
first larval instar.

In the experiments on the development of the parasite under various
temperature-light regimes (13.2.2), 4.6% of the parasites at 28-13.5°C,
1.9% at 22°C, and 0.5% at 23.5-9.5°C entered diapause. Although diapause
may be very important in the survival of the parasite under adverse condi­
tions, the diapause individuals certainly contribute only insignificantly
to the short-term population increase. For simplicity, the observed propor­
tions of diapause are treated as mortality which occur at the end of the
larval stage.

(3) Survival rates of adult females. Fig. 13.3 shows the percent survivors
of adult females at the beginning of each day throughout adult life under
the four temperature-light regimes. Survival rates of adult females are
calculated from these data, and since adult longevity was shown to be
little affected by host density (12.3.3) the same survival rates are assumed
at different host densities.

(4) **Fertility rates.** Fertility rates of the parasite are determined by the "effective" fecundity rates, i.e. the mean number of aphids parasitized during each age interval and the sex ratio of the progeny.

The mean numbers of aphids parasitized per female per day at a host density of 50 aphids per day under the four temperature-light regimes were shown in Fig. 13.3. These data are used to calculate the effective fecundity rates for the parasite at that host density (i.e. 50 aphids per day).

The experiments carried out at 22°C, 14L:10D with different host densities (Chapter 12) showed the pattern with which the fecundity rates of the parasite change in response to varying host densities. The data shown in Table 12.2* are used to calculate the effective fecundity rates of the parasite under 22°C, 14L:10D at different host densities. Similar data were not available for the remaining three temperature-light regimes, thus the construction of the fertility tables at different host densities under these conditions could not be attempted.

The sex ratios of progeny produced daily under the two temperature-light regimes tested (22°C, 20-5°C; Fig. 13.4) remained relatively constant, the proportion of females being about 70% throughout the reproductive life of the parasite. In all life and fertility tables, fertility rates are calculated by multiplying the age-specific fecundity rates by a factor of 0.70 throughout.

13.6.2 Results and Analysis

(1) **Life and fertility table statistics for A. sonchi**

By following the methods described above, life and fertility tables

* The data in Table 12.2 do not include the number of aphids parasitized by each female on the day the female died; such data are included in the calculations here.
were constructed for the parasite reared at four different temperature-light regimes and each provided with 50 second and third instar aphid nymphs daily throughout its adult life (Fig. 13.5). Similarly, life and fertility tables were also constructed for the parasite reared under 22°C, 14L:10D but at different host densities during its adult life (Fig. 13.6). Net reproductive rate \( (R_q) \), intrinsic rate of increase \( (r_m) \) and mean generation time \( (T) \) were calculated on a daily basis for each life and fertility table. The results are shown in Tables 13.7 and 13.8.

**Effect of temperature and photoperiod.** The intrinsic rate of increase of the parasite increased with an increase in temperature and photoperiod (Table 13.7). Since under 20-5°C, 23.5-9.5°C and 22°C, the mortality of the parasite up to the commencement of reproduction was consistently low and the fertility rate curves were all similar (Fig. 13.5), the increase of \( r_m \) at higher temperature levels was largely due to the decreased developmental time. The lower intrinsic rate of increase at 28-13.5°C compared to that at 22°C was caused by (1) longer developmental time and (2) heavier mortality, especially during adult life.

**Effect of host density.** The intrinsic rate of increase of the parasite increased with host density (Table 13.8). The trend of increase of \( r_m \) at the six densities examined shows that under 22°C, 14L:10D, the realization of the potential for maximum population increase requires 200 or more host aphids each day during reproductive life.

(ii) Comparison of life and fertility table statistics between the parasite and the aphid

Fig. 13.7 shows the various life and fertility table statistics of the parasite and the aphid reared under three alternating temperature-light regimes: 20-5°C, 12L:12D; 23.5°C-9.5°C, 13L:11D; and 28-13.5°C, 14L:11D. The data for the parasite were taken from Table 13.7 and those
Fig. 13.5 Age-specific survival rates and fertility rates (i.e. female births per adult female per day) of A. sonchi reared at different temperature-light regimes and provided with 50 second and third instar aphid nymphs daily throughout adult life.
Fig. 13.6 Age-specific fertility rates (i.e. mean number of female births per adult female per day) of *A. sonchi* reared at 22°C, 14L:10D but provided with different numbers of host aphids daily throughout adult life. The age-specific survival rates of the parasite are assumed to remain unchanged with host density; i.e. the survival rates at 22°C shown in Fig. 13.5.
Table 13.7 Net reproductive rate ($R_0$), mean generation time ($T$), and intrinsic rate of increase ($r_m$) of *A. sonchi* reared at various temperature-light regimes and each provided with 50 aphids daily throughout adult life

<table>
<thead>
<tr>
<th>Temperature-light regime</th>
<th>$R_0$</th>
<th>$T$</th>
<th>$r_m$</th>
</tr>
</thead>
<tbody>
<tr>
<td>28–13.5°C 14L:10D</td>
<td>52.5</td>
<td>14.3</td>
<td>0.2775</td>
</tr>
<tr>
<td>22°C 14L:10D</td>
<td>94.9</td>
<td>13.5</td>
<td>0.3375</td>
</tr>
<tr>
<td>23.5–9.5°C 13L:11D</td>
<td>101.7</td>
<td>18.2</td>
<td>0.2545</td>
</tr>
<tr>
<td>20–5°C 12L:12D</td>
<td>105.4</td>
<td>25.1</td>
<td>0.1855</td>
</tr>
</tbody>
</table>

Table 13.8 Net reproductive rate ($R_0$), mean generation time ($T$) and intrinsic rate of increase ($r_m$) of *A. sonchi* reared at 22°C, 14L:10D and provided with various numbers of aphids daily throughout adult life

<table>
<thead>
<tr>
<th>No. of aphids provided per day</th>
<th>$R_0$</th>
<th>$T$</th>
<th>$r_m$</th>
</tr>
</thead>
<tbody>
<tr>
<td>during adult life</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>10.4</td>
<td>13.3</td>
<td>0.1730</td>
</tr>
<tr>
<td>10</td>
<td>23.0</td>
<td>14.0</td>
<td>0.2244</td>
</tr>
<tr>
<td>25</td>
<td>41.2</td>
<td>13.3</td>
<td>0.2802</td>
</tr>
<tr>
<td>50</td>
<td>94.8</td>
<td>13.4</td>
<td>0.3405</td>
</tr>
<tr>
<td>100</td>
<td>124.4</td>
<td>13.2</td>
<td>0.3643</td>
</tr>
<tr>
<td>200</td>
<td>130.2</td>
<td>13.1</td>
<td>0.3720</td>
</tr>
</tbody>
</table>
for the aphid from Table 7.4.

The net reproductive rate (i.e. female replacement per female per generation) of the parasite is much higher than that of the aphid over the temperature range examined. The obvious decline of the parasite's net reproductive rate at the highest temperature is caused mainly by the "premature deaths" of reproducing females under these conditions.

Over the temperature range examined, the mean generation time of the parasite is consistently longer than that of the aphid, being about 1.15 times that of the latter. However, the difference in mean generation times between the parasite and the aphid is much smaller than that between their developmental times: in every case the parasite takes 1.60-1.80 times longer to reach the adult stage. Since prereproductive period (i.e. the time from emergence of adult to the onset of reproduction) is very short in both the aphid and the parasite, the smaller differences between mean generation times than those between developmental times are largely due to the much higher reproductive rates and much shorter reproductive life of the parasite.

However, net reproductive rate and/or mean generation time offer little actual knowledge of the potential capacity of the organisms to increase in numbers. This capacity can be seen only from the intrinsic rate of increase, $r_m$ (Chapter 5). The results of the comparison of $r_m$'s between the parasite and the aphid show that over the temperature range examined their potentials for population increase are very similar. It must be remembered that the $r_m$'s of the parasite shown in Fig. 13.7 were calculated from data obtained from experiments in which each female was provided with only 50 aphids each day throughout her adult life. Higher $r_m$ values can be expected when more host aphids are provided.
Mean daily temperatures (°C)

Fig. 13.7 Comparison of life and fertility table statistics between *A. sonchi* and *H. lactucae* reared under three different alternating temperature-light regimes with a diurnal temperature range of 14-15°C. For further explanations, see text.
13.7 DISCUSSION

The rate of development of *A. sonchi* is directly influenced by temperature, following the curvilinear relationship depicted in Fig. 13.1. Thus, within the favourable range, the speed of development increases with temperature.

The comparison of the effect of constant and alternating temperatures suggests that in *A. sonchi* temperature alternation does not stimulate or retard rate of development. However, the analysis showed that, because of the curvilinear relationship between temperature and speed of development, data obtained under alternating temperature regimes with different diurnal ranges of alternation will result in different estimates of temperature coefficients derived by linear regression. Since the sequences of temperature fluctuations in the field are variable in both space and time, there seems to be little basis for choosing any particular alternating or fluctuating temperature regimes in experiments to determine temperature coefficients for use in field studies. In general, the temperature coefficients derived from constant temperature data may have a wider practical use, as they can give good predictions of the development of the parasite when temperature does not exceed the linear zone of the sigmoid curve. However, as soon as temperature remains outside the linear zone for any considerable lengths of time each day, the numbers of day-degrees calculated is always too low at low temperatures and tends to be too high above the optimum temperature.

The data on the numbers of eggs in the ovaries of the parasites reared under three different temperature-light regimes suggest that the potential fecundity of *A. sonchi* is relatively constant over the range of experimental conditions examined. The mean total numbers of eggs laid per female at 23.5–9.5°C and 20–5°C were not much higher than the mean numbers of eggs
in the ovaries on the day of emergence under these conditions, this supports the evidence of earlier observations (10.4) that egg production after emergence in this parasite is probably very limited.

The oviposition rates achieved by the parasite were very similar under three of the four temperature-light regimes tested. The exception occurred at 28-13.5°C and 14L:10D where the survival of the female parasites was reduced. Since the temperatures during the photophase were very similar in the three temperature-light regimes where similar oviposition rates were observed, the results suggest that oviposition rates of the parasite were largely determined by the temperature during the light period in each day rather than the daily mean temperature. This might be expected, since, as suggested above, egg production and maturing in this parasite are almost completed as soon as the females reach the adult stage. The observed similarity in oviposition rates also suggests that further increase in photoperiod, i.e. longer than 12 h a day, does not result in a corresponding increase of oviposition activity of the parasite. This is in agreement with the results of earlier direct observations, i.e. under these artificial conditions the female parasites concentrate their oviposition activity in the early hours of the photophase during each day.

The relatively uniform, female-predominant sex ratios in the progeny produced throughout the reproductive life of the parasite showed that most of the eggs laid in each successive day were fertilized. Such a high and steady percentage of egg fertilization was probably due to both the short reproductive period and the very limited further production of eggs after emergence in this parasite. However, since the parasite begins oviposition soon after emergence irrespective of mating (10.6.1), the proportion of male progeny will increase if mating is delayed.
With the data obtained here and those for the aphid reported in Chapter 7, it is now possible to make a partial comparison of the bioclimatic characteristics between the aphid and the parasite. The main drawback in the data for such a comparison is the lack of detailed information on the first generation of the aphid reared under medium and low temperatures. However, it seems reasonable to assume that within the medium temperature range where no apparent harmful effects were observed there was little difference between the response of the first and second generation. Based on this assumption, the developmental times and mortality during immature stages of the aphid and the parasite over a wide temperature range can then be attempted.

Over the temperature range examined, *A. sonchi* took at least 1.4 times longer to reach the adult stage than did *H. lactucae* (Table 13.9), indicating that the temperature requirements of the parasite are higher than those of the host. However, both total fecundity and reproductive rates of the parasite were higher than those of the aphid over the middle temperature range. This situation resulted in the similar values of the

<table>
<thead>
<tr>
<th>Temperature-light regime</th>
<th>Mean developmental time in days</th>
<th>% mortality during immature stages*</th>
</tr>
</thead>
<tbody>
<tr>
<td>28°C 14L:10D</td>
<td>6.1</td>
<td>4.0</td>
</tr>
<tr>
<td>26°C 14L:10D</td>
<td>6.6</td>
<td>4.2</td>
</tr>
<tr>
<td>24°C 14L:10D</td>
<td>6.7</td>
<td>4.0</td>
</tr>
<tr>
<td>28-13.5°C 14L:10D</td>
<td>7.2</td>
<td>0.0</td>
</tr>
<tr>
<td>22°C 14L:10D</td>
<td>7.1</td>
<td>0.0</td>
</tr>
<tr>
<td>23.5-9.5°C 13L:11D</td>
<td>9.4</td>
<td>0.0</td>
</tr>
<tr>
<td>17°C 13L:11D</td>
<td>9.5</td>
<td>0.0</td>
</tr>
<tr>
<td>20-5°C 12D:12D</td>
<td>14.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

* The figures for *H. lactucae* represent the percentages from birth to adult; while those for *A. sonchi* represent the percentages in pupal stage only and the total percent mortality from egg to adult can be expected to be higher.
intrinsic rate of increase for the aphid and the parasite under these conditions (Fig. 13.7). At the higher temperatures, *A. sonchi* showed increase in developmental time and suffered heavy mortality, such deleterious effects were not observed with the aphid. These differences in their responses to high temperatures suggest that the aphid can withstand high temperatures better than the parasite.

The data obtained at the lower temperatures tested in this study indicated that both the aphid and the parasite can remain active through rather cool conditions. For example, the aphid did not suffer any apparent harmful effects at the lowest temperature tested where it spent 12 h at 1°C each day (Chapter 7). In case of the parasite, the healthy development and very low mortality at 20-5°C and 12L:12D (Table 13.1) suggest that it can achieve complete development at even lower temperature levels. The data on the oviposition threshold showed that *A. sonchi* can oviposit at temperatures lower than 10°C. However, as the temperatures tested did not include the lower lethal limit for either the aphid or the parasite, the data do not form a suitable basis for a comparison between them of the capability to develop and reproduce through low extreme temperatures.
CHAPTER 14

TWO FIELD CAGE EXPERIMENTS WITH HYPEROMYZUS LACTUCAE AND
AND APHIDIUS SONCHI

14.1 INTRODUCTION

Chapter 8 and Chapter 9 described the population dynamics of *H. lactucae* in a field cage. This chapter reports the two field cage experiments with both *H. lactucae* and *A. sonchi*. The results are used to examine the impact of the parasite on the population dynamics of the aphid by comparing the observed age distributions with those predicted by the aphid model (Chapter 9). Further analyses of the results are carried out with the aphid model after various population processes of the parasite have been incorporated, these analyses will be presented in the next chapter.

14.2 MATERIALS AND METHODS

The field cage used was the same as previously described (Chapter 8), as were the procedures for establishing the plant and aphid populations and the methods for sampling the aphid population.

*Rearing and introduction of parasites.* Second and third instar aphid nymphs from the aphid stock culture were exposed to attack by female parasites drawn from the parasite stock culture. The exposed aphids were maintained on young seedlings in the insectary until mummified. Parasites were introduced into the cage on two occasions by placing specified numbers of mummies in a 25 x 50 cm vial near each plant. The vials were laid down on their sides to prevent the entry of free water. One or two days after all the parasites were expected to have emerged, the vials were collected and brought back to the laboratory to examine the percentage of emergence.
In the meantime, some siblings of the parasites released were reared in an 
environmental cabinet at 22°C and 14L:10D to provide information on their 
age distributions and sex ratio.

Assessment of parasitization. Sixty third instar aphid nymphs (or as 
many as possible when the aphid numbers were low) were removed alive from 
each plant sampled. These third instar aphid nymphs were reared individually 
on detached young leaves in vials for a further eight days at 22°C and 
14L:10D. Daily observations were made to record the number of mummies 
formed.

Experimental design. The experiments were carried out in 1982 during 
the two seasons when the weather was favourable to both the aphid and the 
parasite, i.e. one from March to May (hereafter Third cage experiment) and 
the other one from September to November (hereafter Fourth cage experiment). 
Fig. 14.1 shows the changing temperatures recorded in the cage during the 
periods when samples were taken frequently.

![Temperature Graph](image)

**Figure 14.1** Average weekly maximum, mean and minimum temperatures 
during the periods of the two field cage experiments in 1982. Arrows 
indicate the beginnings of the experiments.
The numbers and types of aphids and parasites introduced into the cage in the two experiments and the times of introductions are shown in Table 14.1. When the Third cage experiment was started, information on many aspects of the parasite biology was not yet available, so the numbers of parasites used and the times of introductions were chosen more or less arbitrarily. By the time the Fourth cage experiment was attempted, the laboratory investigations described in the previous four chapters were nearly completed. Preliminary analysis was carried out at that time on the results obtained and the various components of the host-parasite interrelationships were added to the previously described aphid model. The numbers of parasites used and the times of introductions for the Fourth cage experiment were thus chosen, on the basis of the host-parasite model developed at that stage, to give oscillations of the aphid population throughout the season, which were neither too small to measure nor so large as to be likely to eliminate the hosts.

Table 14.1. Numbers and types of aphids and parasites introduced into the field cage in two experiments and the times of introduction (The numbers shown are averages per plant)

<table>
<thead>
<tr>
<th></th>
<th>Third cage experiment</th>
<th>Fourth cage experiment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aphids used for initial infestation of host plant</td>
<td>$2 N_4$ apt. and 4 newly moulted Aapt.</td>
<td>$3 N_4$ apt. and 3 newly moulted Aapt.</td>
</tr>
<tr>
<td>First parasite introduction</td>
<td>At 160 D$^\circ$C 1.5 mummies *</td>
<td>At 100 D$^\circ$C 4 mummies</td>
</tr>
<tr>
<td>Second parasite introduction</td>
<td>At 290 D$^\circ$C 10 mummies</td>
<td>At 200 D$^\circ$C 15 mummies</td>
</tr>
</tbody>
</table>

* Achieved by placing one and then two mummies on alternate plants.
14.3 RESULTS AND PRELIMINARY ANALYSIS

In both experiments, the plants, aphids and parasites became established and no unwanted insects were found in the cage. Of the parasites introduced 95% emerged and the sex ratios of their siblings reared in the laboratory indicated that the proportion of females in the parasites released was about 70% for all introductions. Tables 14.2 and 14.3 present the mean dry weight of host plants, the mean numbers of aphids in different instars/morphs and the mean percentage of third instar aphid nymphs parasitized on each sampling occasion in the two experiments.

14.3.1 Growth of *S. oleraceus*

The host plants, like those in the first two cage experiments, grew rapidly and appeared succulent. The relation between the increase of plant dry weight and the accumulation of effective temperatures during the sampling periods in both experiments can be described satisfactorily by exponential curves:

\[
Y = 1.370750 e^{-0.006947 x} \quad (r^2 = 0.99, \text{ d.f.} = 4, P < 0.001)
\]

for the Third cage experiment, and

\[
Y = 1.462786 e^{-0.007247 x} \quad (r^2 = 0.98, \text{ d.f.} = 6, P < 0.001)
\]

for the Fourth cage experiment, where \(Y\) is the dry weight of a plant in grams and \(x\) the accumulated D\(_{2}\)C. The curves were transformed to straight lines by plotting \(\log_{10}Y\) against \(x\) (Fig. 14.2). In Fig. 14.2, an extra line derived from the equation for the First cage experiment (8.4.1) was added to compare the growth rates of the plants in different experiments. The growth rates of the plants in the first two cage experiments had been shown to be almost identical. Thus, the similar slopes of the three lines depicted
Table 14.2  Growth of *S. oleraceus*, population of *H. lactuca* and its percent parasitization by *A. sonchi*
in Third cage experiment (March – April, 1982)

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Date</th>
<th>Accumulated D2C</th>
<th>Dry weight of plant (g)</th>
<th>Mean number of aphids per plant</th>
<th>Proportion (%) of N3 parasitized</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>N1</td>
<td>N2</td>
</tr>
<tr>
<td>1</td>
<td>25 March</td>
<td>0.0</td>
<td>1.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>4 April</td>
<td>145.3</td>
<td>3.1</td>
<td>39</td>
<td>43</td>
</tr>
<tr>
<td>3</td>
<td>12 April</td>
<td>240.2</td>
<td>7.5</td>
<td>927</td>
<td>439</td>
</tr>
<tr>
<td>4</td>
<td>19 April</td>
<td>318.6</td>
<td>14.0</td>
<td>1807</td>
<td>1444</td>
</tr>
<tr>
<td>5</td>
<td>26 April</td>
<td>389.0</td>
<td>19.7</td>
<td>10144</td>
<td>5520</td>
</tr>
</tbody>
</table>
Table 14.3. Growth of *S. oleraceus*, population of *H. lactuca* and its percent parasitization by *A. sonchi* in Fourth cage experiment (September - November 1982)

<table>
<thead>
<tr>
<th>Sample No.</th>
<th>Date</th>
<th>Accumulated D8C</th>
<th>Dry weight of plant (g)</th>
<th>Mean number of aphids per plant</th>
<th>Proportion (%) of N3 parasitized</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>N1</td>
<td>N2</td>
</tr>
<tr>
<td>1</td>
<td>16 Sept.</td>
<td>0.0</td>
<td>1.3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>27 Sept.</td>
<td>74.5</td>
<td>2.3</td>
<td>42</td>
<td>25</td>
</tr>
<tr>
<td>3</td>
<td>2 Oct.</td>
<td>98.6</td>
<td>3.2</td>
<td>48</td>
<td>51</td>
</tr>
<tr>
<td>4</td>
<td>7 Oct.</td>
<td>145.6</td>
<td>4.9</td>
<td>117</td>
<td>34</td>
</tr>
<tr>
<td>5</td>
<td>13 Oct.</td>
<td>200.8</td>
<td>6.9</td>
<td>723</td>
<td>290</td>
</tr>
<tr>
<td>6</td>
<td>21 Oct.</td>
<td>272.4</td>
<td>10.8</td>
<td>1855</td>
<td>1243</td>
</tr>
<tr>
<td>7</td>
<td>28 Oct.</td>
<td>353.4</td>
<td>16.5</td>
<td>7719</td>
<td>3399</td>
</tr>
</tbody>
</table>
Figure 14.2. Increases of dry weight of *S. oleraceus* in a field cage. The unfilled and filled circles are data points, the lines are transformed from exponential curves fitted by regression and the dotted line for First cage experiment is drawn here for comparison of the slopes of the lines (See Fig. 8.4).

in Fig. 14.2 suggest that the plants in the four experiments grew at a very similar rate on a physiological time scale.

14.3.2 Changes of Aphid Numbers and Impact of the Parasite on the Aphid Population in Third cage experiment

The aphid population in this experiment increased rapidly. The parasites from the first introduction emerged at the time when the F1 aphid nymphs had just moulted into adults. The weather at that time was sunny and warm, with average daily temperatures of 22°C max. and 6°C min., inside the cage. However, the data of sample 3 taken on 12 April indicated that the proportion of parasitized aphids in the population after the first parasite introduction was very low (Table 14.2). The proportion of parasitized aphids increased only slightly after the second parasite introduction. At the time when the
fifth sample was taken, the aphid population density had reached a very high level: Virtually all actively growing parts of the plants were covered with aphids and large numbers of adults (mostly alatae) were found on the mesh inside the cage. Since it appeared clear by that time that the parasites introduced would not have any substantial impact on the population increase of the aphid, no further samples were taken but general observations continued. The aphid population was heavily infected with a fungus disease subsequently. However, despite the heavy mortality caused by the fungus infection, the aphid population continued to survive at high densities and eventually crashed as the host plants died out in late May.

Since the aphid model described in Chapter 9 allowed the aphid population increase and the changes in age structure with time to be predicted, any substantial impact of the parasite on the aphid population should have resulted in apparent differences between the numbers of aphids observed and those predicted. When such a comparison was made with the data shown in Table 14.2, the observed population trend and changes in age structure were found to be very similar to those predicted by the aphid-only model (see Fig. 15.4). From this and the very low percentage of parasitization observed, it seems clear that the parasite had little impact on the aphid population in this experiment.

14.3.3 Changes of Aphid Numbers and Impact of the Parasite on the Aphid Population in Fourth cage experiment

During the first two weeks after the plants were infested with aphids, it was rainy and the temperature was low. Despite the bad weather, aphids established successfully on every plant and were developing and reproducing normally. Subsequently, the weather remained warm and mostly sunny during the day throughout the experiment (see Fig. 14.1). The parasites from the
first introduction were emerging during the third week when the F1 aphid nymphs had reached the fourth instar, while the parasites from the second introduction were emerging during the fourth week when the adult aphids of the new generation in the cage had just appeared. Although the initial aphid:parasite ratio had been chosen on the basis of laboratory evidence to give high, but not detrimental, percentages of parasitization, the observed proportions of third instar aphid nymphs parasitized were very low throughout the sampling period (Table 14.3). By the end of the sixth week (i.e. the end of October), the number of aphids on each plant had increased to more than 10,000 (Table 14.3). The high aphid density and low percentage of parasitization observed at that time suggested strongly that there was no point in continuing the original experimental design.

However, since it was still in the middle of the favourable season, attempts were made to reduce the aphid density and increase the relative number of parasites in the cage, thereby “starting” another similar cage experiment. As a first attempt, the plants were sprayed with tap water. An observation made 24 h after the spray showed that most of the aphids dislodged by the “heavy rain” had come back to the plants. The plants were then sprayed thoroughly with 2% soapy water. A sample taken three days later showed that the aphid number on each plant was greatly reduced (about 3,000 left on each plant). However, subsequent observations revealed that the soapy water also killed most parasite pupae inside the mummies: of the 72 brought back to the laboratory, only seven produced adult parasite. Thus, neither attempt to revitalize the experiment succeeded. The aphid population continued to increase. Within two weeks after the spray of soapy water, all the plants were covered with aphids again. No fungus-infected aphids were observed in this experiment. The aphid population
crashed in late November when the host plants died out.

The number of aphids used to start the experiment was used to initialise the aphid-only model to simulate the likely increase of aphid population during that season. Interestingly, the numbers of aphids observed in most instars/morphs throughout the sampling period appeared to be higher than those generated by the model (See Fig. 15.5), suggesting that the aphid population in this experiment increased at a higher rate than those in the earlier experiments. But such differences can probably be expected due to likely differences between the materials used to start the different experiments. Nevertheless, the observed population trend and changes in age structure were very similar to those predicted by the model. This, together with the very low percentage of parasitization observed, suggests that, again, the parasite had little impact on the aphid population.
CHAPTER 15
PRELIMINARY MODELLING OF THE HOST-PARASITE SYSTEM AND ANALYSES
OF THE HOST-PARASITE INTERACTIONS IN THE FIELD CAGE

15.1 INTRODUCTION

In this chapter, the dynamics of the host-parasite interactions observed in the laboratory are compared with those observed in the field cage. To make such a comparison possible, the various population processes of the parasite explored in the laboratory experiments were incorporated into the aphid model. The model is then used to simulate the potential impact of the parasite on the aphid populations in the last two field cage experiments and the results of the simulations are compared with the field cage data. Finally, the various mechanisms that may account for the sharply different performance of the parasite in the field cage from that in the laboratory are explored.

15.2 INCORPORATION OF THE POPULATION PROCESSES OF APHIDIUS SONCHI INTO THE APHID MODEL

This section shows how the laboratory data on the parasite were transformed and added to the aphid model.

15.2.1 Physiological Time-Scale

Preliminary overall analyses of the data obtained on the biology of the parasite showed that although the rates of various physiological processes varied with temperature, no one threshold was particularly suitable for modelling all of them. Gilbert et al. (Gilbert et al. 1976; also see Campbell et al. 1974) have pointed out, however, that physiological time scales of $D^o$ based on different thresholds are highly correlated during periods when temperatures rarely approach the threshold. Thus,
the threshold temperature and the time unit used in the aphid model were adopted for use with the parasite. Various pieces of laboratory data were converted to new population values applicable to every 8.5 D°C (1 quip) and incorporated into the model.

15.2.2 Rate of Development

The various problems associated with predicting the development of the parasite in the field have been discussed in some detail previously (13.2.2; 13.7).

Fig. 13.1 shows the relationship between temperature and developmental rate of *A. sonchi*. Strictly speaking, prediction of parasite development should be based on this curvilinear relationship, but this would complicate the model considerably. However, as discussed earlier (13.2.2), because the diurnal ranges of temperature fluctuations during the field cage experiments were similar to the amplitude of temperature alternations used in the laboratory experiments and the duration of each of the two experiments was shorter than two generations, prediction of development based on the temperature coefficients derived from alternating temperature data would probably differ very little from those based on the sigmoid curve. For these reasons, the development threshold and thermal constant calculated from alternating temperature data (Table 13.3) were used. Calculations on the temperature records from the field cage experiments showed that the threshold for the parasite could be lifted to 2.0°C without changing the predictions throughout the two seasons if the thermal constant was reduced by 30 D°. Thus the duration from egg to adult was approximated in the model by 238.0 D°C (28 quips).

Data on the developmental times of the parasite reared individually (Table 11.5) showed that the duration of egg-larval stages is about 56% of
the total time of development. In the model, this period is assumed to be 16 quips (57%) and the pupal stage 12 quips.

15.2.3 Survival Rates

(i) Survival during egg-larval stages

Over the middle temperature range little mortality occurs during the egg-larval stages (see Table 11.6 and 13.5.2) as long as the host aphids do not die before mummification takes place. Since mortality caused by the death of the host aphids will be taken into account as the deaths of the host aphids are modelled, no extra mortality was imposed on the egg-larval stages of the parasite in the model (Fig. 15.1).

(ii) Survival during pupal stage

Table 13.1 shows the percent mortality during the pupal stage and proportions of diapause of the parasite under various alternating temperature-light regimes. In the lower and middle temperature range, the total losses caused by both death and diapause were 5% or less. In the model, diapause is treated as a mortality factor because the diapausing individuals do not contribute significantly to short-term population increase. The total mortality during the pupal stage is thus taken as 5%, occurring at the middle point of the stage, i.e. at the 23rd quip after oviposition (Fig. 15.1).

(iii) Survival during adult life

Data at four different temperature-light regimes (Table 13.5; Fig. 13.3) indicated that survival rates of the parasite were little affected by temperatures below 28°C, with the mean life span being 4-5 days. Thus, strictly speaking, the survival rates of adult females should be modelled on calendar time scale. However, since the daily mean temperatures during the field cage experiments seldom went above 16°C and the adult life span
of the parasite is short, the survival rates of the adult females can be approximated on a selected physiological time-scale throughout without noticeably affecting the timing of the population growth. The survival rates of the adult females reared under 20-5°C (12.5°C mean) and 12L:12D (Fig. 13.3) were converted to D⁰ equivalent and used in the model (Fig. 15.1).

Data at different host densities (Tables 12.1 and 12.2) indicated that the survival of adult females is little affected by host density. In the model, survival is assumed to be unrelated to host density.

![Graph showing age-specific survival rates of A. sonchi in laboratory studies.](image)

**Fig. 15.1** Age-specific survival rates of *A. sonchi* in laboratory studies. Each unit of time on the abscissa equals 8.5 D⁰C.

15.2.4 Effects of Host Instars/Morphs Attacked

Data on the parasites reared from different instars/morphs (Table 11.6) indicated that developmental time and sex ratio are not actually affected by the host instar/morph but the potential fecundity may differ.
However, since the observed differences were only marginally significant, they are not considered in the model. Thus, all attributes of the parasite are assumed to be unaffected by the host instars/morphs attacked.

15.2.5 Sex Ratio

Data on the progeny sex ratio at two different temperature-light regimes (Table 13.6, Fig. 13.4) indicated that the proportions of female progeny vary little from day to day, being about 70% throughout the reproductive life of the adult female parasite. In the model, a constant proportion of 70% females is assumed among the newly emerged parasites throughout.

15.2.6 Fecundity Rates

(i) Effect of temperature

Results of the experiments at 10°C (13.3) indicated that the adult females can lay eggs at even lower temperatures. After the first parasite introductions into the two field cage experiments, temperature remained above 10°C for at least eight hours each day. It is assumed therefore that oviposition can occur throughout the experimental periods.

Data at four different temperature-light regimes (Fig. 13.3) suggested that over much of the temperature range favourable for oviposition the adult females probably oviposit at a similar rate. Thus, the oviposition rates should, strictly speaking, be modelled on a calendar time scale. Based on the same arguments as for adult female survival (15.2.3), fecundity rates are also approximated on a selected physiological time scale throughout (see below).

(ii) Effect of Host Density

Data obtained under 22°C and 14L:10D at six different host densities
(Figs. 12.2 and 12.4) show the relationship between host density and oviposition rates of the female parasites throughout adult life. Since the oviposition rates of the parasite under 22°C, 23.5-9.5°C and 20-5°C at the same host density were very similar (Fig. 13.3), it is assumed that within the favourable temperature range the female parasites respond to host density in the same manner.

To incorporate the density-dependent oviposition rates depicted in Fig. 12.4 into the model, the small number of ovipositions on the 7th day after emergence is ignored and the oviposition period, i.e. six days, is assumed to be eight quips. The model will thus simulate the timing of oviposition correctly when the daily mean temperatures remain at 13.3°C. This time scale is chosen because it is closely equivalent to that selected for survival rates (accurate at 12.5°C mean). To allow for a declining trend the oviposition rates of the adult females at different host densities are assumed to remain the same during quips 1-4 after emergence and then fall to a lower level during quips 5-8.

To derive the equations for describing the relationship between host density and oviposition rates, the total numbers of parasite eggs laid at each of the six host densities during the first three days and those laid during the second three days were each divided by four (4 quips) and the mean numbers so estimated were plotted against host density (Fig. 15.2). The relationship between the two variables in both cases was then described using Holling's (1959b) disc equation. The equations fit the data well (Fig. 15.2) and are used in the model to calculate the numbers of eggs each adult female lays at different host densities throughout her reproductive life. Thus, in each of the first four quips:

\[ N_e = \frac{2.4621N_0}{1+0.0458N_0} \]
Fig. 15.2 Relationships between host density and oviposition rates in *A. sonahi* in laboratory studies. The dots are estimated from experimental results and the continuous lines are fitted according to Holling's (1959b) disc equation.
and in each the second four quips:

\[ N_e = \frac{1.1523N_o}{1+0.0335N_o} \]

where \( N_o \) is the number of aphids available and \( N_e \) the number of eggs laid.

However, it must be remembered that the above equations were derived from experimental data obtained with second and third instar aphid nymphs. Since aphids of different instars/morphs are not equally susceptible to attack, the application of the equations must take into account the different susceptibility between instars/morphs.

(iii) Host instar preference

Table 11.9 shows the mean numbers of eggs laid in different instars/morphs when they were exposed together to attack by \( A. sonchi \). These differences in the mean numbers of eggs laid are used to calculate the different probability of aphids in each instar/morph to be parasitized for use in the model.

Since all the experiments on the oviposition rates of the parasite (Chapters 12 and 13) were carried out with second and third instar aphid nymphs, the third instar is used here as the standard instar to calculate the host instar preference index. Thus:

<table>
<thead>
<tr>
<th>Host instar/morph</th>
<th>( N_1 )</th>
<th>( N_2 )</th>
<th>( N_3 )</th>
<th>( N_4 ) apt.</th>
<th>( N ) al.</th>
<th>A apt.</th>
<th>A al.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preference index</td>
<td>0.55</td>
<td>0.77</td>
<td>1.00</td>
<td>0.64</td>
<td>0.37</td>
<td>0.41</td>
<td>0.08</td>
</tr>
</tbody>
</table>

The preference index is incorporated into the model through the following calculations at each time unit:

(a) Multiply the numbers of aphids in each of the seven instars/morphs by their respective index value. The numbers of aphids so calculated are assumed to have the same probability to be parasitized;

(b) Add together the numbers of aphids calculated in (a) and then use the
total as \( N_0 \), i.e. the number of aphids available (see above) to calculate the number of eggs to be laid and the number of aphids to be parasitized (see below); and

(c) Distribute the number of aphids to be parasitized to each of the seven instars/morphs according to their weighted numbers calculated in (a).

(iv) Superparasitization

Direct observations in the laboratory (10.6.3) showed that the adult females oviposit in previously parasitized aphids as long as the aphids are still alive, i.e. any time before mummification, but only one egg (usually the first laid) can develop into an adult in each aphid. In the model, all live aphids of a given instar/morph, either unparasitized or parasitized, are assumed to have the same probability to be attacked by the parasite, i.e. are equally likely to receive a particular parasite egg, but only the egg first laid in an aphid is taken as effective and all eggs laid subsequently are ignored.

Direct observations (10.6) and data on the distributions of eggs among host aphids (Tables 11.7 and 11.8) indicated that the adult females search for hosts at random. In the model, the total number of eggs to be laid in each quip is assumed to be allocated randomly among the host aphids of given instar/morph and thus the number of aphids to be parasitized is calculated according to the random search equation, i.e.

\[
N_p = N_0 (1 - \exp(-N_e/N_0))
\]

where \( N_p \) is the number of aphids to be parasitized and \( N_0, N_e \) as defined above.

15.2.7 Consequences of Parasitization on the Aphid

Data on the consequences of parasitization (11.2.1) indicated that (1) reproduction of the host aphid is not affected until the parasite has
completed 30% of its total development and then declines to zero within a short time (1-2 days at 17°C), and the aphid is killed when about 56% of the total developmental time of the parasite has elapsed, i.e. at the time of pupating, and (2) the timing of the occurrence of various lethal effects remains unchanged in different instars/morphs. In the model, the duration from oviposition to the end of reproduction of the aphid is approximated by 10 quips (36%), and that from oviposition to the death of the aphid is approximated by 16 quips (57%). During the first 10 quips of the parasite development, the reproduction of the parasitized aphid is taken as normal.

Data on the wing development of parasitized alatiform nymphs (11.2.2) indicated that those which become parasitized in the first instar invariably develop into normal fourth instar apteriform nymphs, while those which become parasitized in the second instar or later will grow wingpads to a varying degree or develop into normal alatae depending on the time of the beginning of parasitization. In the model, all aphids which become parasitized in the first instar and early second instar, i.e. in the first five quips after birth, are assumed to develop into apterae, and alatiform nymphs which become parasitized from the 6th quip after birth onwards are assumed to develop into alatae.

12.2.8 Synopsis of the Host-Parasite Model

The various population processes of the parasite described above were added to the aphid model (Appendix 5). Fig. 15.3 illustrates the sequences of events which now occur in the model.

Since the parasite spends its egg and larval stages inside a live aphid, the ages of both the host and the parasite have to be specified and updated simultaneously. To do this, the model stores the numbers of aphids in two two-dimension arrays, one for apterae and one for alatae.
Input numbers of aphids and parasites at time 0 (I = 0), set up number of day — degrees

$I = I + 8.5$

Apply survival rates to aphids and parasites

Aphids produce progeny

Age parasite pupae and adults

Age aphid population (Note: parasite eggs and larvae are aged along with parasitized aphids)

Sum up numbers of aphids in each instar/morph

Are there any adult female parasites? Yes

No

Sum up number of parasites in each age group

Write out current population status for both aphid and parasite

$I \geq N$? Yes

Stop

Fig. 15.3 Computer algorithm for experimental populations of *H. lactucae* and *A. sonchi.*
With the accumulation of each quip, the numbers of parasitized aphids in each age class of each array are transferred diagonally after the specified mortality factor has been applied.

The priming of the model and the way it is driven remain essentially unchanged, except that the numbers and types of parasites used in the introductions are entered through a series of "if" statements. The model now prints out the numbers of aphids in all instars/morphs and the percentage of third instar aphid nymphs parasitized at the end of each quip after the start of each population (Appendix 5). The output can then be compared with data obtained in the field cage experiments.

15.3 COMPARISON OF MODEL OUTPUT WITH FIELD CAGE DATA

The results of applying the host-parasite model to the two sets of field cage data (Tables 14.2 and 14.3) are shown in Figs. 15.4, 15.5 and 15.6.

As mentioned in Chapter 14, the observed aphid population trend and changes of age structure with time were very similar to those generated by the model when the potential impact of the parasite is not considered. Since both experiments were carried out to examine the dynamics of the host-parasite interactions, the simulated results depicted in Fig. 15.4 show that the design of the Third cage experiment was inappropriate. For even if the parasites introduced had attacked the aphid population at a similar rate to that expected from laboratory experimental evidence, the changes of the aphid population would still have differed little from those in the absence of the parasite throughout the entire season. This problem did not occur in the Fourth cage experiment where, according to the model, the parasite should have had substantial impact on the aphid population. However, the observed population trend shows no evidence of such an effect
Fig. 15.4  Comparison for Third cage experiment of observed and simulated population trends of *H. lactucae*. The dots are actual data points, while the lines are those predicted by the host-parasite model before (solid line) and after (dotted line) the impact of the parasite is incorporated. Arrows indicate the time of emergence of adult parasites from the first introduction.
Fig. 15.5  Comparison for Fourth cage experiment of observed and simulated population trends of *H. lactucae*. The dots are actual data points, while the lines are those predicted by the host-parasite model before (solid line) and after (dotted line) the impact of the parasite is incorporated. Arrows indicate the time of emergence of adult parasites from the first introduction.
Fig. 15.6 Comparison for field cage experiments of observed and simulated percent parasitization of third instar nymphs of *H. lactucae* by *A. sonchi*. The dots are actual data points, while the dotted lines are those predicted by the host-parasite model. Arrows indicate the times of emergence of adult parasites from the first introduction.
(Fig. 15.5). This, together with the wide deviations between the simulated and observed percentages of the third instar aphid nymphs parasitized in both experiments (Fig. 15.6), suggests strongly that the dynamics of the host-parasite interactions in the field cage was grossly different from that demonstrated in laboratory investigations. The greater reduction in the level of parasitization observed in the Fourth cage experiment compared to that in the Third cage experiment indicates that the impact of the parasites on the aphid population as expected from the model was further reduced in this case.

15.4 ANALYSES AND DISCUSSION

In both experiments, the observed percentages of third instar aphid nymphs parasitized were much lower than those calculated by the model immediately after the first parasite introduction. Since the numbers of adult female parasites introduced were accurately known, the obvious reductions in the percentages of parasitization were only likely to be produced by:

(1) shift of the instar preference of the parasite;
(2) heavy mortality during the egg-larval stages; and
(3) reductions of the numbers of parasite eggs laid.

The instar "preference" of the parasite detected in the laboratory trials may change under field cage conditions: in the field cage where the host aphids were not so readily to be found as in the laboratory trials, the instar preference of the parasite may be considerably relaxed, i.e. the aphids encountered were more equally likely to be successfully attacked. The results of some simulation experiments showed that relaxation of the instar preference of the parasite would result in higher proportions of the third instar nymphs being parasitized throughout the sampling periods.
A tightening of instar preference for the fourth instar aphid nymphs and adults to reduce the impact of the parasite seems very unlikely. Thus, the possible shift of the parasite's instar preference can be ignored in the present analysis.

Reductions in survival of the parasite during the egg-larval stages could decrease the observed percentages of parasitization. In this experimental setup, temperature may have been important. In the Third cage experiment, the weather during the period when samples were taken frequently was warm and sunny, with temperatures remaining well within the favourable range (Fig. 14.1; Chapter 13). Thus, the survival of the parasite in this experiment was unlikely to be reduced to any noticeable extent. However, in the Fourth cage experiment, minimum temperatures during early to mid October were usually rather low, ranging from \(-3^\circ\) to \(5^\circ\)C. It was possible that some mortality of the parasite during the egg-larval stages may have been caused by the regular short exposures to temperatures around freezing point.

The above analyses suggest that the observed reductions in the proportions of the third instar aphid nymphs parasitized were mainly a result of the parasites' failure to lay all of their eggs. With the aphid-parasite model, it is possible to simulate what happens when there is a reduction in the numbers of parasite eggs laid compared to the numbers expected from laboratory data. By running the model with different reductions in eggs laid, it became clear that the parasite was achieving only about 20% of its potential fecundity in the Third cage experiment and less than 10% in the Fourth cage experiment (Fig. 15.7). There could have been two factors responsible for this. The first is a reduction in the parasite's host searching efficiency. In the field cage, aphids on each plant aggregated on various young, actively growing parts. The area for the adult females
Fig. 15.7  Comparison of the observed (filled and unfilled circles) and simulated (solid and dotted lines) aphid population trend and level of parasitization for two field cage experiments after the age-specific oviposition rates of the parasite were reduced to 0.20 (A. Third cage experiment) or 0.05 (B. Fourth cage experiment) of those achieved in the laboratory.
to search for hosts without finding them was greatly increased. Such spatial differences in host density were very likely to reduce the searching efficiency of the parasite (cf. Morrison et al. 1980; Parkman and Shepard 1982). Circadian rhythms, as well as climate, may also influence the daily patterns of parasite activity. For example, the studies on *Cercelia gnava* (Klomp 1959) indicated that the searching efficiency may be affected by the amount of sunshine during the searching period. In addition, in the present experiments, although the parasites introduced were confined in the cage, direct observations showed that a few adult parasites, possibly responding phototactically, spent a considerable amount of time walking on the inner walls and roof of the cage. Thus, it was possible that some of the adult females were regularly or even consistently held on the cage screens and away from the aphids on the plants. On the other hand, the adult parasites observed on the cage screens were probably "natural" emigrants and some of them could have returned to the plants in the cage. This latter effect presents a potential problem in any use of field cages to study the dynamics of host-parasite interactions.

The second factor which could have contributed to the much lower numbers of eggs laid is a reduction of the survival of the adult females. In the laboratory experiments on the survival and oviposition rates of the parasite, no extra water and carbohydrates (other than from the plant material and aphids) were provided. Thus if the survival of the adult parasites was reduced in the field cage, it must have been caused by other factors. Again, the most likely important factor was temperature. Thus, as in the case of the survival of immature stages, the survival of the parasite during adult life was likely to be reduced in the Fourth cage experiment but not in the Third cage experiment.
To summarize, then, the obvious failure of the parasite to achieve its potential impact on the aphid populations in the field cage was probably due mainly to a considerable reduction in the parasite's host searching efficiency. The most likely factors responsible were spatial differences in host density, cold weather and modification of the environment by the cage. The further decrease of the potential impact seen in the Fourth cage experiment was apparently caused by the lower temperatures which were also likely to reduce the survival of the parasite.
PART V

GENERAL DISCUSSION
16.1 SPECULATION CONCERNING THE EFFECTIVENESS OF A. SONCHI AS A BIOLOGICAL CONTROL AGENT OF H. LACTUCAE IN SOUTH-EASTERN AUSTRALIA

A number of attributes have been proposed as characteristics of effective biological control agents among insect parasites. These include a high searching efficiency, a marked ability to aggregate in patches of high host density, a high degree of host specificity, a high intrinsic rate of increase relative to the host(s) and the ability to thrive over a wide range of environmental conditions (Huffaker et al. 1971; Waage and Hassell 1982). Although there are important limitations imposed on the validity of laboratory and field cage data for estimating the performance of natural enemies in the field (1.2; Mackauer and van der Bosch 1973), the results obtained in this study tend to suggest that the French strain A. sonchi has limited potential to be an effective biological control agent in south-eastern Australia. This speculation is based on the following features of the aphid-parasite system:

(i) high rates of increases of the aphid populations during both early spring and early autumn;

(ii) low searching efficiency of the parasite, especially at relatively low temperatures; and

(iii) the narrower tolerable limits of temperature of the parasite in comparison with those of the aphid.

The available information on the population dynamics of H. lactucae was reviewed earlier (2.4). In south-eastern Australia, H. lactucae is predominantly anholocyclic on S. oleraceus, reproducing viviparously
throughout the year. In the field, two peaks of abundance and of production of alates are usually observed each year, one in spring and the other one in autumn when the mean weekly temperatures are about 15-17°C and flowering host plants are relatively abundant. During the few weeks prior to the occurrence of the two peaks of aphid numbers each year temperatures in the field are usually ideal for aphid population growth, and there is a vast and expanding population of favourable host plants. Aphid numbers in the absence of natural enemies can then increase at a rate approaching very closely to the intrinsic rate of increase measured under laboratory conditions (see Maelzer 1981). This potential for population increase of *H. lactucae* in the field was demonstrated by the aphid populations in the four field cage experiments conducted in this study: the initial increases of aphid numbers in every case were approximated satisfactorily by the aphid model which was constructed with population values (e.g. speed of development, survival and fecundity rates) determined in the laboratory. The possibility that the rates of population increase of *H. lactucae* in these experiments could have been enhanced by some effects of caging cannot be positively excluded. However, Chambers *et al.* (1983), working with cereal aphids in winter wheat, showed that aphid populations inside large field cages (very similar to the one used in this study) increased at the same rates as those outside during the first few weeks of each season when the numbers of aphid-specific predators in the field were very low. These authors also showed that there were no differences in plant growth stage inside and outside the cages. In view of these reports, it seems probable that the rates of increase of the field cage populations of *H. lactucae* are similar to those in the field under comparable host plant and weather conditions. Thus, the aphid-parasite model developed in this study can be
used to prescribe properties which an effective parasite must possess. The results of some computer simulation experiments along these lines (Appendix 6) suggest that if A. sonchi is to reduce the total number of emigrants on plants infested early in a favourable season (either early spring or early autumn) to less than half, the adults of its first generation must attack at least 15% of all aphids during each quip. The searching efficiency exhibited by the parasites in the last two field cage experiments (see 15.4) suggests that A. sonchi is unlikely to be able to achieve such high levels of parasitization early in the seasons (especially in early spring), even if the population densities of the parasite are relatively high at those times (e.g., 2 parasites/plant). The analyses of the data of the last two field cage experiments (15.4; Fig. 15.7) showed that at those low temperatures (mean weekly temperatures around 10°C) where the searching efficiency (and/or probably also the survival of adults) of the parasite is reduced considerably, the aphid can still develop and reproduce normally. In fact, the rates of increase of the aphid under these conditions are higher than at relatively high temperatures if measured on the physiological time scale (see 9.2.3 and 9.4). This shows the advantages of the aphid over the parasite at the beginning of each season. Furthermore, the comparison of bioclimatic characteristics between the aphid and the parasite (13.7; Table 13.9) indicates that the aphid is more tolerant of high temperatures, suggesting that the aphid can thrive at higher temperatures than the parasite.

Having elaborated these points, it is now necessary to point out that the above speculations are in no way intended as predictions of the field performance of the parasite, as experience has shown that studies carried out in a simplified experimental universe are not to be trusted until they have
been tested in the field (Gilbert et al. 1976; Mackauer and van den Bosch 1973). Nevertheless, these points are the implications of the results obtained in this study on the interactions between the aphid and the parasite and they provide some useful indications for further work on this and probably other aphid-parasite systems.

16.2 TEMPERATURE RELATIONSHIPS: EFFECTS OF CONSTANT AND FLUCTUATING TEMPERATURES ON THE DEVELOPMENT OF INSECTS

In this study, the development of *H. lactucae* and two strains of *A. sonchi* were examined under a range of constant and alternating temperatures (Chapters 7 and 13; Appendix 4). The data obtained have been discussed in some detail in the places where they were presented. Here, an overall discussion on the three sets of data is presented.

The data on the development and survival of both the aphid and the parasite at the higher temperature levels tested showed that under alternating regimes healthy development can proceed during regular exposures to extremes which would be harmful or even lethal if experienced continuously. The results demonstrate that the effects of extreme temperatures depend upon the time patterns of exposure. This has the corollary that tolerable limits for complete development of a given species will vary with the pattern and magnitude of temperature fluctuations. In the field, extreme temperatures result from irregular fluctuations superimposed on diel and seasonal temperature variations. This means that estimates of tolerable limits obtained with standardized animals under controlled conditions are not easily applied to field conditions. The situation is made more complicated by the fact that the ability of insects to tolerate extreme temperatures may vary with their thermal history, i.e. the phenomenon of acclimatization (see review by Bursell 1974).
At the lower temperature levels tested, a constant temperature of 12.5°C and the alternating temperature regimes providing a daily mean of 12.5°C were shown to exert different influences on the development of both the aphid and the French strain of *A. sonchi*. In the aphid, males were produced when the aphid was reared at a constant 12.5°C but not at the alternating temperature regime of 20°-5°C (mean 12.5°C) or at 16°-1°C (mean 8.5°C). In the parasite, a large proportion (37.4%) of the individuals reared at a constant 12.5°C entered diapause, which contrasts sharply with the situation in those colonies maintained at two alternating temperature regimes with the same daily mean where the incidences of diapause were negligible (0.0% at 20°-5°C and 2.4% at 17.5°-7.5°C), although the night temperatures were much lower in these cases. It is noteworthy that 12.5°C is well above the developmental thresholds estimated from constant temperature data for both the aphid and the parasite.

That low constant temperatures favour the induction of diapause has also been observed in the aphid parasite, *Praon exsoletum* (Force and Messenger 1964a; Messenger 1969). With a fixed photoperiod of 12L:12D at all temperature regimes, the incidences of diapause at constant temperatures below 20°C (66% at 18.3°C, > 90% at 15.6°C and 10.0°C) were significantly higher than those observed at fluctuating temperatures with similar daily means (10.8% at 16.1°C, 37% at 12.5°C and 27.8% at 10.5°C). Thus, the data obtained on the relationship between thermoperiod and induction of diapause in the two aphid parasites (i.e. *A. sonchi* and *P. exsoletum*) do not support the applicability of Beck's (1983) suggestion that "thermoperiodic response threshold" was of major importance in determining the induction of diapause, i.e. significant incidences of diapause will occur if the cryophase temperatures (i.e. night-time temperatures) are below a species-specific threshold.
regardless of the amplitude of temperature fluctuations.

The results of analyses on the data of the developmental rates of the two strains of *A. sonahi* showed that within the favourable range, temperature variations neither stimulate nor retard the rate of development in this parasite. However, because the relationship between rate of development and temperature over the whole range is curvilinear, the developmental times at constant temperatures differed considerably from those at the corresponding alternating temperature regimes characterized by the same daily mean. The data thus reemphasize the warning given by Howe (1967) that comparison of the effects of constant and fluctuating temperatures on the rate of development of insects should always be based on cyclic temperature effects rather than on temperature means. This is a simple, but very didactic point. In the literature, claims of developmental acceleration and/or deceleration have frequently been made on the direct comparison with mean temperatures (e.g. Baker 1971; Bradshaw 1980; Hagstrum and Leach 1973; Huffaker 1944; Messenger 1964b, 1969; Wilkinson and Daugherty 1980). Evidently, no significance can be attached to results of such direct comparisons. Indeed, when appropriate weightings are applied according to the precise form of the relationship between temperature and developmental rate determined experimentally for the subject species, e.g. as has been done in this thesis, the rate of development generally turns out to be the same under constant and fluctuating temperatures (e.g. Fye *et al.* 1969; Johnson 1940; Lamb 1961; Munger and Cressman 1948; also see review by Howe 1967).

A single relationship between temperature and rate of development means that the temperature coefficients estimated from data obtained under constant temperatures can be safely used to predict the development of
insects in field conditions, provided that the temperatures do not remain outside the linear zone of the sigmoid curve for long periods. However, as the data on the two strains of *A. sonchi* indicate, considerable development may occur below the notional threshold estimated by extrapolation of the linear zone and the development above the optimum high temperature may be much less than that calculated from the fitted straight line. Thus, if temperatures experienced by the insects in the field remain outside the linear zone for long periods each day, predictions of developmental times from the mean will be too short at higher temperatures, and too long at lower temperatures.
APPENDIX 1

EFFECT OF CROWDING ON THE PRODUCTION OF ALATAE IN HYPEROMYZUS LACTUCAE: STAGES SENSITIVE TO CROWDING

It is generally recognized that in many aphids crowding plays an important role in the determination of wing development but the stages sensitive to crowding vary with the aphid species. In *Macrosiphoniella sanborni* (Gillette) and *Megoura viciae* (Buckton), the sensitivity to crowding seems exclusively prenatal (Kitzmiller 1950; Lees 1961). In other species, such as *Rhopalosiphum insertum* (Walker) and *Brevicoryne brassicae* (L.), aphids are sensitive to crowding only during the early nymphal instars (Noda 1958, Kawada 1965). In yet other species, such as *Aphis craccivora* Koch and *Aphis fabae* Scopoli, both mothers and young nymphs can respond to crowding (Johnson 1965; Shaw 1970a). It is thus clear that any attempt to study the effect of crowding on wing polymorphism in aphids must take into account the possibility of both prenatal and postnatal morph control. In *H. lactucae*, although crowding has been established as a prime factor influencing the production of alatae (see 1.3.6), the developmental stages responding to crowding remain largely unknown. This appendix reports preliminary experiments in which the responsiveness to crowding of both apterous mothers and young nymphs were briefly examined.

A1.1 MATERIALS AND METHODS

Experience in the earlier part of this study had shown that if apterae, which were born and reared to maturity at low densities (i.e. <10 aphids/flowering shoot), were held at a low density after the final moult (i.e. <3 adults/flowering shoot), their progeny, if also reared at low density,
generally did not form wings, i.e. less than 20% of them became alatae. For the purpose of the following experiments, adult and nymphal aphids were regarded as uncrowded if they were held at densities of <3 or <10 per flowering shoot respectively.

Rearing was carried out in environmental cabinets so that temperature and photoperiod could be controlled. In every case, mothers and progeny were reared at the same temperature-light regime.

Preparation of uncrowded apterae. Fourth instar apteriform nymphs from the stock culture were reared to adulthood at a density of 3 per flowering shoot. Nymphs less than 24 h old were collected from these apterae and reared to adulthood at a density of 8-10 per flowering shoot. Apterae among these adults were regarded as uncrowded.

Preparation of crowded apterae. To obtain maximal crowding history, third instar nymphs from a naturally dense population on plants in a field cage were reared to adulthood at densities of 20-30 per flowering shoot. Eighty percent of such nymphs developed wings so that the apterae among them could be regarded as intensely crowded.

A1.2 PRENATAL CROWDING EXPERIMENT

Samples of nymphs from uncrowded apterae and those from crowded apterae were collected within 2 h of birth and reared at a low density of ten per flowering shoot to adults under each of the two temperature-light regimes: 20-5°C, 12L:12D; and 16-1°C, 12L:12D.

The proportions of the nymphs becoming alatae among the progenies of the two types of mothers are shown in Table A1.1. Alatae were more frequent among the progeny of crowded apterae. Since under each temperature-light regime the progenies of both uncrowded and crowded apterae were given identical treatment, the different proportion of alatae must be due to prenatal crowding.
A1.3 POSTNATAL CROWDING EXPERIMENT

This experiment was carried out also with two different temperature-light regimes: 22°C, 12L:12D; and 15°C, 12L:12D. Under each temperature-light regime, samples of nymphs from uncrowded apterae only were collected within 4 h of birth and held on 28 cm² surface of young leaves in plastic jars. Variations in density were achieved by using a specific number of the newly born nymphs together with about the same number of third instar nymphs drawn from the aphid stock culture (see Table A1.2). The latter were much larger and easily differentiated from the experimental nymphs. After the specific exposure period the experimental nymphs were transferred

Table A1.1 Proportions of alatae among progenies of crowded and uncrowded mother apterae

<table>
<thead>
<tr>
<th>Rearing condition of progeny*</th>
<th>Progeny of crowded mothers</th>
<th>Progeny of uncrowded mothers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>Alatae</td>
</tr>
<tr>
<td>20-5°C 12L:12D</td>
<td>62</td>
<td>28</td>
</tr>
<tr>
<td>16-1°C 12L:12D</td>
<td>80</td>
<td>53</td>
</tr>
</tbody>
</table>

* Higher temperature in each 24 h coincides with the light period.

Table A1.2 Effect of crowding during nymphal development on the production of alatae in *H. lactucae*. A 12L:12D photoperiod was used at both constant temperatures

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Experience of crowding</th>
<th>Resultant morph</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Density*</td>
<td>Morphology</td>
</tr>
<tr>
<td></td>
<td>Hours</td>
<td>End of crowing</td>
</tr>
<tr>
<td>22</td>
<td>40 N₁ + 30 N₃</td>
<td>1-24 Late 1st instar</td>
</tr>
<tr>
<td></td>
<td>40 N₁ + 30 N₃</td>
<td>1-48 Early 2nd instar</td>
</tr>
<tr>
<td></td>
<td>80 N₁ + 80 N₃</td>
<td>1-24 Late 1st instar</td>
</tr>
<tr>
<td></td>
<td>80 N₁ + 80 N₃</td>
<td>1-48 Early 2nd instar</td>
</tr>
<tr>
<td></td>
<td>80 N₁ + 80 N₃</td>
<td>1-72 End 2nd instar</td>
</tr>
<tr>
<td>15</td>
<td>80 N₁ + 80 N₁</td>
<td>1-60 End 1st instar</td>
</tr>
<tr>
<td></td>
<td>80 N₁ + 80 N₃</td>
<td>1-120 End 2nd instar</td>
</tr>
</tbody>
</table>

* The numbers shown are rearing densities per 28 cm² leaf area.
to new young leaves and reared to adulthood at a low density of 10 per 28 cm² leaf surface under the same temperature-light regime as during exposure to crowding.

The proportions of nymphs becoming alatae in relation to exposure density, exposure period and exposure temperature are shown in Table A1.2. At 22°C, the proportion of alatae was consistently higher at the higher density, and at the higher density increased exposure periods gave higher proportions of alatae. Increased exposure period at 15°C did not increase the proportion of alatae.

A1.4 DISCUSSION

The results obtained in the prenatal crowding experiment show that in *H. lactuca* crowding of the apterous mothers increases the proportion of alatae among their progeny. However, as the progeny in this experiment were reared in small groups, it is not clear whether the morph of the progeny could be determined during late embryonic development or crowding of the mothers only increased the potential of their progeny to become alatae during nymphal development.

The results obtained in the postnatal crowding experiment demonstrate the promoting effects of crowding during nymphal development on wing production in this aphid. However, although considerable mortality occurred in the original third instar nymphs where 80 newly born nymphs and 80 third instar nymphs were held together for more than 24 h, in no case did the proportion of alatae exceed 60%. Presumably, the relatively low proportions of alatae produced were mainly due to absence of prenatal crowding. If this is true, the absence of increase in proportion of alatae with longer duration of crowding at 15°C may well be caused by the low potential of the progeny to develop into alatae. It is also possible that
the use of young leaves as substratum contributed partially to the relatively low proportions of alatae, as the aphids reared on young leaves mostly fed on the veins and maximum tactile interaction could not be achieved despite the high mortality.

To sum up, the results in the two experiments show that in *H. lactucae* both prenatal crowding and postnatal crowding favour the production of alatae, and that in postnatal crowding the nymphal stages sensitive to crowding probably cover the whole duration of the first two instars.
APPENDIX 2
THE APHID MODEL

A2.1 Glossary of Fortran Symbols

alden  alatae density, number of alate aphids in each age class
alfec  alate fecundity rates
apal  nymphs in late first instar developing into either apterae or alatae
apden  apterae density, number of apterous aphids in each age class
apfec  apterae fecundity rates
avtemp  average temperature experienced during nymphal development and early adult life
degree  number of day-degrees being run
dens  aphid density, defined as mean number of aphids per gram dry weight of plant
fact  correction factor for effect of temperature on fecundity rates
fact 1  array for storing correction factors for effect of temperature on fecundity rates of apterae
fact 2  array for storing correction factors for effect of temperature on fecundity rates of alatae
gram  dry weight of plant in grams
mt  daily mean temperature applying to each quip
nd  number of day-degrees to be run
nq  number of quips to be run
nquip  number of the current quip being run
perc  a function calculating the proportion of nymphs developing into alatae
resurv  correction factor for survival rates
stage  developmental stages of the aphid
surv  survival rates
temp  a symbol copying the number of day-degrees being run for temporary use
tempt  total of mean temperatures experienced during nymphal development and early adult life
total  total number of aphids per plant
young  young produced during the current quip
A2.2 Program Listing (Final Version)

(With initial input of Second cage experiment)
if (apdens(i).eq.0.0.and.aldens(i).eq.0.0) go to 15
continue
end if
if (apdens(15).le.0.0.and.aldens(16).le.0.0) go to 18

if (avtemp.eq.10.0) avtemp=10.0
fact1=0.00756-0.33697*avtemp
fact1(15), fact2(16)= fact
continue

young=0.0
do 19 j=15,65
young=young*apdens(i)*apfec(j)*fact1(j)
do 19 continue

apa1 =apdens(4)
do 30 k=70,6,-1
apdens(k)=apdens(k-1)
aldens(k)=aldens(k-1)
do 30 continue

35 apdens(i)=apdens(i-1)
aldens(i)=aldens(i-1)
do 35 continue

avtemp=avtemp+32
if (avtemp.eq.10.0) avtemp=10.0
fact1=0.00756-0.33697*avtemp
fact1(15), fact2(16)= fact
continue

do 150 iquip=1,7
stage(i)=total*apdens(i)
do 150 continue

155 do 70 iquip=1,7
stage(1)=stage(1)+apdens(i)
do 70 continue

if (degree.ge.50) degree=50
if (degree.ge.500) degree=500
if (degree.ge.5000) degree=5000
gram=1.071342*exp(0.006558*degree)

160 function perc(degree,total,dens)

calculate the proportion of alatoids
dens=total/gram
perc=exp(-29.9647/(dens**0.7456))
if (perc.le.0.1) perc=0.1
return

end
A2.3 An example of output of the model
(Second cage experiment)

<table>
<thead>
<tr>
<th>no. cut</th>
<th>instar 1</th>
<th>instar 2</th>
<th>instar 3</th>
<th>instar 4</th>
<th>instar 5</th>
<th>instar 6</th>
<th>adult male</th>
<th>adult female</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.35</td>
<td>.90</td>
<td>.65</td>
<td>.50</td>
<td>.45</td>
<td>.40</td>
<td>.35</td>
<td>.30</td>
<td>.30</td>
</tr>
<tr>
<td>2</td>
<td>1.38</td>
<td>1.00</td>
<td>.30</td>
<td>.20</td>
<td>.10</td>
<td>.05</td>
<td>.05</td>
<td>.05</td>
<td>.05</td>
</tr>
<tr>
<td>3</td>
<td>1.40</td>
<td>1.00</td>
<td>.50</td>
<td>.40</td>
<td>.30</td>
<td>.20</td>
<td>.10</td>
<td>.10</td>
<td>.10</td>
</tr>
<tr>
<td>4</td>
<td>1.42</td>
<td>1.00</td>
<td>.60</td>
<td>.50</td>
<td>.40</td>
<td>.30</td>
<td>.20</td>
<td>.20</td>
<td>.20</td>
</tr>
<tr>
<td>5</td>
<td>1.45</td>
<td>1.00</td>
<td>.70</td>
<td>.60</td>
<td>.50</td>
<td>.40</td>
<td>.30</td>
<td>.30</td>
<td>.30</td>
</tr>
<tr>
<td>6</td>
<td>1.47</td>
<td>1.00</td>
<td>.80</td>
<td>.70</td>
<td>.60</td>
<td>.50</td>
<td>.40</td>
<td>.40</td>
<td>.40</td>
</tr>
<tr>
<td>7</td>
<td>1.50</td>
<td>1.00</td>
<td>.90</td>
<td>.80</td>
<td>.70</td>
<td>.60</td>
<td>.50</td>
<td>.50</td>
<td>.50</td>
</tr>
<tr>
<td>8</td>
<td>1.52</td>
<td>1.00</td>
<td>1.00</td>
<td>.90</td>
<td>.80</td>
<td>.70</td>
<td>.60</td>
<td>.60</td>
<td>.60</td>
</tr>
</tbody>
</table>

274
PRELIMINARY STUDIES ON DIAPAUSE OF *APHIDIUS SONCHI*

A3.1 THE INFLUENCE OF FOOD ON THE INDUCTION OF DIAPAUSE

This experiment was carried out in the insectary during September and October, 1981 (22-25°C, 14L:10D, 50-60% R.H.). Two mated, 2-3 days post-emergent female parasites from the parasite stock culture were introduced into each of five caged pots each containing a flowering shoot bearing approximately 100 second and third instar aphid nymphs from the aphid stock culture. After a 24 h period, all the female parasites were removed. The exposed aphids were divided randomly into two groups. Aphids in one group were reared on growing young seedlings in a 15 cm plastic pot containing soil, while those in the other were reared individually on detached young leaves placed on nutritive agar in a vial. The pot and the vials were placed side by side in the insectary.

Table A3.1 The incidence of diapause in *A. sonchi* at 22-25°C and 14L:10D when its host aphids were reared on young seedlings and detached young leaves

<table>
<thead>
<tr>
<th>Substrate for aphids</th>
<th>N</th>
<th>Resultant parasites</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>No. non-diapause</td>
<td>No. diapause</td>
</tr>
<tr>
<td>Young seedlings in soil</td>
<td>240</td>
<td>222 (92.5%)</td>
<td>18 (7.5%)</td>
</tr>
<tr>
<td>Detached leaves on agar</td>
<td>112</td>
<td>42 (37.5%)</td>
<td>70 (62.5%)</td>
</tr>
</tbody>
</table>

Table A3.1 shows the results of this experiment: the proportion of parasite progeny that entered diapause was much higher when the host aphids were reared on detached young leaves than when reared on growing seedlings. Although the light intensity in the vials might have been somewhat different from that in the pot, it is unlikely that the eight-fold difference observed could have been caused by the slight difference in light intensity. Thus,
It seems difficult to escape the conclusion that the observed difference was mainly due to the different substrates on which the host aphids were reared.

A3.2 THE INFLUENCE OF TEMPERATURE AND PHOTOPERIOD ON THE INDUCTION OF DIAPAUSE

See 13.2 and Table 13.1. The data collected indicated that with a photoperiod of 12L:12D, low constant temperature favours the induction of diapause in comparison with the alternating temperature regimes providing the same daily mean.

A3.3 DEVELOPMENTAL RATE OF DIAPAUSE AND NON-DIAPAUSE INDIVIDUALS

Female parasites and aphids used were obtained from their respective stock cultures. Freshly parasitized second and third instar nymphs were reared individually on young leaves set in the vial under two different temperature-light regimes (Table A3.2) during August and September, 1981, and the time from oviposition to mummification was recorded for each individual. Classification of the parasites, i.e. diapause or non-diapause, was carried out by keeping all the mummies individually in 4 x 1 cm vials under the experimental conditions until about one week after the non-diapause adults emerged and then dissecting all the unproductive mummies to see the live larvae inside.

Table A3.2 Mean duration of time from oviposition to mummification of non-diapause and diapause individuals of *A. sonchi*

<table>
<thead>
<tr>
<th>Rearing conditions</th>
<th>Time in days from oviposition to mummification</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Non-diapause (N)</td>
</tr>
<tr>
<td>22°C 14L:12D</td>
<td>6.0 (71)</td>
</tr>
<tr>
<td>17°C 13L:11D</td>
<td>10.2 (23)</td>
</tr>
</tbody>
</table>
The results of this experiment (Table A3.2) suggest that individuals which are going to enter diapause and those which are not going to enter diapause develop at a similar rate during the egg and larval stages.

A3.4 DURATION AND TERMINATION OF DIAPAUSE

About 300 mummies housing diapausing parasites collected in various experiments were maintained in the insectary. These mummies were observed every ten days in the first three months and thereafter observed once a month. All the unproductive mummies were dissected at the end of twelve months. Results of the observations can be summarized as follows: Under the insectary conditions, about 30% of the diapausing parasites resumed development and emerged successfully after two to three months (the developmental time from egg to adult for non-diapause parasites was 10-12 days under the same conditions). The remaining parasites (about 70%), on being dissected out of their mummies at the end of twelve months, were all found dead. As it was not possible to specify the developmental stage of the dead individuals, it could not be determined if any of the parasites had resumed development before dying.

A3.5 DIFFERENCES BETWEEN THE TWO STRAINS

All the descriptions of and results of experiments on diapause presented in Chapter 10 (10.9) and above refer exclusively to the French strain of A. sonchi (see 4.5).

During the course of this study, no diapause individuals were found in the Japanese strain, either in the stock culture of this strain maintained in the insectary, or in experimental populations of this strain reared at various temperature-light regimes (Appendix 4).
A4.1 INTRODUCTION

This appendix presents the results of some laboratory experiments on the development, body size and potential fecundity of the Japanese strain *A. sonchi* reared under various temperature-light regimes. The experiments were carried out concurrently with the same experiments on the French strain *A. sonchi* described in 13.2. Their purposes were to compare the bioclimatic characteristics of the two strains and their responses to constant and alternating temperatures.

A4.2 MATERIALS AND METHODS

The test aphids used and the experimental procedures were the same as described for the French strain in 13.2.1. Adult parasites used to start the experimental cultures were 1-2 days post-emergent, mated females obtained from the stock culture of the Japanese strain *A. sonchi* (see 4.5). The experiment under each of the twelve temperature-light regimes used (Table A4.1) was started on the same day as the equivalent experiment with the French strain and the experimental cultures of the two strains were maintained in the same environmental cabinet.

A4.3 RESULTS AND ANALYSIS

A4.3.1 Rate of Development and Diapause

Time from oviposition to emergence of adults increased with decreased temperatures, either constant or alternating (Table A4.1). In every case, males reached the adult stage a little earlier than females. However,
since the differences between sexes were consistently small, the analysis of developmental rate was carried out on the pooled data.

The general pattern of developmental rate in response to constant and alternating temperatures was very similar to that of the French strain: as in the French strain (Table 13.1), the Japanese parasites reared under alternating temperatures reached the adult stage earlier in the cooler regimes but took longer to develop in warmer regimes, and under the three temperature regimes with a daily mean of 12.5°C, the developmental time decreased as the amplitude of temperature alternation increased (Table A4.1).

The various considerations that must be taken into account in the comparison of the effects of constant and fluctuating temperatures were discussed in 13.2.2. For the Japanese strain, the data obtained under constant temperatures were also found to be described satisfactorily by the empirical Pearl-Verhulst logistic curve (Fig. A4.1; see Davidson 1944). The data obtained at 28°C were excluded from the curve fitting as the reversal in trend of development at this temperature was again obvious. With the fitted curve, the rate of development observed over the range 26-11.5°C under variable regimes can be examined to show the effect, if any, of temperature fluctuations. The results indicated that, as in the French strain, developmental rates of the parasites were very similar under constant and alternating temperatures as shown by the following table:

<table>
<thead>
<tr>
<th>Temperature-light regime</th>
<th>Percent development per day</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>26-11.5°C, 14L:10D</td>
<td>7.75</td>
<td>218</td>
</tr>
<tr>
<td></td>
<td>7.88</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-1.68</td>
<td></td>
</tr>
</tbody>
</table>

Thus, the data again suggest that within the mid range temperature alternation neither accelerates nor retards the development of the parasite. As discussed
in 13.2.2, if one accepts the assumption that when a temperature outside this range is alternated with a temperature within it, the effect of the latter on the developmental rate of the parasite is still that specified by the constant-temperature curve, the amount of development experienced at the temperature extreme can be estimated. Such estimates were made with the data obtained under the four alternating temperature regimes including the extremes. The estimated rates of development at the extreme temperatures generally agreed closely with those extrapolated from the curve for the constant temperature (Table A4.2).

The results suggest that the relationship between temperature and rate of development in the Japanese strain *A. sonchi* is very similar to that for the French strain (see Fig. 13.1). Thus, the considerations with regard to the interpretation of temperature effects based on daily means for the French strain (13.2.2) also apply here. Accordingly, if the reciprocals of developmental times (or the reciprocals multiplied by 100) are plotted against daily mean temperatures and a linear regression is used to estimate the developmental threshold and thermal constant (see Campbell *et al.* 1974), different values will be obtained with data collected under temperatures with different patterns of fluctuations. The calculations with the data shown in Table A4.1 (within the appropriate range) show that the threshold temperature estimated from data obtained under alternating temperature regimes with a diurnal range of 14–15°C was 5.6°C lower than that estimated from constant temperature data (Table A4.3; Fig. A4.2). Although the thermal constant estimated from alternating temperature data was higher, the two sets of temperature coefficients will give quite different predictions of the development of the parasite in the field, especially when temperature remains long outside the linear zone of the sigmoid curve.

In contrast with the French strain in which diapause occurred in most
Table A4.1  Mortality during pupal stage, developmental time of the Japanese strain
A. sonahi under various temperature-light regimes

<table>
<thead>
<tr>
<th>Rearing conditions*</th>
<th>N</th>
<th>Mortality during pupal stage</th>
<th>Mean time in days from oviposition to emergence of adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Male (N)</td>
<td>Female (N)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>28°C</td>
<td>14L:10D 50-80% R.H.</td>
<td>188 34 (18.1%)</td>
<td>9.6 (39)</td>
</tr>
<tr>
<td>26°C</td>
<td>14L:10D 50-80% R.H.</td>
<td>139 11 (9.2%)</td>
<td>9.2 (30)</td>
</tr>
<tr>
<td>24°C</td>
<td>14L:10D 50-70% R.H.</td>
<td>127 3 (2.4%)</td>
<td>9.5 (19)</td>
</tr>
<tr>
<td>28-13.5°C</td>
<td>14L:10D 40-80% R.H.</td>
<td>117 1 (0.9%)</td>
<td>11.8 (23)</td>
</tr>
<tr>
<td>22°C</td>
<td>14L:10D 70-90% R.H.</td>
<td>102 2 (2.4%)</td>
<td>10.7 (28)</td>
</tr>
<tr>
<td>26-11.5°C</td>
<td>14L:10D 70-90% R.H.</td>
<td>223 5 (2.2%)</td>
<td>12.8 (40)</td>
</tr>
<tr>
<td>20°C</td>
<td>14L:10D 60-90% R.H.</td>
<td>100 2 (2.0%)</td>
<td>11.8 (24)</td>
</tr>
<tr>
<td>23.5-9.5°C</td>
<td>13L:11D 60-85% R.H.</td>
<td>183 3 (1.7%)</td>
<td>15.5 (23)</td>
</tr>
<tr>
<td>17°C</td>
<td>13L:11D 70-90% R.H.</td>
<td>104 1 (1.9%)</td>
<td>17.1 (20)</td>
</tr>
<tr>
<td>20-5°C</td>
<td>12L:12D 70-85% R.H.</td>
<td>128 1 (0.8%)</td>
<td>22.3 (22)</td>
</tr>
<tr>
<td>17.5-7.5°C</td>
<td>12L:12D 70-85% R.H.</td>
<td>276 4 (1.5%)</td>
<td>25.6 (50)</td>
</tr>
<tr>
<td>12.5°C</td>
<td>12L:12D 70-80% R.H.</td>
<td>104 3 (2.9%)</td>
<td>29.9 (39)</td>
</tr>
</tbody>
</table>

* In case of alternating temperature regimes, the higher temperature coincides with the light period each 24 h, and the data of each alternating temperature regime and those of the corresponding constant temperature are grouped more closely by extra horizontal space.
Fig. A4.1 Developmental rate of the Japanese strain *A. sonohi* at constant temperatures. The circles on the graph are observed values.

\[ y = \frac{15.1159}{1 + e^{3.546400 - 0.180802x}} \]

Fig. A4.2 Rate of development of the Japanese strain *A. sonohi* at constant temperatures and that at alternating temperatures with an alternating amplitude of 14-15°C. The filled and unfilled circles are observed values and lines are drawn according to the linear regressions shown in Table A4.3.
Table A4.2  Comparison between the estimated developmental rates of *A. sonchi* under some extreme temperatures which were each alternated with a favourable temperature and developmental rates under these temperatures as extrapolated from the constant-temperature curve

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Percent development per day</th>
<th>Estimated*</th>
<th>Extrapolated</th>
<th>Difference (%)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.0</td>
<td>1.00</td>
<td>1.01</td>
<td>-1.00</td>
<td></td>
</tr>
<tr>
<td>7.5</td>
<td>1.61</td>
<td>1.51</td>
<td>+5.60</td>
<td></td>
</tr>
<tr>
<td>9.5</td>
<td>2.24</td>
<td>2.09</td>
<td>+6.70</td>
<td></td>
</tr>
<tr>
<td>28.0</td>
<td>11.58</td>
<td>12.39</td>
<td>-6.56</td>
<td></td>
</tr>
</tbody>
</table>

* See text for methods of estimation.
† Differences expressed as the percent increase of the estimated value in comparison with the extrapolated.

Table A4.3  Temperature coefficients and regression equations for the relationship between temperature and rate of development in the Japanese strain of *A. sonchi*

<table>
<thead>
<tr>
<th>Temperature regime</th>
<th>Development threshold, t (°C)</th>
<th>Thermal constant, K (D°C)</th>
<th>Linear regression Equation†</th>
<th>r²</th>
<th>D.F.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td>7.49</td>
<td>158.86</td>
<td>100/Y=0.6295x-4.7152</td>
<td>0.9906</td>
<td>4</td>
</tr>
<tr>
<td>Alternating*</td>
<td>1.83</td>
<td>240.51</td>
<td>100/Y=0.4158x-0.7570</td>
<td>0.9987</td>
<td>3</td>
</tr>
</tbody>
</table>

* Alternating with an amplitude of 14-15°C.
† In the equations, Y is the number of days required to develop from egg to adult under the daily mean temperature x.

Table A4.4  Head width and number of eggs on the day of emergence of adult females of the Japanese strain *A. sonchi* reared at three different temperature-light regimes

<table>
<thead>
<tr>
<th>Rearing condition</th>
<th>N</th>
<th>Head width*</th>
<th>No. eggs on the day of emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean ± S.E.</td>
<td>Mean ± S.E.</td>
</tr>
<tr>
<td>28-13.5°C 14L:10D</td>
<td>30</td>
<td>25.23±0.16</td>
<td>187.97±7.81</td>
</tr>
<tr>
<td>23.5-9.5°C 13L:11D</td>
<td>30</td>
<td>24.80±0.18</td>
<td>207.53±9.34</td>
</tr>
<tr>
<td>20-5°C 12L:12D</td>
<td>30</td>
<td>24.83±0.18</td>
<td>182.97±9.06</td>
</tr>
</tbody>
</table>

* Head width is presented in units, 50 units = 1.00 mm.
of experimental cultures, no diapause individuals were observed in the Japanese strain under all the temperature-light regimes tested.

A4.3.2 Mortality During Pupal Stage

Mortality during the pupal stage was consistently low within the range of daily mean temperatures from 12.5°C to 24°C, either constant or alternating (Table A4.1). Under constant temperatures above 24°C, the mortality during pupal stage evidently increased as temperature rose. The substantial mortality and the obvious reversal in trend of developmental rate shown by the parasites reared at 28°C suggest that the upper lethal constant temperature for complete development was being approached.

A4.3.3 Body Size and Number of Eggs in the Ovaries

The mean head widths and the mean numbers of eggs in the ovaries of the parasites reared under three different temperature-light regimes are shown in Table A4.4. Analysis of variance showed that there were no significant differences in the two attributes between the three cohorts of parasites (for head widths F = 1.96 and for number of eggs F = 2.19, d.f. = 2/87, in both cases P > 0.05).

A4.4 DISCUSSION

It has long been recognized that insects with broad geographic distributions have often evolved ecotypes adapted to different types of climate (Messenger & van den Bosch 1971). Populations of the same species from different climatic zones often exhibit different responses to temperature and other climatic factors (Campbell et al. 1974; Flint 1980). The two stocks of *A. sonchi* examined in this study originated from widely separated parts of the species' range: the Drome Department, France and Kyoto, Japan. Climatic conditions in the two localities are similar and can be broadly classified
Table A4.5 Climate data of the collection sites of two strains of *Aphidius sonchi* (Temperature in Celsius)

<table>
<thead>
<tr>
<th>Collection site</th>
<th>Altitude (m)</th>
<th>Mean annual temperature</th>
<th>Mean annual precipitation (mm)</th>
<th>Mean daily temperature of the coldest month</th>
<th>Mean daily min. temperature of the coldest month</th>
<th>Mean daily temperature of the hottest month</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kyoto (Japan)</td>
<td>43</td>
<td>13.8</td>
<td>1600</td>
<td>2.0</td>
<td>-2.0</td>
<td>25.0</td>
</tr>
<tr>
<td>Valence* (France)</td>
<td>126</td>
<td>12.3</td>
<td>904</td>
<td>3.0</td>
<td>0.2</td>
<td>22.0</td>
</tr>
<tr>
<td>Vernoux* (France)</td>
<td>580</td>
<td>11.3</td>
<td>1214</td>
<td>2.0</td>
<td>0.6</td>
<td>21.0</td>
</tr>
</tbody>
</table>

* The collection site of the French strain is about 15 km south of Valence and Vernoux, and is considered to have a type of climate intermediate between the two localities.
as humid with cold winters (Table A4.5; Walter and Lieth 1967). However, the summers in the collection site in France are generally cooler and less humid than those in Kyoto. The data collected in this study showed that the two strains have very similar temperature requirements for complete development (Tables 13.3 & A4.3; Figs. 13.2 & A4.2), but the Japanese strain is more tolerant of high temperatures (as indicated by the systematic differences in mortality during the pupal stage under higher temperature regimes between the two strains, see Fig. A4.3). Thus, the results tend to support the concept that the bioclimatic characteristics of different populations of an insect are adjusted to local conditions (see above).

![Fig. A4.3 Percent mortality during pupal stage of two strains of *A. sonchi* at high temperatures.](image)

Under all the temperature-light regimes tested, no diapause individuals were found in the Japanese strain, while a low incidence of diapause was observed in nearly all the experimental cultures of the French strain (Table
The marked differences between the two strains in this aspect of their physiology cannot be explained. In fact, it is quite odd to see that no diapause was induced in the Japanese strain over the whole temperature/photoperiod range tested. This is because the climate in Kyoto is characterized by hot summers and cold winters and the data obtained in this study on the development of this strain suggest strongly that the local population there must possess the ability to enter diapause to survive through both extreme cold and hot seasons. It is possible that the temperature-light regimes tested did not include the lower temperature/photoperiod threshold for induction of hibernal diapause in this strain. However, at the highest temperature combined with long photoperiod tested, i.e. 28°C, 14L:10D, the parasites suffered obvious deleterious effects (Table A4.1), yet no diapause occurred.

The relationship between temperature and rate of development over the whole range in the Japanese strain was shown to be very similar to that in the French strain, being characterized by a shallow-sigmoid curve. Also, like in the French strain, little evidence was found for a developmental acceleration or deceleration caused by temperature alternations.

The data on the body size and number of eggs in the ovaries of the Japanese strain showed that within the range examined temperature and photoperiod exert little effect on these two attributes of the parasite. This is again equivalent to the situation in the French strain (13.2.2, Table 13.4). Subsequent comparison showed that there were no significant differences in either of the two attributes between the two strains under each of the three temperature-light regimes tested (by t-test, in each case, P > 0.05).
APPENDIX 5

THE APHID-PARASITE MODEL

A5.1 Glossary of Fortran Symbols

alate  an array storing % of alatiform nymphs
apal  nymphs aged 12 developing into either apterae or alatae
egg1  eggs to be laid in the current quip by "waspl"
egg2  eggs to be laid in the current quip by "wasp2"
para  total aphids to be parasitized in the current quip
para3 percentage of 3rd instar aphid nymphs parasitized
pden  an array storing the number of parasites in each age class
pref  an array storing weighted numbers of aphids in each instar/morph
prob probability of each weighted aphid to be parasitized in the current quip
psurv an array storing survival rates of parasite
sum  total of weighted aphid numbers in the current quip
totegg total number of parasite eggs to be laid in the current quip
tpara total number of parasites
up3  proportion of unparasitized 3rd instar aphid nymphs
waspl female parasites aged 29-32
wasp2 female parasites aged 33-36

(For all the rest of the Fortran symbols, see A2.1)
A5.2 Program Listing  
(With the initial input of the Fourth cage experiment)
2. apply survival rates to parasites

\[ \text{do } i = 22, 37 \]
\[ \text{pden}(i) = \text{pden}(i) \times \text{psurv}(i) \]

3. aphids produce babies

\[ \text{aphids produce babies}(n \cdot b \cdot \text{parasitoid aphids}) \]
\[ \text{produce normally until the parasite larva inside reaches age 10, then stop reproducing} \]

3.1 calculate the correction factor for effect of temperature on fecundity rates of aphids

\[ \text{do } i = 65, 16 \]
\[ \text{fact}1(i) = \text{fact}1(i-1) \]
\[ \text{fact}2(i) = \text{fact}2(i-1) \]
\[ \text{if} \left( \text{ntau} < \text{eq}1 \right) \text{then} \]
\[ \text{temp} = 0.0 \]
\[ \text{do } i = 45 \]
\[ \text{temp} = \text{temp} + \text{t}(i-16) \]
\[ \text{avtemp} = \text{temp} / 33.0 \]
\[ \text{fact}1(i) = 1.820750 - 0.036937 \times \text{avtemp} \]
\[ \text{do } i = 46, 70 \]
\[ \text{fact}1(i), \text{fact}2(i) = \text{fact}1(i), \text{fact}2(i) \]
\[ \text{end if} \]

4. calculate the number of young to be produced

\[ \text{do } j = 15, 65 \]
\[ \text{young} = \text{young} + \text{apdens}(j, i) \times \text{apfec}(j) \times \text{fact}1(j) \]
\[ \text{continue} \]

4.2 age the population

4.2.1 age parasite pupae and adults

\[ \text{do } i = 37, 18 \]
\[ \text{pden}(i) = \text{pden}(i-1) \]
\[ \text{continue} \]
\[ \text{pden}(17) = 0.0 \]
\[ \text{do } i = 12, 70 \]
\[ \text{pden}(17) = \text{pden}(17) + \text{apdens}(i, 17) + \text{aldens}(i, 17) \]
\[ \text{continue} \]
\[ \text{do } i = 78 \]
\[ \text{aldens}(i, 17) = 0.0 \]
\[ \text{continue} \]
\[ \text{do } i = 16, 70 \]
\[ \text{fact}1(15), \text{fact}2(16) = \text{fact}1(15), \text{fact}2(16) \]
\[ \text{continue} \]

4.2.2 age aphids in all other age classes

4.2.2.1 unparasitized apterous aphids

\[ \text{do } i = 12, 2 \]
\[ \text{do } j = 17, 3 \]
\[ \text{apdens}(i, j) = \text{apdens}(i-1, j-1) \]
\[ \text{continue} \]

4.2.2.2 parasitized apterae and alatae, 4th instar onwards

\[ \text{do } 100 \]
\[ \text{iif} (i < 13) \text{go to } 90 \]
\[ \text{apdens}(i, 1) = \text{apdens}(i-1, 1) \]
\[ \text{continue} \]
\[ \text{apdens}(1, 1) = \text{young} \]

4.2.2.3 aphids instar 1–3, parasitized

\[ \text{do } 110 \]
\[ \text{iif} (i < 15) \text{go to } 90 \]
\[ \text{apdens}(i, 1) = \text{apdens}(i-1, 1) \]
\[ \text{continue} \]
\[ \text{apdens}(1, 1) = \text{young} \]

4.2.2.4 alatoid aphids, unparasitized, 4th instar onwards

\[ \text{do } 120 \]
\[ \text{aldens}(k, 1) = \text{aldens}(k-1, 1) \]
\[ \text{continue} \]

4.2.3 alatoid aphids, parasitized

\[ \text{do } 130 \]
\[ \text{iif} (j < 16) \text{go to } 90 \]
\[ \text{apdens}(i, j) = \text{apdens}(i-1, j-1) \]
\[ \text{continue} \]

4.2.4 alatoid aphids, unparasitized, 4th instar onwards

\[ \text{do } 140 \]
\[ \text{aldens}(k, 1) = \text{aldens}(k-1, 1) \]
\[ \text{continue} \]

\[ \text{do } 145 \]
\[ \text{iif} (i < 16) \text{go to } 90 \]
\[ \text{apdens}(i, j) = \text{apdens}(i-1, j-1) \]
\[ \text{continue} \]

\[ \text{do } 150 \]
\[ \text{iif} (j < 16) \text{go to } 90 \]
\[ \text{apdens}(i, j) = \text{apdens}(i-1, j) \]
\[ \text{continue} \]

\[ \text{do } 155 \]
\[ \text{iif} (i < 16) \text{go to } 90 \]
\[ \text{apdens}(i, j) = \text{apdens}(i-1, j) \]
\[ \text{continue} \]
5. calculate the actual number of aphids in each instar, either parasitized or not, then sum the total number of aphids
   do 230 i=1,7
      stage(i)=0.0
   continue
   do 270 i=1,4
      stage(1)=stage(1)+apdens(j,i)
   continue
   do 310 i=5,17
      stage(2)=stage(2)+apdens(j+4,i)
   continue
   do 350 i=18,70
      stage(3)=stage(3)+apdens(j+8,i)
   continue
   do 390 i=1,17
      stage(4)=stage(4)+apdens(j,i)
   continue
   do 430 i=1,13
      stage(5)=stage(5)+aldens(j,i)
   continue
   do 470 i=1,17
      stage(6)=stage(6)+apdens(j,i)
   continue
   do 510 i=1,13
      stage(7)=stage(7)+aldens(j,i)
   continue
   5.6 total number of aphids
   total=0.0
   do 390 j=1,37
      total=total+stage(j)
   continue
   6. calculate number of unparasitized aphids in each age class to be parasitized during the current quip
   6.1 test whether there are any female adult parasite present, if not, go straight to sum the current population status
   female=0.0
   do 395 j=29,37
      female=female+apdens(j)
   continue
   if(female.eq.0.0) go to 100
   apply the instar preference index to the actual number of aphids in each instar, then calculate the total of the calculated numbers
   pref(1)=stage(1)*0.55
   pref(2)=stage(2)*0.77
   pref(3)=stage(3)
   pref(4)=stage(4)*0.64
   pref(5)=stage(5)*0.37
   pref(6)=stage(6)*0.41
   pref(7)=stage(7)*0.08
   sum=0.0
   do 400 i=1,7
      sum=sum+pref(i)
   continue
   6.3 use the sum above to calculate the number of aphids (either parasitized previously or unparasitized) to be parasitized during the current quip
   6.3.1 calculate the total number of eggs to be deposited (73% of the adult parasites are assumed to be female)
wasp1,waspl,egg1,egg2,tot = 0.0
wasp1(pden[20] + pden[30] + pden[31] + pden[32]) * 0.70
if (wasp1.ep[0] > 0.0) goto 450
egg1 = (1.4661 * sum(1 + 0.0458 * sum)) * wasp1
continue
wasp2 = (pden[33] + pden[34] + pden[35] + pden[36]) * 0.70
if (wasp2.ep[0] > 0.0) goto 480
egg2 = (1.4661 * sum(1 + 0.0458 * sum)) * wasp2
continue
totegg = egg1 + egg2

5.2 calculate the number of aphids to be parasitized
para = sum * (1 - exp(-totegg/sum))

5.4 calculate the probability of each aphid (the number after the preference
index has been applied) to be parasitized
prob = para/sum

5.5 now calculate the number of unparasitized aphids in each
age class to be parasitized

5.5.1 1st instar
do 500 i = 1, 4
apdens(i,2) = apdens(i,1) * 0.5 * prob
apdens(i,1) = apdens(i,1) - apdens(i,2)
500 continue

5.5.2 2nd instar
do 510 i = 5, 12
apdens(i,2) = apdens(i,1) * 0.77 * prob
apdens(i,1) = apdens(i,1) - apdens(i,2)
510 continue

5.5.3 3rd instar
do 520 i = 13, 20
apdens(i,2) = apdens(i,1) * prob
apdens(i,1) = apdens(i,1) - apdens(i,2)
520 continue

5.5.4 4th instar apterous
do 530 i = 21, 28
apdens(i,2) = apdens(i,1) * 0.64 * prob
apdens(i,1) = apdens(i,1) - apdens(i,2)
530 continue

5.5.5 adults apterous
do 540 i = 29, 70
apdens(i,2) = apdens(i,1) * 0.37 * prob
apdens(i,1) = apdens(i,1) - apdens(i,2)
540 continue

5.5.6 4th instar alate

do 550 i = 31, 38
aldens(i,2) = aldens(i,1) * 0.41 * prob
aldens(i,1) = aldens(i,1) - aldens(i,2)
550 continue

5.5.7 adults alate

do 560 i = 39, 70
al dens(i,2) = al dens(i,1) * 0.36 * prob
al dens(i,1) = al dens(i,1) - al dens(i,2)
560 continue

7. calculate the percentage of 3rd instar nymphs which have been
parasitized
para3 = (1 - up3) * 100

8. calculate the number of parasites in each age class and
sum up the total number of parasites
para = para3 / stage(3)
do 570 i = 1, 16
pden(i) = pden(i) + apdens(i,1)
do 610 j = 1, 70
pden(i) = pden(i) + aldens(i,1)
do 670 i = 1, 16
pden(i) = pden(i) + al dens(i,1)
do 660 i = 1, 70
pden(i) = pden(i) + al dens(i,1)
do 690 i = 1, 16
pden(i) = pden(i) + al dens(i,1)
d0 630 continue
6.5 sum up the total number of parasites

do 660 i=1,137
   tpara = tpara + pden(i)

write out the results

do 680 i=1,7
   if(stage(i),le.1.0) stage(i)=1.0
   if(tpara,le.1.0) tpara=1.0
   format(4x,5x,3x,7(f9.2,1x,f10.2,1x,f5.1))

function perc(degree,total,dens)

find out the dry weight of plants in grams

if(degree.ge.500) degree=500
   gram=1.071612*exp(0.00655*degree)

calculate the percentage of alactos

dens=total/gram
   perc=exp(-29.9547/(dens**0.7456))
   if(perc.le.0.1) perc=0.1

end
### A5.3 An Example of Output of the Model

(Fourth cage experiment, see Fig. 15.5)

<table>
<thead>
<tr>
<th>no. cage</th>
<th>instar 1</th>
<th>instar 2</th>
<th>instar 3</th>
<th>instar 4</th>
<th>instar 4</th>
<th>adult aptera</th>
<th>adult alate</th>
<th>total aphids</th>
<th>% of 3rd</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.28</td>
<td>1.27</td>
<td>1.26</td>
<td>1.24</td>
<td>1.23</td>
<td>1.23</td>
<td>1.25</td>
<td>1.25</td>
<td>1.25</td>
</tr>
<tr>
<td>2</td>
<td>1.30</td>
<td>1.28</td>
<td>1.26</td>
<td>1.25</td>
<td>1.24</td>
<td>1.24</td>
<td>1.25</td>
<td>1.25</td>
<td>1.25</td>
</tr>
<tr>
<td>3</td>
<td>1.32</td>
<td>1.31</td>
<td>1.29</td>
<td>1.28</td>
<td>1.27</td>
<td>1.27</td>
<td>1.28</td>
<td>1.28</td>
<td>1.28</td>
</tr>
<tr>
<td>4</td>
<td>1.34</td>
<td>1.33</td>
<td>1.31</td>
<td>1.30</td>
<td>1.29</td>
<td>1.29</td>
<td>1.30</td>
<td>1.30</td>
<td>1.30</td>
</tr>
<tr>
<td>5</td>
<td>1.36</td>
<td>1.35</td>
<td>1.33</td>
<td>1.32</td>
<td>1.31</td>
<td>1.31</td>
<td>1.32</td>
<td>1.32</td>
<td>1.32</td>
</tr>
<tr>
<td>6</td>
<td>1.38</td>
<td>1.37</td>
<td>1.35</td>
<td>1.34</td>
<td>1.33</td>
<td>1.33</td>
<td>1.34</td>
<td>1.34</td>
<td>1.34</td>
</tr>
<tr>
<td>7</td>
<td>1.40</td>
<td>1.39</td>
<td>1.37</td>
<td>1.36</td>
<td>1.35</td>
<td>1.35</td>
<td>1.36</td>
<td>1.36</td>
<td>1.36</td>
</tr>
<tr>
<td>8</td>
<td>1.42</td>
<td>1.41</td>
<td>1.39</td>
<td>1.38</td>
<td>1.37</td>
<td>1.37</td>
<td>1.38</td>
<td>1.38</td>
<td>1.38</td>
</tr>
<tr>
<td>9</td>
<td>1.44</td>
<td>1.43</td>
<td>1.41</td>
<td>1.40</td>
<td>1.39</td>
<td>1.39</td>
<td>1.40</td>
<td>1.40</td>
<td>1.40</td>
</tr>
</tbody>
</table>

Note: The table represents the output of the model for different instars and stages of development.
This appendix describes some simulation experiments on the interactions between *H. lactucae* and *A. sonchi*, using the aphid-parasite model developed in this study (Appendix 5). The purpose of the experiments is to provide information for a tentative assessment of the effectiveness of the parasite as a biological control agent of the aphid in south-eastern Australia (Chapter 16).

A6.1 Assumptions of the simulation experiments

The central assumptions implicit in these simulation experiments have been discussed in 16.1. To make the simulation experiments possible, further assumptions on the population status of *H. lactucae* at the beginning of the season and the timing of the first parasite attack are needed.

(i) Population status of *H. lactucae* at the beginning of the season

In the field, populations of *H. lactucae* spend the winter and the summer in low numbers on the few flowering plants and the inner leaves of non-flowering rosette forms of *S. oleraceus*. As the favourable seasons approach and progress, the rosette forms of *S. oleraceus* start to elongate and produce flower heads. Meanwhile, many new plants emerge and grow rapidly. These new plants are then infested at various times through the season. It is thus obvious that the distribution of aphids during the initial stages of a natural infestation is very variable. Rather obviously, if a colony is started late in a favourable season, it will not have enough time to increase to very high number. Therefore, it can be considered that the colonies which contribute most to the observed peak numbers (see 2.4)
fall broadly into two categories: (1) colonies which start at the end of the previous favourable season on a rosette form plant, pass the adverse seasons in low numbers (presumably mostly apteriform nymphs and apterae) and then develop rapidly as soon as the favourable seasons start and the host plants begin to grow; and (2) colonies which start with various numbers of alate emigrants shortly after the beginning of a favourable season.

Based on the considerations given above, two kinds of aphid colonies are considered in the simulation experiments.

(a) colonies which start with various numbers of apterous aphids (both nymphs and adults); and

(b) colonies which start with various numbers of newly-emerged alatae.

According to the model, the fecundity rates of the aphid are affected by temperature, so a daily mean temperature of 15°C, which is typical during the seasons when populations of *H. lactucae* in the field are increasing rapidly, is used throughout.

(ii) Timing of first parasite attack

No information is yet available on the seasonal history of *A. sonchi* in Australia. The data on the bioclimatic characteristics of the parasite obtained in this study (Chapter 13) indicate that in most regions of southeastern Australia, the summers are too hot and dry and the winters are probably too cold for the parasite to remain active. In addition, the numbers of aphids during these two adverse seasons are usually low (Martin, 1979). Thus, for *A. sonchi* to prosper in these regions, it is probably essential that large numbers pass the adverse season in diapause (or in a state of quiescence) and resume their activity early in the favourable seasons. In these simulation experiments, it is thus assumed that the parasite survives through the adverse seasons as diapausing larvae and
adults of its first generation emerge at quip 12, i.e. after pupal develop-
ment. Aphid colonies of category (a) are then assumed to receive first
parasite attack at quip 13 and aphid colonies of category (b) at quip 5.
The timing of parasite attack on alate colonizers in category (b) assumes
that there is likely to be some delay before the parasite finds newly-
established colonies.

A6.2 Simulation experiments and results

Analysis of plant growth in the field cage experiments (8.4.1; 14.3.1)
showed that sowthistle plants under these conditions remain actively growing
for about 500 D\textsuperscript{2}C. As \textit{H. lactucae} is a typical "flush" feeder and leaves
the plant when the latter becomes unfavourable, simulations of the interac-
tions between the aphid and the parasite are restricted to the first 60
quips (510 D\textsuperscript{2}C).

As discussed in 2.6, the main objective of the parasite introductions
is to reduce the aphid numbers below the density conducive to the development
of alatae resulting, consequently, in a reduction in the numbers of virus-
infected alate emigrants landing on lettuce crops. Thus, the success of the
parasite as a biological control agent should be judged by the magnitude of
the reduction of emigrants.

Fig. A6.1 shows the development of a colony started with eight apterous
aphids (2 N_2, 2 N_3, 2 N_4 apt. and 2 newly-moulted A apt.). If the parasite
is to prevent the colony from reaching its likely peak of over 30,000 and
thereby reduce the total number of emigrants to less than half, the adults
of its first generation must attack about 20% of all aphids during each
quip. The percentages of parasitization of N_2 and N_3 resulting from such a
rate of attack through the season are shown on the top half of the figure.

Figure A6.2 shows the development of a colony started with two newly-
Figure A6.1. (A) simulated population trends of *H. lactucae* before (solid line) and after (dotted line) the level of parasitization by *A. sonchi* depicted in (B) is incorporated; see text for explanation.
Fig. A6.2  (A) Simulated population trends of *H. lactucae* before (solid line) and after (dotted line) the level of parasitization by *A. sonchi* depicted in (B) is incorporated (Note that the scale for No. emigrants/quip is different from that in Fig. A6.1); see text for explanation.
moulted alatae. In this case if the parasite is to prevent the colony from reaching its likely peak of over 10,000 and reduce the total number of emigrants to less than half, the adults of its first generation must attack about 15% of all aphids during each quip. Again the percentages of parasitization of N2 and N3 resulting from such a rate of attack are shown at the top half of the figure.

A6.3 Discussion

Martin (1979) showed that in Adelaide the population densities of H. lactucae during both winter and summer are usually about five to ten aphids per plant. Since the distribution of aphids in the field is usually very variable, the initial numbers of aphids on many plants can be expected to be higher than those used in the simulation experiments. Obviously, the higher the number of aphids at the beginning of the season, the higher the level of parasitization that is required to achieve the same degree of reduction in the number of emigrants. Thus, the results of the simulation experiments show that even in aphid colonies which are started with low numbers, the parasite must attack a large proportion of the aphids very early in the season to achieve a substantial reduction of the total number of emigrants. On the other hand, it is interesting to note that for the parasite to achieve a 50% reduction of emigrants, it does not have to suppress the aphid density to a very low level. This latter feature suggests that, the aphid, in its role as a virus vector, is a favourable candidate for biological control (see 2.6).

While the results of the simulation experiments appear instructive, it is important to remember that the aphid model used has been tested only against the data collected in the field cage experiments. As mentioned in 8.4.1 and 9.4, the growth of the plants in these cage experiments is above
the average observed in the field. Thus, the simulation results only show the possible response patterns which are likely to occur on those plants whose growth and eventual size are above the average. But these results can be considered indicative as those "better" plants undoubtedly form an important part of the food resources of the aphid in the field.
REFERENCES


302


