ECOLOGICAL STUDIES ON *CHLENIAS PACHYMELA* LOWER (LEPIDOPTERA : GEOMETRIDAE)

by

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October, 1979

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SUMMARY

The biology and ecology of the indigenous and polyphagous *Chlenias pachymela* Lower on the exotic *Pinus radiata* D. Don were studied between 1976 and 1979.

Outbreaks of this geometrid defoliator have occurred periodically in the past 50 years, some of which necessitated chemical control. With one possible exception at Bundaleer, (the species here was probably not *C. pachymela*) such outbreaks have been confined to the radiata pine plantations of the South-East region of South Australia.

The insect is univoltine. Pupation takes place in the ground beneath the forest litter where the pupa spends the summer and autumn months. Moths emerge in winter to mate and lay their eggs. The larvae eclode in spring and pass through 6 instars before pupating in early summer.

The seasonality of the insect is influenced by its diapause which in turn is influenced by temperature. The insect enters diapause during the pharate adult stage. Two models of the processes that take place, from pupation to adult emergence, are postulated and discussed.

Laboratory studies, the results of which were confirmed in the field, suggest that pine shoots are an inadequate food resource and that pine pollen must be present as well to ensure maximum survival and growth of young larvae. The foliage of other host plants tested, namely, *Melaleuca armillaris* Sm. and *Cupressus macrocarpa* Hartweg, was superior to that of *P. radiata*

for the parameters measured (i.e. survival-rate and growth-rate).

The natural enemies of *C. pachymela* were identified and discussed. An ichneumonid parasite, *Lissopimpla excelsa* Costa, which has been considered instrumental in terminating past outbreaks of the pine looper was specially studied and its role in the population dynamics of *C. pachymela* was appraised.

Life table studies indicate that the probable key factors are those that (1) operate on the first-instar larvae, and (2) have a differential effect on the sex ratio.

The hypothesis is advanced that the availability of pollen to feed on by the young larvae is a key factor in the population dynamics of *C. pachymela*. This hypothesis is consistent with the results of the study and explains both the distribution and abundance of the insect in South Australia.

Suggestions are made for the future control of *C. pachymela* in *P. radiata* plantations without the use of insecticides. Two of these suggestions, namely alteration of tree phenology and planting of male-sterile trees, are based on the assumption that pollen is a key factor. It is considered impracticable to alter tree phenology, but the planting of male-sterile pine trees is favoured because this suggestion, if adopted, may not only prevent future outbreaks of *C. pachymela* but should also divert energy normally expended in pollen production to vegetative growth, thereby increasing timber yield. A third suggestion for the control of *C. pachymela* involves the retention of large areas of native forests dispersed within pine plantations. Such a practice is desirable both from the viewpoint of better wildlife conservation and from the increase in the numbers of parasites and predators of *C. pachymela* it could stimulate.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and, to the best of my knowledge and belief, contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

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(Khoo Khay Chong)

October, 1979.

ACKNOWLEDGEMENTS

I am most grateful to my supervisors Dr. F.D. Morgan and Dr. D.A. Maelzer for their guidance and their constructive criticisms during the course of this study.

I am indebted to members of the Entomology Department, all of whom have helped me in various ways. In particular, I would like to record my sincere appreciation to Professor T.O. Browning and Professor H.G. Andrewartha for their advice and useful suggestions and to Mr. N.C. Stewart, Mr. K.M. Wilkinson and Mr. R. Schaumloffel for field assistance.

I am grateful to the Woods and Forests Department of South Australia for its cooperation in provision of areas to carry out field studies at Noolook forest and data from its files on the pine looper. It has also provided me with Fig. 1.2. I would like to especially thank its officers, Mr. R.S. Bungey and Mr. J. Chapman.

I wish to thank the following for the identification of specimens : my colleague Mr. R.B. Coles, Mr. D.E. Symon of the Agronomy Department, Waite Agricultural Research Institute; Dr. J. Cardale and Dr. I.F.B. Common of C.S.I.R.O.; Dr. W.R.M. Mason of Biosystematics Research Institute, Canada.

Thanks are due to Mr. B. Palk for Fig. 5.1 and for printing the photographs and to Miss P. Perera for typing the thesis.

This study was made possible by an Australian-Asian Universities Cooperation Scheme award and I thank the Commonwealth of Australia for this. I would like to thank the Universiti

Pertanian Malaysia for granting me the period of leave required to carry out this study.

Finally, my thanks to my wife, Kim, for her help and her encouragement.

CHAPTER 1

INTRODUCTION

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INTRODUCTION

The pine looper, *Chlenias pachymela* Lower, an insect indigenous to Australia, is one of the major insect pests of the introduced *Pinus radiata* D. Don in South Australia.

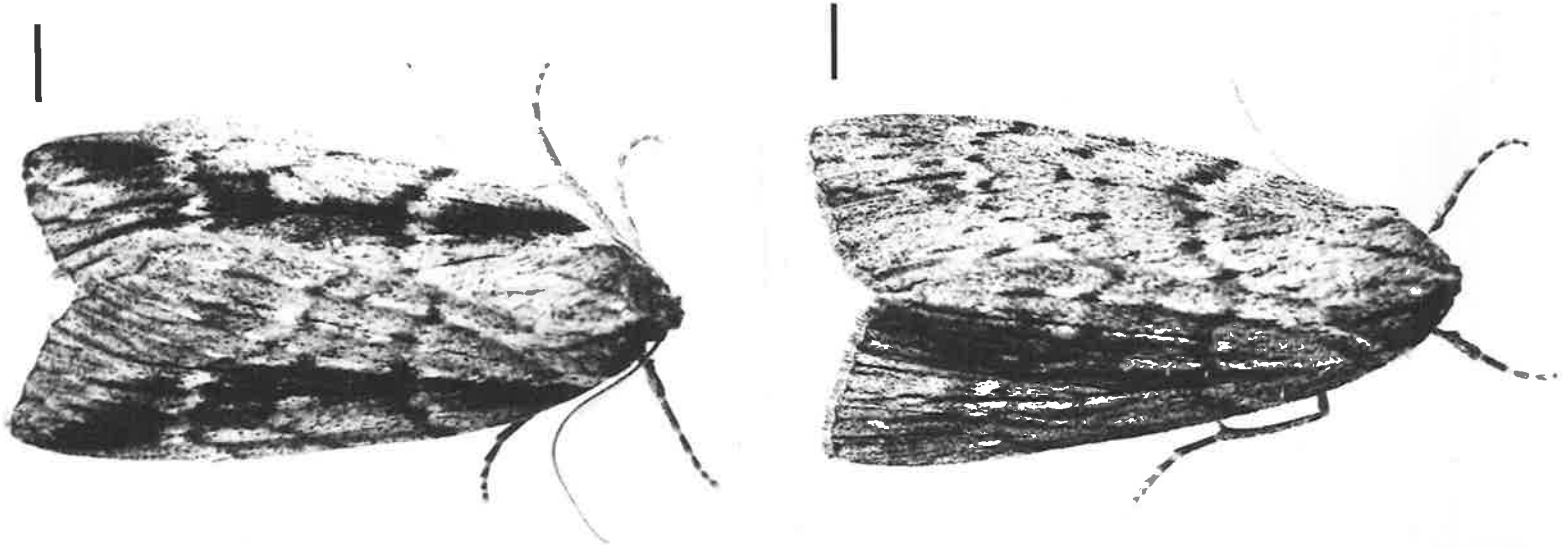
The Woods and Forests Department of South Australia has kept good records of *Chlenias* attacks on *P. radiata* since 1927. It has also carried out several investigations in cooperation with F. D. Morgan of the Waite Agricultural Research Institute. The frequent references in subsequent sections to unpublished reports of the Woods and Forests Department of South Australia and to those of Morgan are based on the Department's records.

The early literature concerns the taxonomy of species of *Chlenias* attacking *P. radiata* (Lower, 1893; Meyrick, 1891; Tindale, 1928). Recently some aspects of the diapause (Monro, 1972), biology and population ecology (Madden and Bashford, 1977a, 1977b) have been investigated.

1.1 Taxonomy

Two variations in the pattern of the forewing (Fig. 1.1) can be found in both male and female moths. The morph with the black streak running from the base of the costa to the apex has been named *C. pachymela* by Lower (1893), and that without the black streak, *C. pini* by Tindale (1928). However, Morgan (personal communication) and Boros (personal communication) who have worked on the taxonomy of the genus, consider them to be conspecific. I have carried out numerous crossings which confirm this. The name *C. pachymela* is adopted here since it has precedence over the name *C. pini*.

Fig. 1.1 Two morphs of *Chlenias pachymela* both females. The morph without the black streak in the forewing (top) was thought to be a different species from that with the black streak (bottom). The former was named *C. pini* and the latter *C. pachymela*. Scales represent 2.8 mm (top) and 2.7 mm (bottom).



There is a third form of *Chlenias* infesting *P. radiata*. The larva and adult of this form are distinctly different from those of *C. pachymela* although it is difficult to distinguish between the two when they are tiny larvae. The larva and adult of this third form fit the description of *C. zonaea* given by Meyrick (1891); this species was first described by Guest (1886) under Meyrick's manuscript name. *Chlenias zonaea* was found in the study area, but its occurrence was rare (<5%) compared with *C. pachymela* and no attempt was made to differentiate between the two species when sampling for life table studies.

Both *C. pachymela* and *C. zonaea* are present in the forests of the Lower South-East. The former species appears to predominate in number over the latter.

1.2 The host

The earliest record of the introduction of *P. radiata* into Australia was in 1857; the species was found growing in South Australia by 1866 (Fielding, 1957). Radiata pine was one of the tree species planted in the first forest plantation in South Australia at Bundaleer in 1876 (Lewis, 1975).

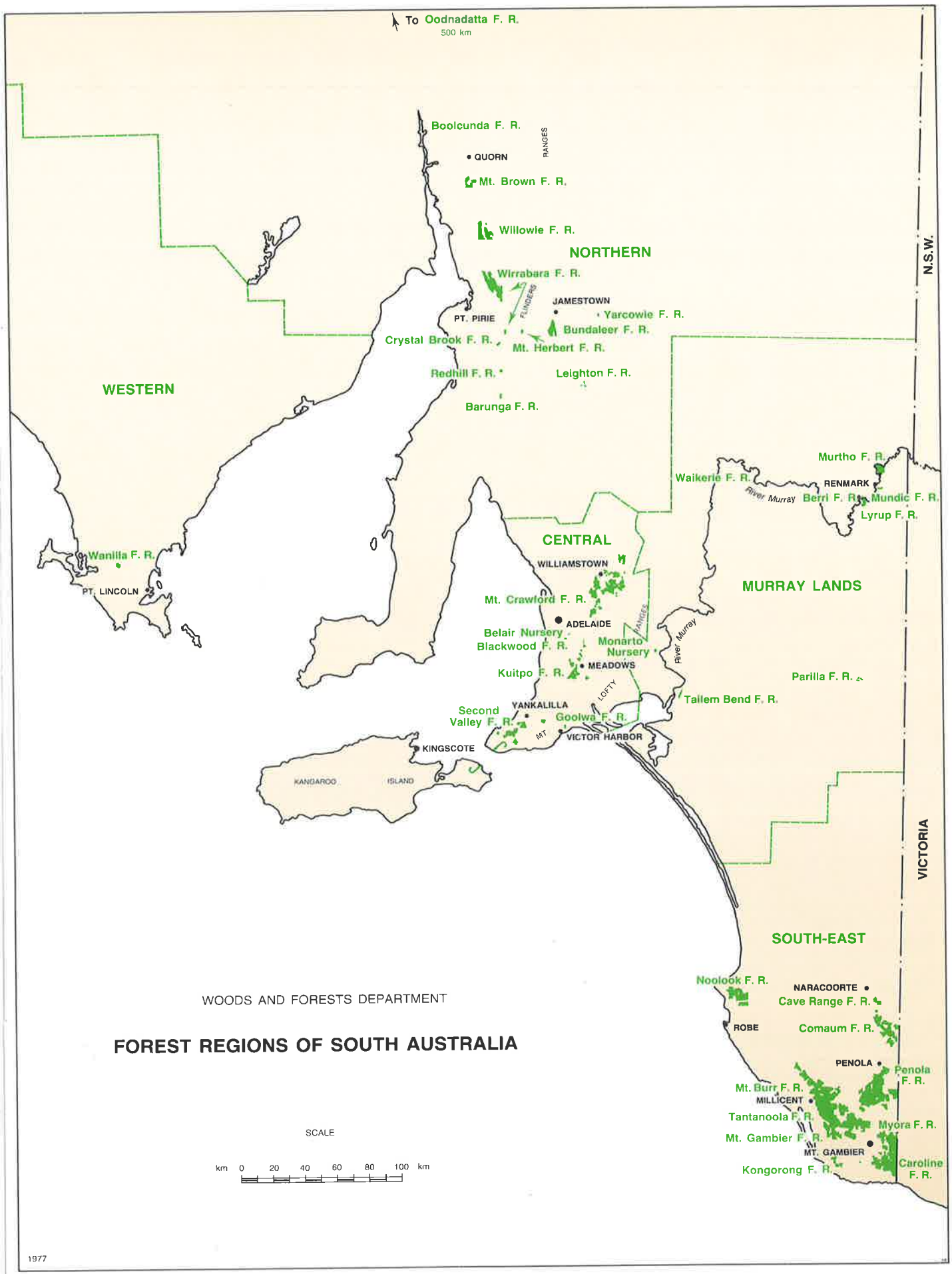
Today *P. radiata* is the most extensively planted forest-tree species in Australia. Plantations are established within a narrow coastal belt in Western Australia and south-east Australia, as well as Tasmania. In South Australia, exotic softwoods accounted for approximately 99% of the planted forest area at 31 March 1977 of which *P. radiata* is of predominant importance (Table 1.1). The majority of the planted forest in South Australia is in the Lower South-East (Fig. 1.2).

Table 1.1 Plantation areas (ha) in South Australia, 31 March 1977.

	Pinus radiata	Other *Pinus*	Hardwoods
State forests	69872.1	6692.0	1049.5
Private forests	17103.0		99.0
Total	93667.1		1148.5

Source : Leonard (1978)

Fig. 1.2 Forest regions of South Australia.


To Oodnadatta F. R.
500 km
Boolcunda F. R.
QUORN
RANGES
Mt. Brown F. R.
Willowie F. R.
NORTHERN
Wirrabara F. R.
FLINDERS
JAMESTOWN
PT. PIRIE
Yarcowie F. R.
Bundaleer F. R.
Crystal Brook F. R.
Mt. Herbert F. R.
Redhill F. R.
Leighton F. R.
Barunga F. R.
WESTERN
N.S.W.
Murtho F. R.
Waikerie F. R.
RENMARK
River Murray
Berri F. R.
Mundic F. R.
Lyrup F. R.
CENTRAL
Wanilla F. R.
WILLIAMSTOWN
PT. LINCOLN
MURRAY LANDS
Mt. Crawford F. R.
ADELAIDE
Belair Nursery
Blackwood F. R.
Monarto Nursery
MEADOWS
River Murray
Kuitpo F. R.
Parilla F. R.
Tailem Bend F. R.
LOFTY
YANKALILLA
Second Valley F. R.
Goolwa F. R.
MT
VICTOR HARBOR
KINGSCOTE
KANGAROO
ISLAND
VICTORIA
SOUTH-EAST
Noolook F. R.
NARACOORTE
Cave Range F. R.
ROBE
Comaum F. R.
PENOLA
Penola F. R.
Mt. Burr F. R.
MILLICENT
Tantanoola F. R.
Myora F. R.
Mt. Gambier F. R.
MT. GAMBIER
Caroline F. R.
Kongorong F. R.
WOODS AND FORESTS DEPARTMENT
FOREST REGIONS OF SOUTH AUSTRALIA
SCALE
km 0 20 40 60 80 100 km
1977

Scott (1960) reviewed various aspects of *P. radiata* including its botany and protection. Of the large volume of literature on this coniferous species, those by Fielding are particularly useful in understanding the present study. Many of his observations made at Canberra also apply to the trees in the study area. A brief account of some aspects of the botany of *P. radiata* has been given below and is based on 3 publications by Fielding (1953, 1955, 1960).

The tree consists of a central axis or trunk supporting a crown made up of whorls of branches. Unlike most other species of *Pinus*, *P. radiata* is typically multinodal and produces from 1 to 4 or more whorls per year. The number of branches in the whorl varies from 1 to 10 or more. The branches bear needles of various ages; needles may be retained for up to 6 years. But for the present study the term "mature foliage" refers to needles about a year old, i.e. the needles just behind the new shoot.

Radiata pine is typically monoecious and produces both seed and pollen on the same tree. However, all gradations occur between trees that are completely male and those that are completely female. Male flowers are first produced at about 3 years of age and female flowers at about 4. The male flower is also known as a staminate/male strobilus and the female flower as an ovulate/female strobilus.

As used here, a shoot is the young growth of a stem which is less than a year old. Ontogenetically, the male strobili are dwarf shoots and occupy the position of needle fascicles. Therefore shoots may be of two kinds - pollen-producing or purely foliar. The seasonal growths of these 2 kinds of shoots differ. Growth of the purely foliar shoot is rapid in spring and very slow elongation takes place the rest of the year, with growth in autumn and early winter almost at a standstill.

The pollen-producing shoots elongate throughout the year with the exception of a resting period in summer. The male strobili develop in autumn and pollen is shed in early spring. Growth of the shoot continues with the development of foliage above the male strobili and ceases in early summer.

1.3 History of the association of *Chlenias* spp. with *Pinus radiata*

The following account of past occurrences of *Chlenias* spp. on *P. radiata* in South Australia is based on documents in the files of the Woods and Forests Department of South Australia unless otherwise mentioned.

The first outbreak of loopers in South Australia was reported in 1927. A letter from forester F. Kay to the Conservator of Forests in Adelaide mentioned the presence of looper caterpillars in plague proportions on *P. radiata* in the Mount Burr area. Kay had seen the caterpillars before but had never known them to cause perceptible damage. Since then the pine looper has been reported in various plantations (Table 1.2). It will be noted that, with the exception of Bundaleer, all the recorded occurrences of *Chlenias* have been in the South-Eastern region. The outbreaks at Bundaleer were probably not caused by *C. pachymela* but by another species of *Chlenias* (Morgan, personal communication).

It is probable that pine loopers are endemic to the forests in the South-East. Although the Table (Table 1.2) lists every recorded occurrence, it is by no means complete. It is likely that many light infestations have gone unnoticed or were not reported. For example, I have found larvae in the Tantanoola plantation and this was a locality not previously reported. In 1976 Myora was the only plantation mentioned as being infested (South, 1978) but I have found the larvae at Caroline, Mount Burr and Penola as well as at Noolook.

Table 1.2 Recorded occurrences of *Chlenias* spp. on *Pinus radiata* in plantations of South Australia.

Year	Location
1927	Mount Burr
1936	Mount Burr
1940	Myora
1947	Comaum
1960	Caroline, Myora, Noolook
1961	Caroline*, Comaum, Mount Burr, Myora, Noolook*
1962	Bundaleer, Caroline*, Comaum*, Mount Burr, Myora*, Noolook*
1963	Caroline*, Kongorong, Mount Burr*, Noolook*
1964	Caroline*, Mount Burr*, Myora*, Noolook*
1965	Mount Burr, Myora, Noolook
1966	Mount Burr, Myora, Penola
1967	Mount Burr, Penola
1968	Mount Burr
1969	Bundaleer
1970	Bundaleer *
1971	Noolook
1976	Caroline, Mount Burr, Myora, Penola, Noolook, Tantanoola

* Treated with insecticide

Source : The information above was obtained from the files of the Woods and Forests Department of South Australia with the exception of that for 1976 which was derived from a survey I carried out in the plantations of the South-East.

1.4 Damage caused by *Chlenias*

Except where otherwise stated, the following assessment of the importance of the pest is based on the records of the Woods and Forests Department of South Australia.

Trees of all ages are attacked. Caterpillars have been reported damaging new plantings. On the other extreme they were seen in the crown of a 23-year old tree felled in a thinning operation. It is believed that the caterpillars found in new plantings were brought there by the wind from older stands nearby. This is probably correct : I have searched for eggs in new plantings at Caroline and Noolook without any success although I did find many late-instar larvae. These larvae did not appear to have penetrated deep into the stands, being generally confined to the margin nearest the older stands.

Attacks on natural regenerations have been reported in Penola and are common in Mount Burr. But natural regenerations are not presently being utilised and the loopers do not therefore pose a problem.

The reported infestations vary in intensity. The damage done ranged from very light to complete defoliation.

Trees have a good chance of recovery if the defoliation is not severe. A study carried out after an outbreak at Bundaleer in 1969 showed that where defoliation was complete the trees were likely to die.

However, the proportion of trees killed as a direct consequence of defoliation by looper caterpillars is small. An attack by insect pests in general rarely results in mortality of radiata pine, except in natural regeneration under a canopy of older trees (Minko, 1965) as has happened in Tasmania between 1968-1971 (Madden and Bashford, 1977a). Where mortality has been high in planted stands as in the

infestation at Bundaleer in 1969, climatic conditions were considered to be contributory factors.

Branch tips and leaders are often killed in a severe infestation (Bednall, 1962). Such damage to a tree may eventuate in one of several stem defects known as dead-top, forking and stem kinks and bends. These defects and the resultant losses have been described by Wright et al. (1967) and the following account is taken from their papers :

1. Dead-top : Death or severe damage to the terminal shoot of a tree may be followed by subsequent development and assumption of terminal dominance of several lateral branches from lower down the stem. The main effects of dead-topping are the reduction of the length of the merchantable log, and reduction of tree vigour. If the secondary leaders develop to merchantable size, there is a strong possibility that one or more of these secondary leaders will be broken by the wind. In addition the smaller size of these secondary leaders and the prevalence of stem kinks greatly reduce their value.
2. Forking : A forked tree is one with more or less equal-sized leaders replacing the normal terminal shoot. Forking may not result in any loss of total volume. However, the stems that make up the fork are smaller than the stem of a normal tree and thus the value of a forked tree is reduced. As in the case of dead top, there is a strong possibility of windthrow.
3. Stem kinks and bends : Displacement of the leading shoot from a vertical position often results in the formation of permanent stem kinks and bends. The quality of sawn timber cut from kinked logs is affected by the distorted and sloping grain resulting from the kinks. Kinks are also associated with wandering pith, compression wood and an increase in the

deleterious effect of the lower density core-wood. The quantity of sawn timber recovered may also be reduced by severe kinking.

Injury to *P. radiata* by *Chlenias* spp. may render the tree more vulnerable to attacks by other insects. Severe defoliation of 1-16 year old regeneration in Tasmania between 1968 and 1971 resulted in the death of many trees and predisposed many of the survivors to attack by the woodwasp, *Sirex noctilio* F. (Madden and Bashford, 1977a). A serious attack on 15-20 years old plantations at Bundaleer in 1969 killed many trees that were completely defoliated and caused some of the survivors to succumb to *Ips grandicollis* Eichh. (Thomas, 1971). Fortunately, neither *S. noctilio* nor *I. grandicollis* have been found in the important South-East as yet.

Between 1961 and 1964 there were severe outbreaks in several plantations in the South-East and chemical control became necessary. Fogging with DDT readily brought the pest under control. The other forest regions of South Australia have remained free from outbreaks with the exception of Bundaleer in the Northern region.

There have been other occasions when it appeared that the insect would be a serious threat judging from the numbers of eggs and early instar larvae present. As it turned out, mortality was high and the larvae were reduced to innocuous levels.

Outbreaks of *Chlenias* seem to be characterised by their sudden appearance and disappearance. Reports by foresters suggest that there is no gradual build-up over several seasons. Many outbreaks which had reached the stage where the larvae were causing noticeable defoliation ended abruptly without intervention by man.

The genus is neither limited to South Australia nor is its host only *P. radiata*. In Victoria the larvae attack a wide range of trees and shrubs including species of *Eucalyptus*, *Cupressus macrocarpa* Hartweg. and *Pinus* spp. (Minko, 1965). There was an outbreak in a *P. radiata* plantation in Gippsland, Victoria in 1959 (Morgan, unpublished report). *Chlenias* larvae have been recorded defoliating apricot trees, *C. macrocarpa* and *P. radiata* in Tasmania (Tindale, 1928; Madden and Bashford, 1977a).

In South Australia itself many host species are known. Morgan (unpublished reports) has recorded the following hosts : *Acacia mearnsii* De Wild., *Cassinia laevis* R. Br., *Banksia marginata* Cav., *Kunzia* spp. and *Leptospermum* sp. I have found them feeding on *Melaleuca armillaris* Sm., *Cupressus macrocarpa* Hartweg, *Pittosporum undulatum* Vent., *Citrus* sp., *Prostanthera ovalifolia* R. Br. and *Camellia japonica* L.

1.5 The study area

Field studies were carried out at Noolook forest. The forest is located 341 km (by road) to the south-east of Adelaide.

The forest is largely planted to *P. radiata*, but other conifers, in particular *P. pinaster*, are also grown. The trees are planted in rows running in a north-south direction. The forest is divided into stands, called compartments, by roads and breaks. The trees within a compartment are of the same age.

Life table studies were carried out in compartment number 68 (see Section 7.2.1); other studies and collection of experimental materials, e.g. pupae, eggs, pollen, were done in the adjacent compartments. The trees in these compartments, including compartment 68, were planted in 1969.

The basic features of the climate in the study area are much like that of the rest of South Australia, i.e. hot dry summers with relatively mild nights, and cool but not severe winters. Highest temperatures recorded during the summer months, December to February, were 38, 35 and 36°C in 1976, 1977 and 1978 respectively. Temperatures start to fall during the autumn months of March, April and May. The winter months, June to August, are the coldest; lowest temperatures recorded in 1976, 1977 and 1978 were -1.5, -1, -1°C respectively. Temperatures gradually rise in the spring months of September, October and November.

Most of the rains are experienced between May and September. Rainfall during the rest of the year is generally light and unreliable although heavy rains do occur occasionally.

Air temperature and rainfall recorded at Noolook during 1976, 1977 and 1978 are summarised in Appendices 1 and 2.

1.6 Scope of the study

In broad terms, the present study investigates the biology and ecology of *C. pachymela*. The study includes : (1) aspects of the biology, especially those aspects useful for an understanding of the population dynamics of the insect, (2) construction and analysis of life tables to determine the factor(s) which strongly influence the population trend, (3) identification of natural enemies and evaluation of the importance of some of these enemies in the biological control of the insect, (4) evaluation of the role of food in the population dynamics of the insect, and (5) examination of the diapause processes in order to understand the phenology of the insect.

CHAPTER 2

GENERAL MATERIALS AND METHODS

CHAPTER 2

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2.1 Rearing

The various stages of *Chlenias* used in experiments were obtained either from a laboratory culture or from the field.

The laboratory rearing procedure described below starts with the adult and ends with the pupae. The same procedure was used when larvae collected from the field were being reared e.g. for parasites, or when, say, eggs were desired.

Eggs were obtained by placing 2 adult males and 1 adult female together in a clear polystyrene container 20 cm deep and 20 cm in diameter together with a sprig of pine foliage for egg laying and 10% sucrose solution for food. The female showed a strong preference to oviposit on the pine foliage; in the absence of this ovipositional substrate, irregular masses a single layer deep were deposited anywhere on the cage - this happened even when paper towel was provided.

The eggs were sterilised with 0.15% sodium hypochlorite solution and rinsed twice with distilled water. They were then placed over distilled water in a closed container and incubated at 15°C.

Larvae were reared in 120 ml capacity "pomade" jars. Initially, 20 first-instar larvae were placed in each jar; the density was progressively reduced with each instar until in the sixth instar there was only 1 larva per jar. The larvae are not cannibalistic but this procedure was followed to minimise possible stress from

overcrowding.

The larvae were fed an abundance of foliage from a hedge of *Cupressus macrocarpa*. The foliage of *C. macrocarpa* growing as a hedge differs from that growing as a tree in that the former has a preponderence of juvenile foliage whilst the latter produces mainly mature foliage. The terms "juvenile" and "mature" are used here in the ontogenetic sense. Younger larvae, especially the first instars, seemed to fare poorly on mature foliage of *C. macrocarpa*. The older instars, however, could be fed new mature foliage without any apparent ill-effects.

Larvae could also be reared on new foliage of *Melaleuca armillaris* and that of various species of *Eucalyptus* e.g. *E. camaldulensis* Dehnh., *E. cladocalyx* F. Muell. The problem with using the foliage of these species is that they tend to wilt and dry very quickly. *Pinus radiata* is a poor host (see Chapter 5) and was not used to feed larvae.

Larvae were successfully reared to the pupal stage on an artificial diet published by Twine (1971). However, the larvae did not appear to be as healthy as those fed *C. macrocarpa* foliage. Whether the artificial diet could be improved or another better diet found were aspects not pursued because of the univoltine and slow-growing nature of the insect and the shortage of time.

It is worth noting that the food plants of *Chlenias* belong to genera which are rich in essential oils e.g. *Pinus, Citrus, Eucalyptus, Leptospermum, Melaleuca, Cupressus.* Furthermore it was observed that larvae clustered around a wooden case containing vanillin which was placed under an infested *Prostanthera ovalifolia* tree. Essential oils and other strong-smelling organic compounds like vanillin may act as attractants and/or phagostimulants for

Chlenias larvae; it may be necessary to add this kind of substance when preparing artificial diets for the insect. The addition of essential oils to artificial diets for Lepidoptera has also been recommended by Dickson (1976).

When the larvae reached the prepupal stage, they were allowed to pupate in vermiculite.

2.2 Constant temperature rooms and cabinets, and insectary room

Experiments carried out at constant temperatures of 15, 20, 25 and 30°C were done in constant temperature rooms where the variation was ± 1°C; photoperiod was maintained at 12:12 (L:D).

Experiments at other constant temperatures were carried out in cabinets where the variation was ± 1°C and photoperiod was set at 8:16 (L:D).

Temperatures in the insectary room remained at about 20°C most of the time, but the range recorded by a thermograph was 17-27°C. The source of light was indirect sunlight coming in through the window of the insectary.

In no instance was humidity controlled.

2.3 Light trapping

The light trap comprised the following : (1) a 160 watt mercury vapour lamp (Philips MLL-N) suspended 1 m above the ground, (2) power provided by a 1000 watt 240 volt generator, and (3) two clear polythene sheets to cover an area of ground 6 m square with the lamp at the centre of the square. Moths landing within the area covered by the sheets were caught and recorded.

The trap was set up before sunset and trapping was terminated when no moths were caught for 20 minutes.

2.4 Counting of eggs

Eggs occur in masses a single layer deep and adhere tenaciously to each other as well as to the ovipositional substrate. A technique had to be devised to facilitate the counting of individual eggs. This was accomplished by the use of a "Rotring" drawing pen with a 0.25 mm nib. Counting was done under a dissecting microscope; each egg counted was marked with a spot of black drawing ink. Larvae ecloding from eggs thus marked did not seem to be adversely affected by the procedure. If necessary, an egg mass was re-counted by the use of ink of another colour. Where the egg mass was deposited on a pine needle, handling was made easier by enclosing one end of the needle in a small piece of plasticine.

2.5 Measurement of dimensions

Where an object was sufficiently small, e.g. eggs, its dimensions were determined with a calibrated ocular micrometer placed in the eye-piece of a microscope (Wild M5).

Larger objects such as pupae were measured with a pair of vernier calipers.

CHAPTER 3

THE BIOLOGY

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3.1 Introduction

A considerable amount is known about the biology of the species of *Chlenias* attacking *P. radiata* through the work of Tindale (1928), Morgan (unpublished reports), the Woods and Forests Department of South Australia (unpublished reports) and Madden and Bashford (1977a). However, the account given by Madden and Bashford, albeit a detailed one, is not of direct relevance here as they have asserted that the species with which they were working was not one of those described by Meyrick (1891), Lower (1893) and Tindale (1928).

The biological studies which I have carried out seek to cover gaps in the present knowledge and to provide information which would be useful in the understanding of the population dynamics of the species in a *P. radiata* forest.

3.2 Egg

A description of the egg is provided by Tindale (1928); measurements of 50 eggs are summarised in Table 3.1. The incubation period has been given by Morgan (unpublished report) as 24-28 days in the field and 24-36 days in the laboratory. The ambient temperatures were not mentioned.

Prior to emergence the first-instar larva is clearly visible through the transparent chorion. The larva emerges by eating a hole in the chorion.

Table 3.1 Length and breadth (in mm) of eggs

	Width	Length
n	50	50
$\bar{x}$	0.68	0.779
Range	0.594 - 0.642	0.720 - 0.828
S.E.	0.002	o.004

After the larvae have hatched, the shells remain attached to the substrate for a long time, many for at least a year. Previous seasons' egg shells are easily distinguished from the current season's; the former are yellowed and covered with grit whereas the latter have a clean opalescent appearance.

3.2.1 Egg development at constant temperatures

Newly-laid eggs (n=220) were kept in an environment of 100% humidity (by holding the eggs above distilled water in a closed container) at each of the following temperatures : 5, 10, 12, 15, 19, 25 and 30°C. The eggs were laid by 11 female moths; 20 eggs of each female were allocated at random to each of the 6 temperatures. The eggs were examined daily and the numbers hatching were recorded.

The results are summarised in Table 3.2. The median rather than the arithmetic mean is more appropriate here because it eliminates the effect of extreme response and provides a statistic with the desired characteristic of minimum variability (Messenger and Flitters, 1958).

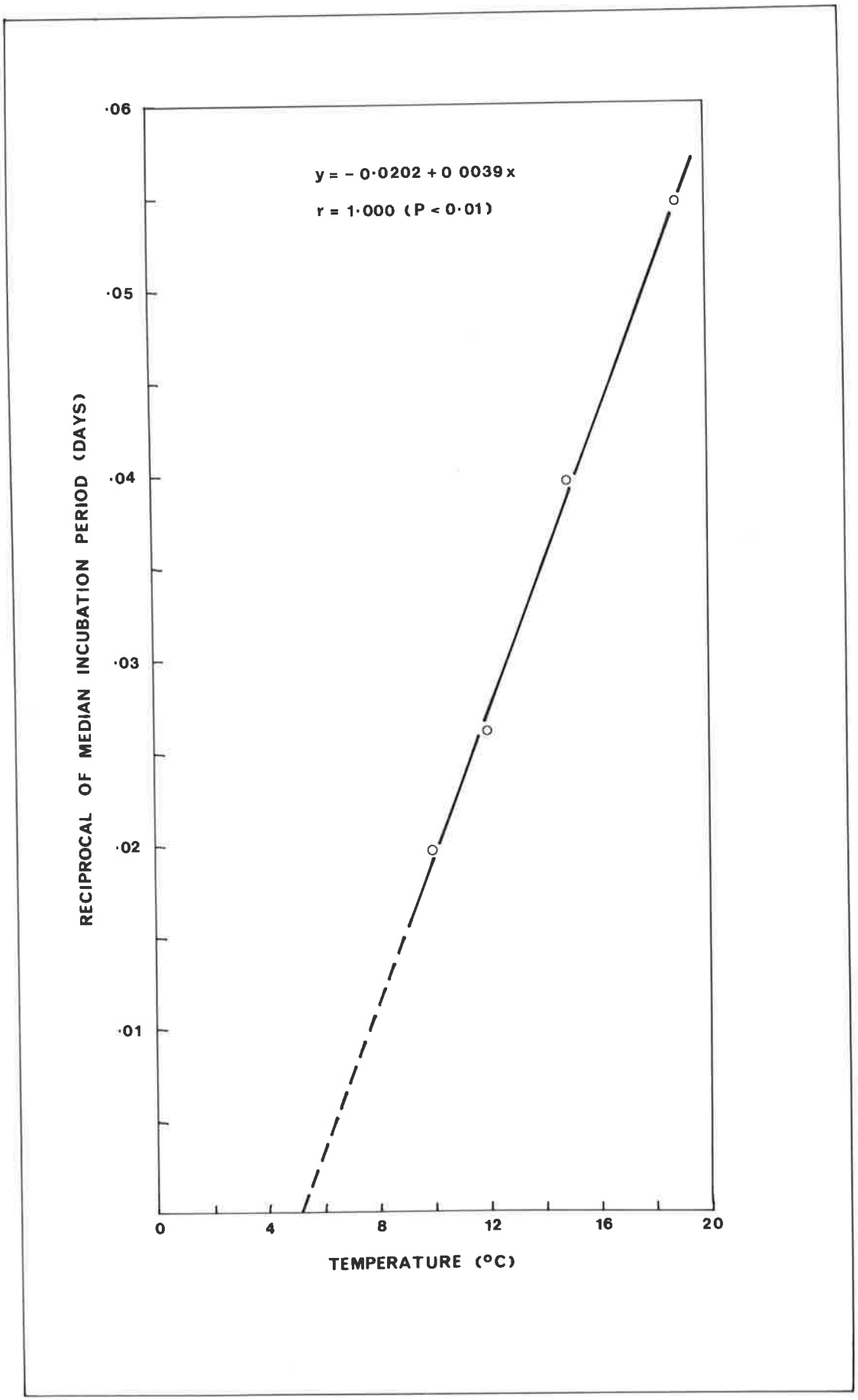
At 5°C eggs eventually turned a bronze colour but did not hatch. Eggs also failed to hatch at 25 and 30°C.

When the reciprocals of the median incubation periods were plotted against temperature, the relationship could be adequately fitted by a straight line (Fig. 3.1). The straight line was then extrapolated back to the X-axis, as has been done by many workers (e.g. Campbell et al., 1974; Obrycki and Tauber, 1978) for other insect species, to obtain the theoretical threshold of development. The estimated value was 5.1°C.

Table 3.2 Effect of various constant temperatures on egg development. (n=220 eggs per treatment)

Temperature (°C)	Median Incubation period (days)	Range Incubation period (days)	% Hatch
5	-	-	-
10	50.7	47 - 62	85.5
12	38.2	36 - 49	83.0
15	25.2	23 - 34	84.5
19	18.3	17 - 25	76.5
25	-	-	-
30	-	-	-

Fig. 3.1 Linear regression of the reciprocal of median incubation period on temperature.


y = - 0·0202 + 0 0039 x
r = 1·000 (P < 0·01)
·06
·05
·04
·03
·02
·01
0
4
8
12
16
20
RECIPROCAL OF MEDIAN INCUBATION PERIOD (DAYS)
TEMPERATURE (°C)

The thermal constant (K) was then calculated from the equation $K = y(D-t)$, where y = median developmental time (days), d = temperature (°C), t = theoretical threshold for development (°C) (Andrewartha and Birch, 1954). The K value was estimated at 253 D°.

3.2.2 Egg development in the field

A total of 25 egg masses in 5 samples of 5 egg masses each were tagged over the entire egg-laying period in 1978. The incubation period recorded for an egg mass ranged from 48-68 days and the mean ± S.E. 58.2 ± 0.55 days.

From the data the estimated thermal constant (K) was calculated for each sample using the threshold temperature from the laboratory (t = 5.1°C) and the mean temperature in the field during the time at which the eggs were developing. Similarly, the estimated threshold temperature was estimated from the field data assuming that the thermal constant (K) was 253 D° as determined in the laboratory. The results are shown in Table 3.3. The mean of the estimated K values was 269.5 D°. and the mean of the estimated t values was 5.4°C, which may be considered to be reasonably close to the values of K and t obtained in the laboratory i.e. 253 D° and 5.1°C respectively.

3.2.3 Moisture requirement for eclosion

Moisture is required for the proper development of the eggs of many insects. This moisture requirement is met by absorption of free liquid water : absorption of water vapour by eggs of arthropods has not been demonstrated (Edney, 1977).

Table 3.3 The mean number of days for eggs to hatch in the field in samples comprising 5 egg masses; and the estimated values of thermal constant (K) and of the threshold temperature (t) for each sample

Sample No.	Mean days to hatch	Estimated K (D°)	Estimated threshold (°C)
1	56	252.0	5.1
2	61	268.4	5.4
3	61	262.3	5.3
4	57	285.0	5.7
5	56	280.0	5.6
$\bar{x}$	58.2	269.5	5.4

In *C. pachymela* the egg is able to develop normally in an environment of low humidity until the first-instar larva is visible through the translucent chorion. At this point high humidity or actual wetting of the egg is essential for eclosion. A similar situation has been observed in *Uraba lugens* (Walker) Morgan and Cobbinah, 1977). In both species it is clear that moisture is required for eclosion of the first-instar larva as distinct from the moisture requirement of the embryo.

An experiment was undertaken to determine the range of humidity within which eclosion would take place. Newly laid eggs were placed in jars in which the relative humidity was controlled by the use of various saturated salt solutions. The salts were selected from the table of Winston and Bates (1960). The salts used and the corresponding humidities obtained at 15°C were as follows : H_2O, 100%; Na tartrate, 94%; $(NH_4)_2SO_4$, 78%; NH_4NO_3, 57%; $Ca(NO_3)_2$, 52%; K_2CO_3, 44%.

A high percentage eclosion occurred within the 78-100% range (Table 3.4). Below 78% only a very small proportion of the eggs hatched.

Buxton (1932) postulated that the deleterious effect of "dry" air on the egg may be a fatal loss of water from the embryo or because it results in the egg shell becoming hard and impenetrable. The latter explanation probably applies to *C. pachymela*. On the other hand, eggs kept in an atmosphere of low humidity were sometimes found to have holes eaten in them and yet the larvae had failed to escape. It is possible that the first-instar larvae requires moisture to initiate normal activities.

Examination of egg masses collected from the field after larval eclosion showed that fertile eggs always hatched.

Table 3.4 Percentage eclosion of eggs at various relative humidities (temperature 15°C).

Relative humidity (%)	n	% Hatch
44	319	0
52	383	3.9
57	251	5.6
78	339	84.7
94	205	94.1
100	301	95.0

Obviously the moisture requirement for eclosion is met in nature. Moisture is available from the frequent rainfalls, the high relative humidities prevalent at this time of the year, and dew.

3.3 Larva

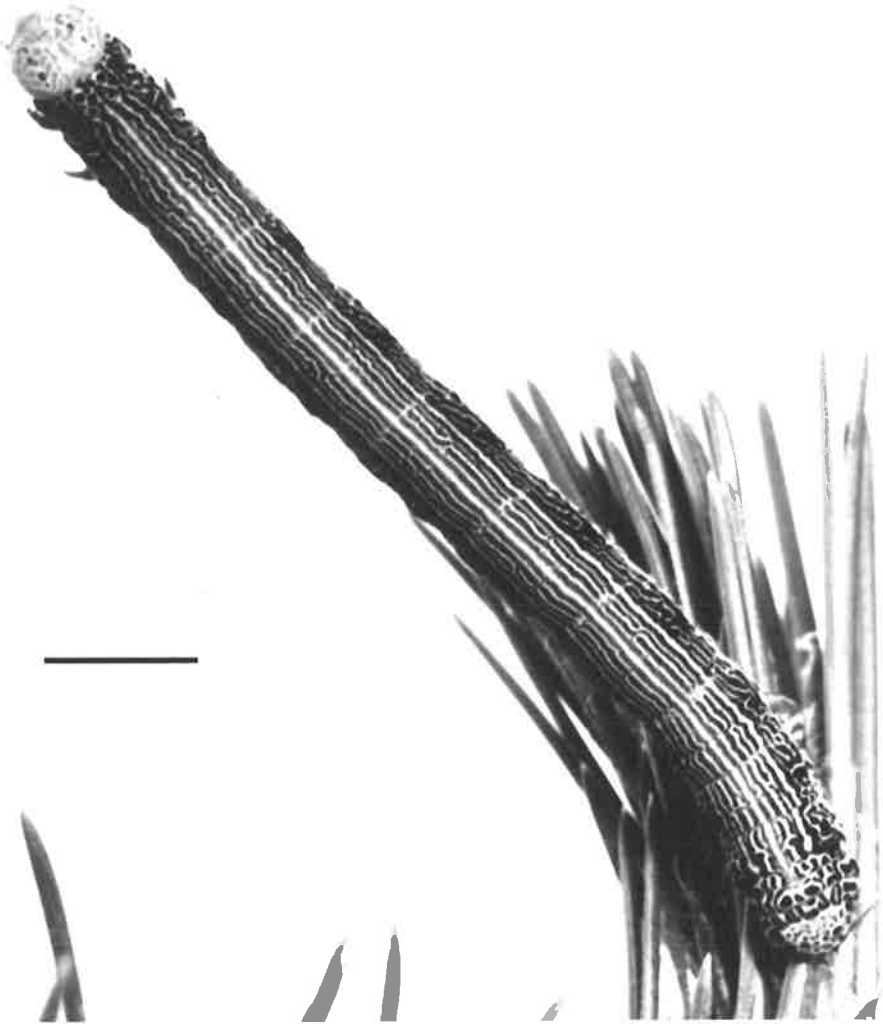
A description of the larval instars was given by Tindale (1928). Variation in colour is common. For example Tindale described the head and prothorax of the final-instar larva as " ... bluish green in colour with scattered blackish marks and spots". Many individuals conform to this description but there are a number with head capsules which are ochreous in colour with the blackish maculations being replaced by whitish ones to varying degrees. A sixth-instar larva is shown in Fig. 3.2.

3.3.1 Behaviour

Neonate larvae are extremely active and exhibit marked positive phototaxis. They soon suspend themselves from silk threads and can be easily dispersed by air currents to other branches and trees. Observations in the field and in the laboratory suggest that almost all first-instar larvae undergo an initial dispersal episode. Dispersal has been discussed at length by Andrewartha and Birch (1954); they observed that most animals have an innate tendency to disperse, and that this tendency may be accentuated by various factors like crowding, hunger, warmth and wind. It has been demonstrated that the first-instar larvae of *Lymantria dispar* (L.) disperse more frequently in the presence of unacceptable food or when denied food, than when in the presence of favoured food (Capinera and Barbosa, 1976).

Fig. 3.2 *Chlenias pachymela*, sixth-instar larva.

Scale represents 6.5 mm.



Starvation, food quality and larval density were examined as factors influencing the tendency of first-instar larvae of *C. pachymela* to disperse; the results were inconclusive.

The early larval instars are restricted in their choice of food materials. They show a strong preference for pine pollen and can often be seen burrowing into the mature male strobili. Pollen seems to be an important constituent of the diet of young larvae. This importance is examined in Chapter 5.

Other than pollen, the stem tissue of new shoots is the exclusive diet of the young larva. By the time it reaches the third-instar the larva is feeding on the proximal ends of new needles. Up to the end of the third-instar's feeding period the damage to its host is not noticeable.

Fourth and later instar larvae are voracious feeders. Entire needles may be eaten. Frequently, needles are eaten at the proximal end and then the presence of larvae can be detected by bits of green needles scattered on the ground under an infested tree. Current season's needles are still preferred although needles of all ages are eaten when the population is dense and food is scarce.

When the larva is disturbed it drops from the branch and dangles by a silk thread. After some time it will climb up the thread onto its previous perch. This behaviour is more evident in later instars.

Like the neonate larva, other instars are also positively phototactic but the response seems to be much weaker. A reversal in the normally photopositive response has been observed to take place at high temperatures. Whilst sampling for larvae in the field, all 10 larvae sampled from one tree were found on the

trunk; the ambient air temperature was 36°C. On another tree, 15 of the 17 larvae sampled were also found on the trunk; the temperature recorded was 38°C. The larvae concerned were in their fifth and sixth-instars. In the laboratory sixth-instar larvae were seen to move rapidly away from the window when the ambient temperature was 32°C. This reversal in the normal response to light has also been observed and investigated for other Lepidoptera (Wellington and Henson, 1947; Sullivan and Wellington, 1953). The response is probably a thermoregulatory one but may also be influenced by relative humidity and starvation. The effects of physical factors on the behaviour of *C. pachymela* larvae require further investigation.

3.3.2 Thermal requirements

Larvae were reared at 5 constant temperatures on *Cupressus macrocarpa* foliage using the method outlined in Section 2.1. The larvae were examined daily; the developmental time was recorded for each larval instar (ecdysis to ecdysis) and also for the entire larval stage of both sexes; the median developmental times are given in Table 3.5. The median value was used in preference to the arithmetic mean for the reason given in Section 3.2.1.

The reciprocal of the median developmental time (rate of development) was plotted against temperature (Fig. 3.3). The rate of development at 25°C deviated from the linear relationship for all larval instars, so linear regressions of the rate of development on temperature were based on the data for the other temperatures. The threshold temperatures and thermal constants

Table 3.5 Developmental times (days) of larval instars of *Chlenias pachymela* at various temperatures.

Larval instar	Statistic	Temperature (°C)				
		11	13	15	20	25
I	Median	18	15	12	7	7
	Range	16-24	12-20	10-17	6-10	5-9
	n	80	93	99	79	64
II	Median	16	12	9	5	5
	Range	13-28	9-15	7-13	4-7	4-6
	n	60	92	98	79	58
III	Median	22	12	8	5	5
	Range	10-34	9-14	7-11	4-8	4-8
	n	45	82	97	79	58
IV	Median	21	12	9	6	7
	Range	15-34	10-19	6-14	4-8	4-8
	n	35	80	94	74	57
V	Median	-	15	12	8	8
	Range	-	11-27	8-21	6-14	4-12
	n	-	77	93	72	56
VI	Median	-	38	30	20	19
	Range	-	31-53	26-43	17-32	16-29
	n	-	74	88	72	52
♂ :I-VI	Median	-	100	80	52	49
	Range	-	90-115	68-97	45-68	43-60
	n	-	58	66	64	39
♀ :I-VI	Median	-	109	85	61	59
	Range	-	100-115	77-101	56-69	52-66
	n	-	15	21	7	12

Fig. 3.3 Linear regressions of median developmental rate on temperature for larval instars I-VI (L_1-L_6) of *Chlenias pachymela*. The regression functions are as follows :

L_1 : $y = -0.060 + 0.010x$ ($r = 0.989$, $P<0.05$)

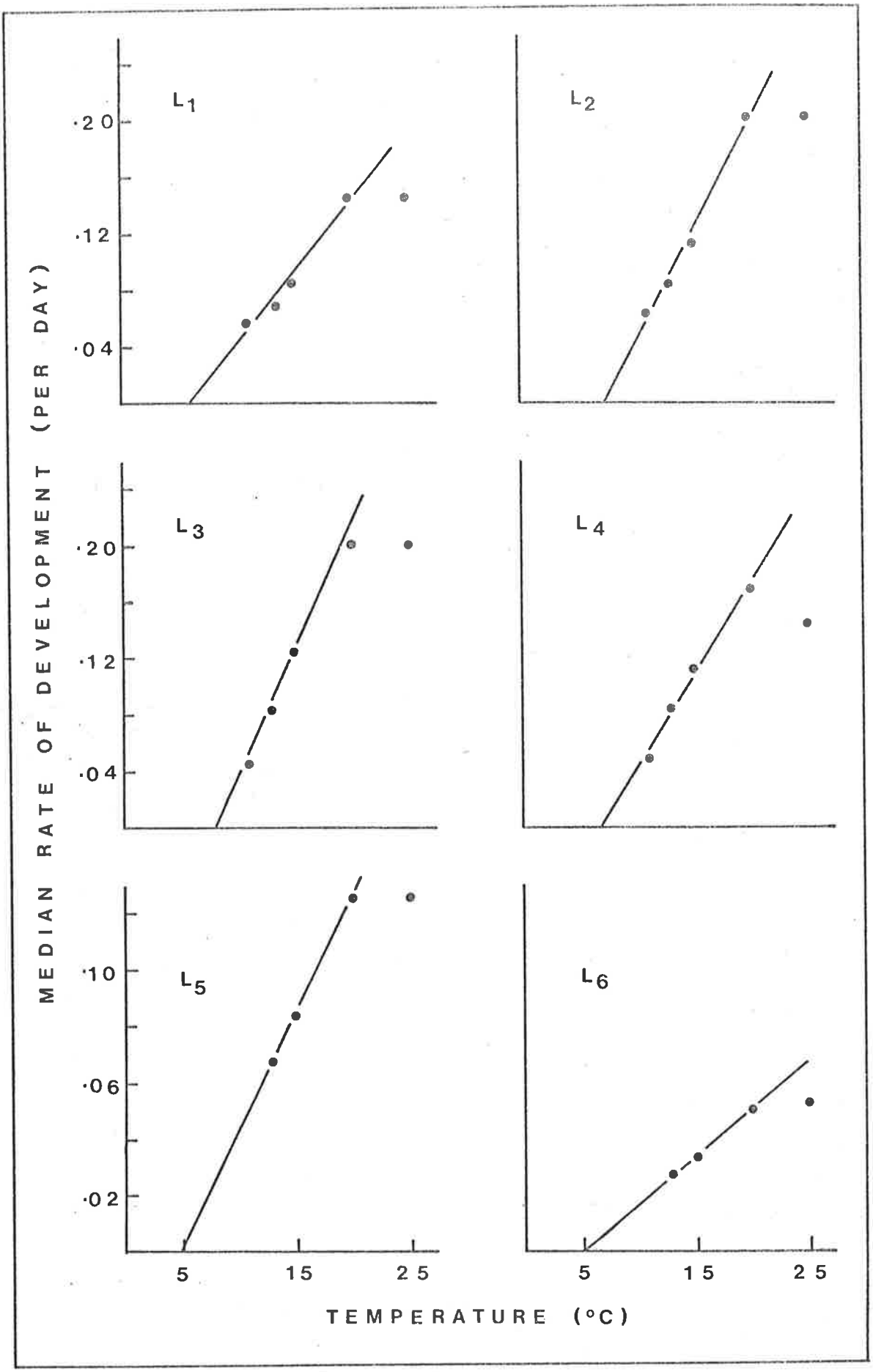
L_2 : $y = -0.116 + 0.016x$ ($r = 0.994$, $P<0.01$)

L_3 : $y = -0.139 + 0.017x$ ($r = 0.997$, $P<0.01$)

L_4 : $y = -0.089 + 0.013x$ ($r = 0.994$, $P<0.01$)

L_5 : $y = -0.042 + 0.008x$ ($r = 1.000$, $P<0.01$)

L_6 : $y = -0.018 + 0.003x$ ($r = 1.000$, $P<0.01$)


L1
L2
L3
L4
L5
L6
·20
·12
·04
·10
·06
·02
5
15
25
MEDIAN RATE OF DEVELOPMENT (PER DAY)
TEMPERATURE (°C)

were estimated using the method given in Section 3.2.1 (Table 3.6).

It should be noted that figures given for the sixth larval instar included the "prepupa". The prepupa is distinguished by several behavioural and physical features : (1) feeding ceases, (2) the body contracts, (3) the colourful markings turn dull, and (4) the cuticle acquires a greasy appearance. However, apolysis does not occur in the sixth instar until formation of the pupa. Therefore, the prepupa may not be considered as a separate instar or stage.

3.4 Pupa

The larva pupates within a silken cocoon encrusted with soil particles (Fig. 3.4). Ecdysis was completed in less than 24 hours at a temperature of 20°C. Newly-formed pupae are greenish in colour but quickly acquire a light brown colouration which deepens with time. A brief description of the pupa is given by Tindale (1928).

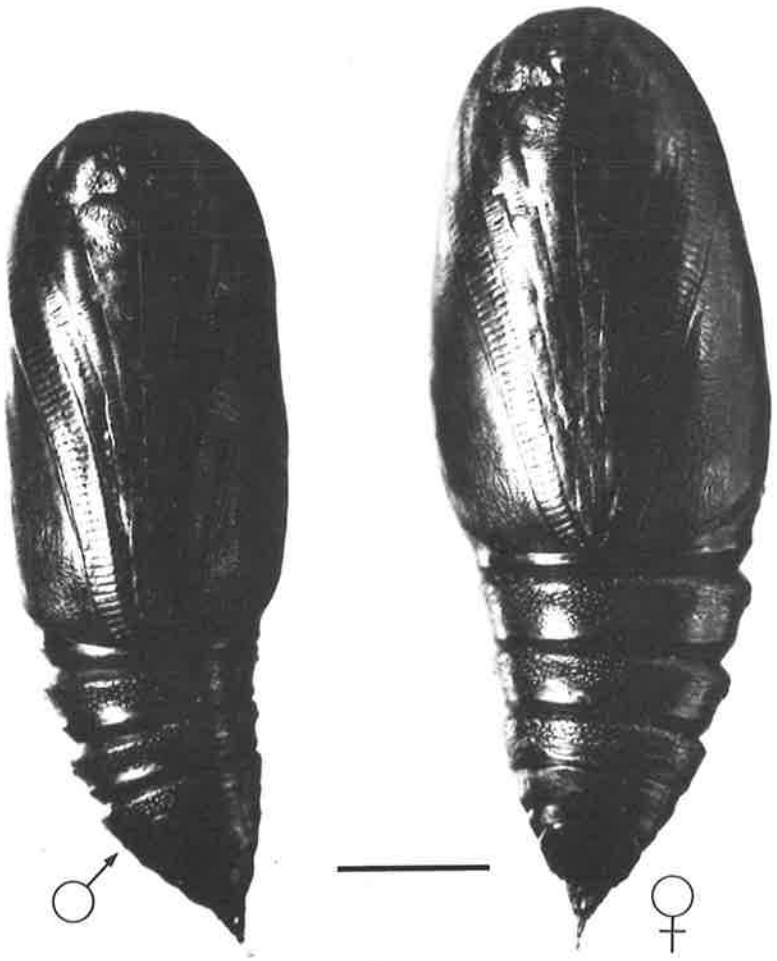
Pupae may be sexed on the basis of genital "scars" : the male has one on sternum 9 and the female one each on sterna 8 and 9. Female may frequently be distinguished from males because the former are bigger in size. However, sexing pupae on the basis of size is unreliable as there is considerable overlap in pupal dimensions (Table 3.7).

In the forest, pupae were commonly found either at the soil surface beneath the litter or immediately below the soil surface. They were rarely found more than 5 cm below the soil surface, and none were found in the tree.

Table 3.6 Developmental threshold temperatures (t) and thermal constants (K) for the 6 larval instars of *Chlenias pachymela*.

Larval instar	t(°C)	K(D°)
I	6.0	100.5
II	7.4	66.7
III	8.1	59.2
IV	6.8	79.1
V	5.0	119.8
VI	5.2	294.7

Fig. 3.4 *Chlenias pachymela* : pupae (top) and soil-encrusted cocoons (bottom).
Scales represent 2.7 mm (top) and 11.2 mm (bottom).



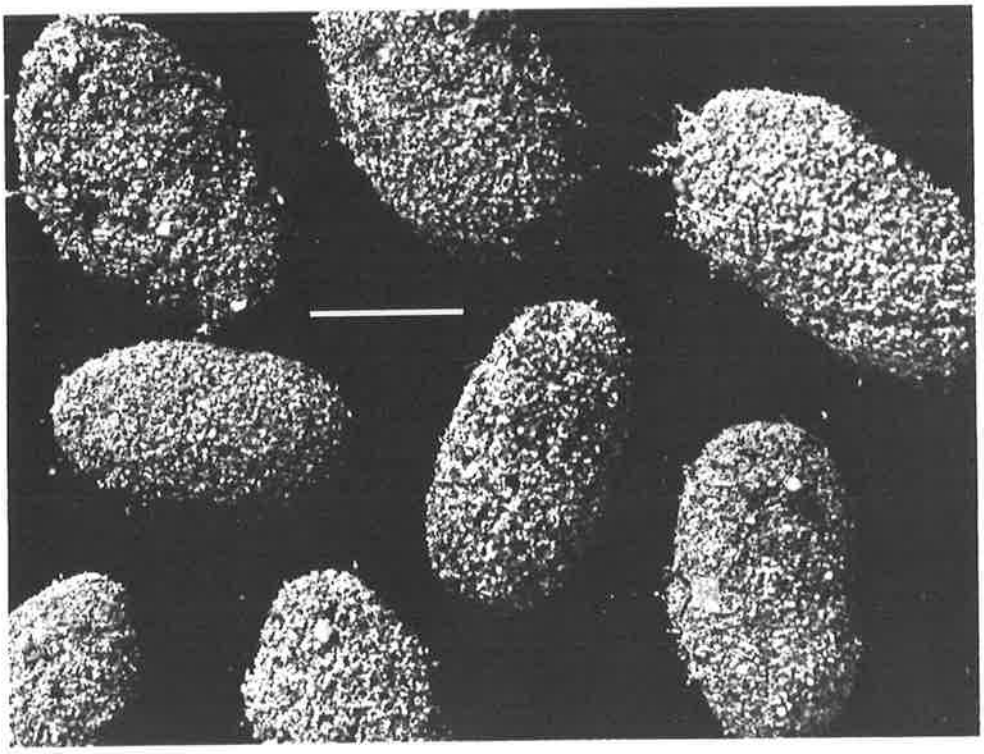


Table 3.7 Dimensions (in mm) of pupae.

	Male		Female	
	Length	Maximum diameter	Length	Maximum diameter
n	20	20	20	20
$\bar{x}$	16.0	5.7	16.6	6.1
Range	13.7-17.8	4.6-6.7	13.1-19.8	4.9-7.7
S.E.	0.22	0.11	0.46	0.16

The pupae remain in the ground for 5-6 months. Since the greater part of this time is hot and dry, I decided to find out the extent of weight loss that would take place. Samples of pupae were collected periodically from the study area over the entire pupal period. The mean weight of each sample for each sex is given in Table 3.8. An analysis of variance showed no significant difference ($P>0.05$) between the weights of pupae collected at the various times for either sex (Appendix 3). These results suggest that the pupae are able to endure the rigours of the summer and autumn months without showing any significant loss in weight.

If the weight of the female pupa is correlated with potential fecundity as has been shown for other Lepidoptera (Baker, 1968; Klomp, 1968; Cobbinah, 1978; Capinera, 1979), then a sample collected at any time from the field can be used to estimate potential fecundity for the population. The relationship between pupal weight and potential fecundity was examined in an experiment.

Female pupae (n=14) collected from the field on 15 January 1979 were washed, air-dried, and weighed. At emergence each individual was dissected and the number of mature and immature ova counted. The data is presented in Table 3.9.

Analysis of the data showed that good correlations were obtained between pupal weight and number of mature ova ($r=0.92$, $P<0.01$), and pupal weight and total number of ova ($r=0.70$, $P<0.01$); however, pupal weight was poorly correlated with immature ova ($r=0.39$, $P>0.05$). The statistic r^2 gives

Table 3.8 Mean weights (in mg) of pupae collected periodically at Noolook in 1978.

Sex	Date of collection	n	Mean ± S.E.
Female	11 Jan	11	306.0 ± 20.4
	17 Feb	20	353.2 ± 11.7
	23 Mar	20	323.0 ± 17.0
	27 Apr	20	369.3 ± 12.6
	19 May	20	336.2 ± 15.2
Male	11 Jan	20	251.2 ± 6.0
	17 Feb	20	262.9 ± 6.1
	23 Mar	20	250.7 ± 6.2
	27 Apr	20	270.3 ± 5.5
	19 May	20	249.6 ± 8.8

Table 3.9 The weights of female pupae of *Chlenias pachymela*, and the numbers of mature, immature and total ova found within moths (<24 h old) emerging from these pupae.

Weight of pupae (mg)	No. mature ova	No. immature ova	Total ova
180.3	438	482	920
332.8	643	492	1135
331.1	601	498	1099
338.1	708	666	1374
300.6	533	1261	1794
280.6	555	723	1278
320.6	614	654	1268
394.3	710	1014	1724
355.3	743	668	1411
320.0	615	659	1274
322.9	604	666	1270
185.9	316	512	828
272.2	459	466	925
288.8	583	552	1135

the proportion of the variance of y that can be attributed to its linear regression on x (Snedecor and Cochran, 1967). The pupal weight (x) may be used as an estimator of the total number of ova, i.e. potential fecundity (y), but the estimate will be relatively crude because only about half (r^2=0.49) the variance of y was associated with x.

A comparison was made of the weights of pupae collected from the study area in 1976, 1977, 1978 and 1979. The mean weight for each sex in each year is shown in Table 3.10. Analyses of variance showed no significant difference (P>0.05) in the weights of pupae between years for either sex (Appendix 4). The results suggest that the potential fecundity of pupae were similar during the period of study.

Contact water is not required for pupal development or adult emergence although the soil in the field is usually wet at about the time of adult emergence. In the laboratory, normal healthy adults ecloded from pupae kept throughout in unmoistened vermiculite. Adults were able to mate and the females to lay their normal complement of eggs.

Emergence of adults takes place between dusk and dawn. This limited period emergence is probably determined by a circadian rhythm as has been demonstrated in many insects e.g. *Hyphantria cunea* (Drury) (Hirai, 1977). The subject of circadian rhythm in arthropods is a complex one and has been much investigated (see reviews by Danilevsky et al., 1970 and Harker, 1961).

Table 3.10 Mean weights (in mg) of pupae of *Chlenias pachymela* collected from Noolook in 1976, 1977, 1978 and 1979.

Sex	Year	No. of pupae	$\bar{x}$ ± S.E.
Male	1976	20	226.9 ± 8.8
	1977	20	209.1 ± 10.6
	1978	20	223.9 ± 10.4
	1979	20	231.2 ± 4.5
Female	1976	20	285.5 ± 12.1
	1977	20	281.4 ± 12.3
	1978	11	305.9 ± 20.4
	1979	20	290.4 ± 57.5

3.5 Adult

The 2 adult forms (see Section 1.1) are present in both sexes. These forms have been described by Lower (1893) and Tindale (1928) under the names of *C. pachymela* and *C. pini* respectively.

The onset of dusk appears to be a cue for adult activity : flight, mating and oviposition all take place in the period between dusk and dawn. Temperatures recorded at a height of 1 m above the forest floor during adult flight ranged between 5.0 and 9.5°C. During the day, adults may fly or walk short distances if disturbed but usually feign death.

Both male and female moths are attracted to light. Dissections of moths caught in light traps revealed that only 2 out of 29 females had a sizeable number of mature eggs (347 and 453). The rest retained less than 100 eggs each, and out of these, 10 were devoid of any mature ova. All the females examined had few or no immature ova. These data suggested that only females which have laid at least some of their eggs responded to light.

The absence of fully gravid females caught in light traps suggested that such females do not respond positively to light or are simply too heavy to fly far. This behaviour resembles that of the spruce budworm, *Choristoneura fumiferana* (Clemens), the female of which will deposit her first few egg masses upon the tree on which she emerges before becoming capable of active flight (Wellington and Henson, 1947).

Eggs are usually laid on mature green needles (Fig. 3.5). However, egg masses have been found on weeds, immature needles, as well as on dead needles. The eggs are deposited along the length

Fig. 3.5 *Chlenias pachymela* ovipositing on the needles of *Pinus radiata*.

of a pine needle so that they are in contact with one another, much like grains of corn on a cob. The mean numbers of eggs per mass for 1976, 1977 and 1978 are presented in Table 3.11.

Both the male and female moths are fully mature at eclosion : mating usually takes place within a few hours after their wings have expanded and dried.

The presence of a single spermatophore in each light-trapped female dissected indicates that the female moth only mates once in her life. However, spermatophore counts may only be used as evidence of mating frequency if the spermatophore can always be recognised even though subject to erosion,collapse and considerable dissolution with time (Burns, 1968). The following experiment was performed to examine the stability of the spermatophore within the bursa copulatrix.

Newly emerged females were kept in a cage with about twice the number of males. The following day the females were removed and each kept in a cage with a sprig of pine needles for egg-laying. Longevity of the females was prolonged by supplying them with 10% sucrose solution. At death those females which had laid fertile eggs were dissected and the condition of the spermatophore examined.

Each female (n=24) dissected retained a recognisable spermatophore and most of the spermatophores did not show any sign of erosion or dissolution. The evidence suggests that females of *Chlenias* are largely monogamous. In the laboratory some females were found to contain 2 spermatophores. However, such females were caged with males throughout their lives - a condition not comparable with that in nature.

The male to female sex ratios based on pupae collected at Noolook were : 1976, 1.5:1 (n=237); 1977, 6.3:1 (n=51); 1978, 1.5:1 (n=811); 1979, 2.4:1 (n=81). The sex ratio based on the total number of moths caught in light traps during 1977 was

Table 3.11 Sizes of egg masses collected from Noolook in 1976, 1977 and 1978.

	1976	1977	1978
No. egg masses	191	21	17
$\bar{x}$	163.7	202.2	214.1
Range	6 - 848	22 - 593	27 - 649
S.E.	11.8	41.5	54.9

3.8:1, again favouring males. However, this ratio varied throughout the season (Fig. 3.6).

The longevity and reproductive capacity of adults are dependent on the availability of sugar to feed on. In the laboratory, the longevity of adults was extended when given a diet of 10% sucrose solution (Table 3.12). Females generally lived longer than males with or without sucrose.

At emergence the abdominal cavity of a female is filled with mature (chorionated) and immature ova in various stages of development. Each female has 8 ovarioles. There is a sharp demarcation of mature and immature ova within each ovariole. The mature ova are recognizable by their pale green colour and are much harder than the immature ova which are buff-coloured.

Fourteen newly-emerged females were dissected and the number of mature and immature ova counted to get an estimate of the potential fecundity. Immature ova were counted as far up the ovariole as individual ones could be discerned at 50 times magnification. The results are summarised in Table 3.13. The potential fecundity as represented by the total number of ova is probably a slight underestimate.

When fed on 10% sucrose solution, the mean (± S.E.) number of eggs laid per female was 1021 ± 58 (range = 838-1148, n=6). A proportion (1-20%) of eggs were infertile but infertile eggs were rarely (<0.1%) found in the forest. The first batch of eggs laid was always the biggest and constituted 57-71% of the total number of eggs. Subsequent batches were laid at infrequent intervals almost up to the time of death.

Fig. 3.6 Light trap catches at Noolook in 1977 and resultant sex ratio.

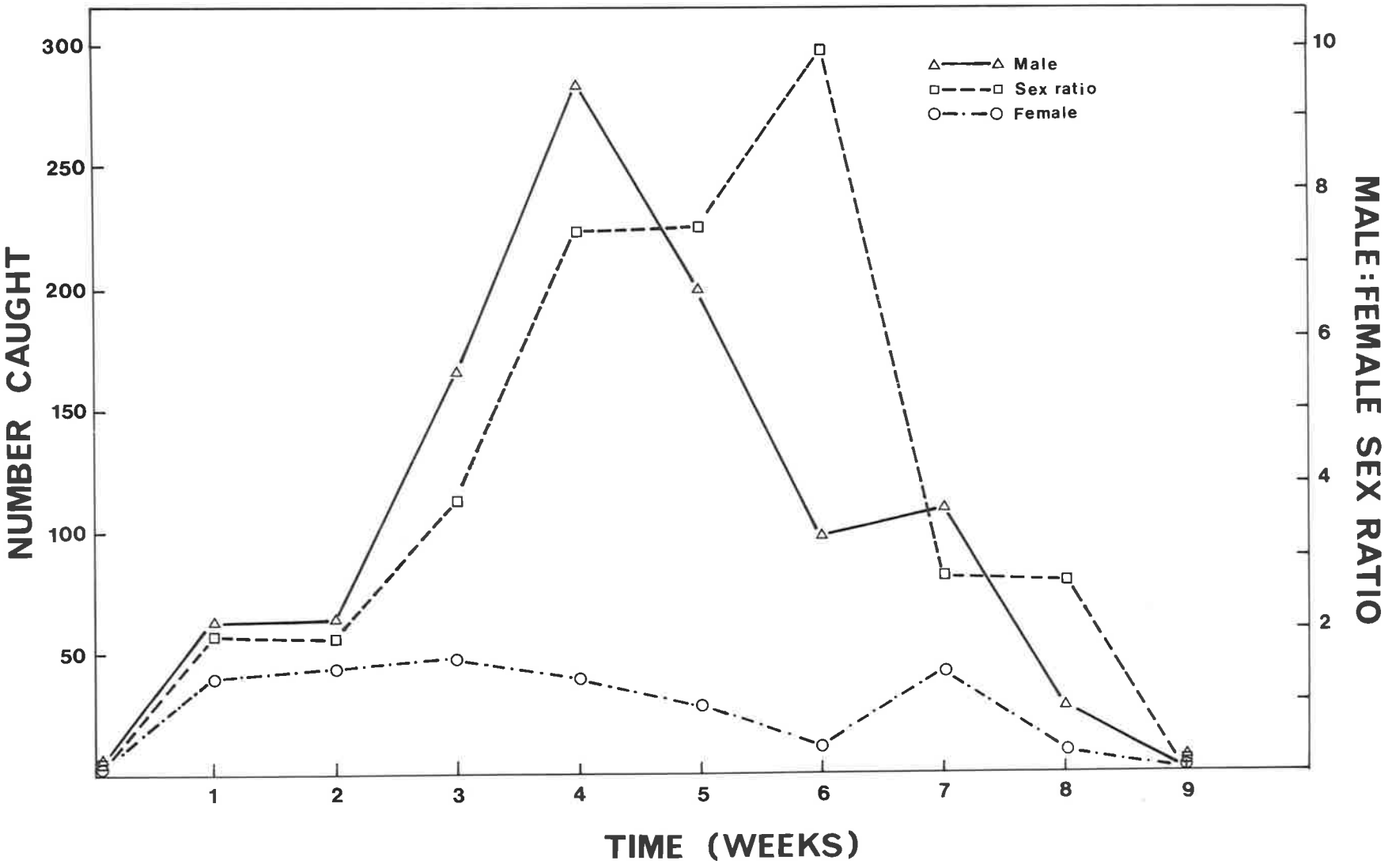

NUMBER CAUGHT
300
250
200
150
100
50
1
2
3
4
5
6
7
8
9
TIME (WEEKS)
10
8
6
4
2
MALE:FEMALE SEX RATIO
Male
Sex ratio
Female

Table 3.12 Longevity (in days) of adult moths at 15°C when supplied with 10% sucrose solution, water or neither.

	Sucrose solution		Water		No sucrose or water	
	♂	♀	♂	♀	♂	♀
n	58	35	33	27	42	25
$\bar{x}$	14.2	16.6	7.0	11.3	7.1	10.8
Range	4 - 38	5 - 35	4 - 12	6 - 19	2 - 12	2 - 19
S.E.	1.03	1.43	0.37	0.66	0.31	0.82

Table 3.13 Number of mature and immature ova in newly-emerged female moths (n=14).

	Mature ova	Immature ova	Total ova	% Immature ova
Mean	580.1	665.2	1245.4	42.9
S.E.	31.0	59.7	74.3	8.7
Range	316-743	466-1261	828-1794	43.4-70.3

The potential fecundity of a female moth is probably realised in nature. Out of 29 light-trapped females, 19 had less than 20 mature and immature ova each. When deprived of sucrose, females were able to mate and lay eggs at the same rate as those which had access to sucrose; but the egg-laying activity ceased after a few days although these females continued to live for some time. At death such females were found to retain large numbers of mature and immature ova. These data suggest that moths in the field do have access to sugar, but the source is not known.

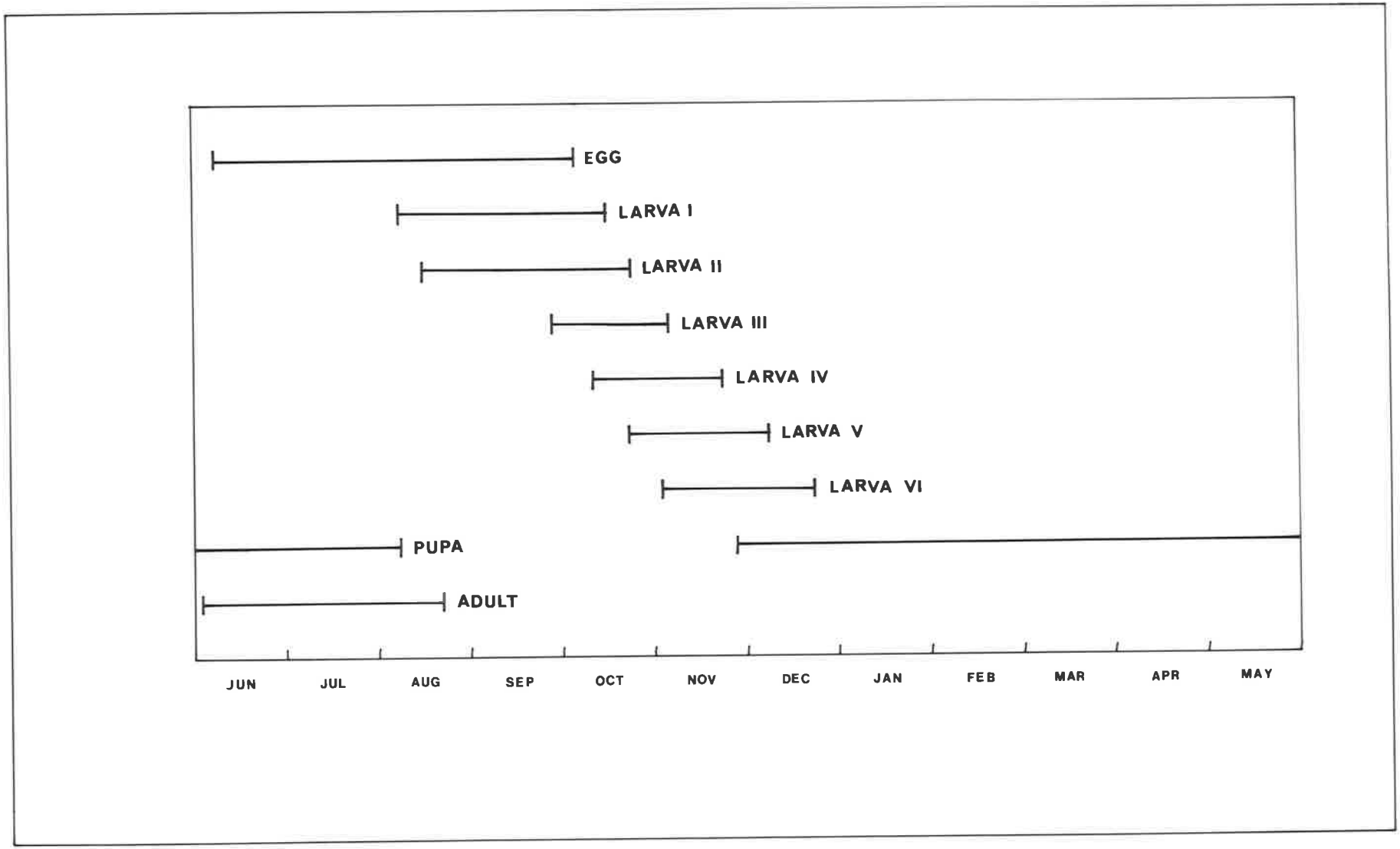
In the laboratory, unmated females may lay a few small batches of eggs, but the majority died without laying any. For this reason the presence of unmated females may not be detected in the field. Furthermore, the eggs laid detached readily from the substrate : in the field such eggs would not remain on the needles for long.

3.6 Seasonal occurrence

C. pachymela has a univoltine life cycle and the times of occurrence of the different stages during the year were similar in the 3 generations studied at Noolook (Fig. 3.7).

Pupae can be found in the forest from late November until about early August. Adult emergence commences in early June and moths can be observed until about mid-August. Egg-laying activity follows adult activity closely but because eggs take some 2 months to hatch, unhatched eggs can be found in the field until late September or early October. First-instar larvae emerge in early to mid-August. The larval period extends to late

Fig. 3.7 Seasonal occurrence of *Chlenias pachymela* at Noolook.


EGG
LARVA I
LARVA II
LARVA III
LARVA IV
LARVA V
LARVA VI
PUPA
ADULT
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY

December. Pupation begins in the latter part of November and is completed by mid-January. In seasonal terms, pupae are in the ground during summer and autumn. Adult activity takes place in winter. The larval period begins in late winter and ends in early summer.

CHAPTER 4

DIAPAUSE

CHAPTER 4

DIAPAUSE

4.1 Introduction

The phenology of many insects is regulated by the phenomenon known as diapause. It is well known that diapause in insects serves to synchronise activity with favourable weather and seasonally available biotic resources such as food, mates, oviposition sites, and periods free from natural enemies. When in diapause, the insect is at that stage of its life when it is most able to survive unfavourable weather.

The habitat of *Chlenias pachymela* has a Mediterranean climate characterised by hot dry summers and cool wet winters. The long summer greatly stresses many organisms through the high temperatures, general lack of moisture and associated shortages of food. The pine looper has responded to these stresses by evolving the habit of spending about half of each year, largely during summer and autumn, in diapause in the litter and soil beneath its host trees. The adults emerge in mid-winter to mate and the females to lay their eggs. The larvae hatch in spring when new vegetative growth, vital to survival of the first-instar, is abundant. Pupation begins in late spring when temperatures start to rise and is completed by early summer. The insect is therefore in synchrony with its environment. In a radiata pine plantation, however, this diapause does not ensure maximum survival of the population (see Chapters 5 and 8).

"Pupal" diapause has previously been studied in *Ciampa arietaria* Guen. (Monro, 1972) which is closely related to

Chlenias pachymela and is also univoltine with an obligate diapause lasting through the summer months. From the results of his investigations, Monro concluded that this species has a "terminal" diapause, i.e. diapause occurs when morphogenesis is almost completed. This diapause was apparently eliminated during low temperatures such as are found in autumn. Monro further found that moisture had no influence on diapause termination. From some initial studies upon *Chlenias pachymela* he indicated that diapause in this species was similar to that in *Ciampa*.

My preliminary experiments with *Chlenias* showed that diapause development is a temperature-dependent process. The present series of experiments was therefore devoted to examining the influence of temperature on diapause.

A number of experiments were done before the mechanism underlying diapause in this insect became apparent. For the sake of brevity and clarity, only those experiments which illustrate the mechanism are reported here.

In the following sections the words "high" and "low" when referring to temperature are used in a relative sense. Temperatures of 25°C and above are "high" and 20°C and below are "low". The terms "morphogenesis" and "diapause development" are used in the sense defined by Andrewartha (1952) and the terms "pupa" and "pharate adult" as defined by Hinton (1973).

4.2 A preliminary model of the diapause processes

A preliminary model to describe the processes in the pupa leading up to adult emergence was based on the following observations and results from preliminary experiments :

1. When newly formed pupae were placed at constant temperatures of 11, 13, 15, 20, 25 and 30°C, adults eventually emerged at the lower temperatures but not at 25° and 30°C.
2. Weekly dissections of pupae kept at 25°C showed that some morphogenesis ensued from the time of pupation and continued until the pharate adult stage was reached. This latter stage resembled the imago externally in every way except that the scales on the body and the wings were not pigmented. This stage was reached in about 5-6 weeks at 25°C; no further change occurred for as long as the insect was kept at this temperature. The pharate adult is therefore the diapausing stage in this species.
3. Dissections also showed that development of the pupa and the pharate adult up to the time when it went into diapause, progressed faster at high temperatures than low.

From these preliminary observations, the following tentative model of the successive processes in the diapause stage was suggested :

1. Development and apolysis of the pupa. This process has a high temperature optimum (25-30°C).
2. Morphogenesis of the pre-diapause pharate adult. This process has a high temperature optimum (25-30°C).
3. Diapause development in the pharate adult. The optimum temperature has yet to be determined.

4. Morphogenesis of the post-diapause pharate adult.

The optimum temperature has yet to be determined.

4.3 Experiment 1 : Pupae exposed to high temperatures for varying periods and then kept at 13°C till adult emergence.

The test animals were reared in the laboratory using the method described in Section 2.1. Pupation took place over a period of 20 days and the experiment was started on the day on which enough pupae had formed.

Groups of 20 pupae were first exposed to a high temperature of either 25 or 30°C for varying lengths of time of 2, 4, 8 or 16 weeks and then transferred to 13°C till adult emergence. A control group was also kept at 13°C continuously.

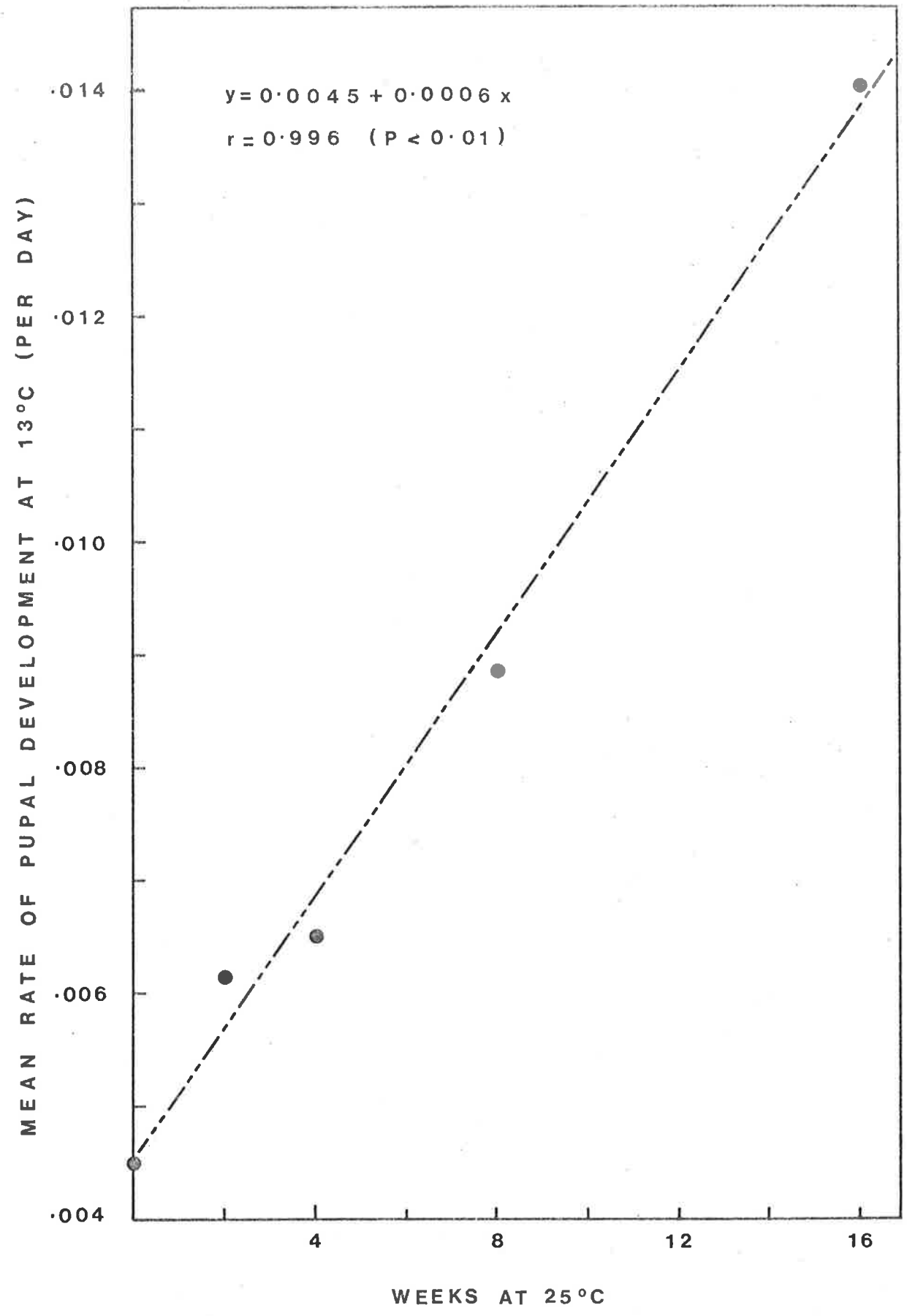
The results given in Table 4.1 show that increasing the length of the initial exposure to high temperatures had the effect of reducing the time spent at 13°C. For the pupae initially exposed to 25°C there was a linear regression of the mean rate of development at 13°C on the length of initial exposure at 25°C (Fig. 4.1). From this it may be inferred that diapause development was favoured by a high temperature.

When pupae were exposed to only 2 weeks at 30°C, the number of adults emerging and the mean duration at 13°C were comparable to those at 25°C. A t-test showed no significant difference between the means at P=0.05. However, when the initial exposure at 30°C was longer than 2 weeks there was a progressive decrease in the percentage of successful emergence as the length of exposure was increased, suggesting that there was a deleterious effect on pupae. An adverse effect was also

Table 4.1 Diapause Experiment 1 : The percentage emergence, the mean number of days to emergence at 13°C, and the total number of days to emergence of pupae exposed to high temperatures for varying periods and then kept at 13°C. Initial number of pupae per treatment was 20

Initial treatment		% emergence	No. of days to emergence at 13°C: $\bar{x} \pm$ S.D.	Total no. of days to emergence
Temperature (°C)	Period (weeks)			
13	continuous	94	221.7 ± 34.3	221.7
25	2	100	163.1 ± 35.3	177.1
	4	94	153.8 ± 36.1	181.8
	8	89	112.9 ± 31.5	168.9
	16	100	71.2 ± 12.0	183.2
30	2	100	165.2 ± 32.5	179.2
	4	65	133.1 ± 23.3	161.1
	8	55	96.7 ± 18.4	152.7
	16	40	68.8 ± 11.0	180.8

Fig. 4.1 Diapause Experiment 1 : Estimated linear relationship between mean rate of pupal development at 13°C and period of initial exposure to 25°C.


y = 0·0045 + 0·0006 x
r = 0·996 (P < 0·01)
·014
·012
·010
·008
·006
·004
MEAN RATE OF PUPAL DEVELOPMENT AT 13°C (PER DAY)
4
8
12
16
WEEKS AT 25°C

observed in adult females that emerged from pupae exposed to 30°C for 4 weeks or longer. Many of these females were adjudged to be abnormal because : (1) they contained a large amount of fat body within the abdomen, and (2) they had very few ova, especially mature ones. In a normal adult female the fat body was scattered amongst the organs, and ovarioles were packed with ova, whereas in an abnormal one the fat body dominated the abdominal cavity to the extent that the ovary was hidden by it and there were frequent gaps between the ova of each ovariole.

Thus it may be concluded that 25°C is approximately the optimum constant high temperature for diapause development. Higher temperatures are tolerated and will even allow diapause development but prolonged exposures to such temperatures seem to be harmful.

Since high temperatures eliminate diapause but did not permit adult emergence, post-diapause morphogenesis must therefore occur at low temperatures. Post-diapause morphogenesis is investigated in Experiment 3 (Section 4.5).

4.4. Experiment 2 : Pupae exposed to 25°C for 36 weeks and then kept at 13°C till adult emergence

When the preceding experiment was being designed, 16 weeks was considered the maximum period of exposure to constant high temperatures as in nature such a period of high temperatures would be unlikely. Despite these natural conditions, the data indicate that diapause development may continue if the length of exposure to 25°C was extended beyond 16 weeks. The following experiment was conducted to test the hypothesis that diapause development

would continue even when pupae were exposed to 25°C for 36 weeks.

Pupae (n=18) were kept at 25°C from the time of pupation (between 26 September and 9 October 1978) until 13 June 1979 when they were transferred to 13°C.

The time to adult emergence at 13°C was 38.8 ± 1.0 days ($\bar{x}$ ± S.E.) for 10 pupae. The adult females when dissected, showed abnormalities similar to those found in heat-stressed females described in the preceding section. Examination of the remaining 8 pupae showed that they were apparently healthy; and the pharate adult within was moist and the tissues fresh; its development had passed the diapause stage and scale pigmentation was obvious but not complete. However, when such pupae were mechanically disturbed, they failed to respond, as do normal pupae, by slow but perceptible movements of their abdomens.

The results suggest that diapause development can be induced to progress to a point where adult emergence will take place in a fairly short time after being returned to 13°C. But the conditions under which this was brought about was highly artificial and had adverse effects on some if not all of the test animals. In other words, it is not possible to reach the theoretical limit of diapause development without subjecting the pupae to great stress. Some indication of this limit may have been obtained by reducing the exposure period at 25°C to 20 or 24 weeks.

In nature it is probable that low temperatures supervene before the end of diapause development and diapause development is completed at these temperatures.

4.5 Experiment 3 : Pupae initially exposed to 25°C and then kept at various low temperatures till adult emergence

Pupae were collected from Noolook on 27 March 1978 and placed at 25°C on the following day. After 40 days at 25°C, the pupae were divided into groups of 20 and each group was transferred to one of the following low temperatures : 7, 11, 13, 15 and 20°C. A control group was not exposed to 25°C at all but was kept at 13°C continuously.

The date (7 May) when the pupae were taken out of 25°C and transferred to the low temperatures coincided with a time of falling temperatures in the field (see Appendix 1), it being late autumn. Thus the pupae, when transferred to the low temperatures were probably very near the end of diapause development. A comparison of the mean time to adult emergence at the various low temperatures should therefore indicate the optimum temperature for post-diapause morphogenesis.

The results are summarised in Table 4.2. The number of successful emergences in all treatments, except when pupae were incubated at 20°C, were similar. Disregarding the "control" at 13°C, the mean time to adult emergence declined from 7°C to 13°C and then increased to be maximal at 20°C. The mean time to adult emergence at 13°C was shorter when the pupae were previously exposed to 25°C than when they were not (control). Disregarding the control treatment again, the trend in the values of the standard deviation follows that observed for the means.

Diapause development was not completed when the pupae were brought in from the field. This is suggested by the shorter time at 13°C after an initial exposure to 25°C for 40 days compared with the control. If it can be assumed that diapause development

Table 4.2 Diapause Experiment 3 : The percentage emergence and the time required at 13°C until adult emergence for pupae collected from field on 27 March 1978, exposed to 25°C for 40 days, and kept at various low temperatures till adult emergence. Initial number of pupae per treatment was 20.

	Control (13°C direct)	Low temperatures (°C)				
		7	11	13	15	20
% emergence	90	90	95	90	95	75
$\bar{x}$ (days)	82.3	96.9	71.7	61.7	70.7	106.5
S.D.	16.3	13.8	13.2	8.7	9.5	42.5

was completed after the initial treatment at 25°C, then the results suggest that the rate of post-diapause morphogenesis was optimal at about 13°C.

It has been shown in Section 4.4 that the mean time at 13°C could be as low as 39 days if the exposure to 25°C was long enough. Assuming that diapause development was not completed when the pupae were taken out of 25°C in the present experiment, then the time spent at the low temperatures included time for diapause development as well as post-diapause morphogenesis. If this was indeed so, then post-diapause morphogenesis was fastest at a temperature of 13°C or lower. Temperatures of 15°C and above may be ruled out as being favourable temperatures because diapause development is optimised by high temperatures and yet the durations of the diapause period at 15 and 20°C were longer that at 13°C.

4.6 Discussion

Diapause in *C. pachymela* is more conveniently discussed by dividing the "pupal" stage into the pupa and pharate adult stages. The pharate adult stage itself may be divided into the following phases with respect to diapause : pre-diapause, diapause and post-diapause stages.

It is generally understood that in those Lepidoptera with a pupal diapause, diapause development comprises the period from the formation of the pupa to the time when the pupa is competent to initiate pharate adult development (Bodnaryk, 1977). *Chlenias pachymela* is an exception to this rule. As soon as pupation occurs, morphogenesis proceeds in the pupa and continues in the pharate adult up to a point which is reached when the external

features of the pharate adult resembles the imago except that wing and body scales are not pigmented. Morphogenesis in the pupal stage and pre-diapause pharate adult is optimum at temperatures of about 25-30°C.

No further change in the external features of the pharate adult is evident when further exposed to 25°C. Instead, the animal proceeds with diapause development at this temperature and after an adequate period of exposure to 25°C, morphogenesis resumes when the pupa is exposed to low temperatures. Post-diapause morphogenesis is optimal at 13°C or lower.

The temperature range for diapause development usually overlaps that for post-diapause morphogenesis. But post-diapause morphogenesis does not occur at temperatures of 25°C and above. In many insects, diapause is terminated during exposure to temperatures that are too low to permit morphogenesis (Lees, 1956). *C. pachymela* is unusual in that the reverse is true, i.e. diapause is terminated during exposure to temperatures that are too high to permit post-diapause morphogenesis.

However, this is not the only species which requires relatively high temperatures to terminate diapause. The highest optimum temperature for diapause development is recorded for *Halotydeus destructor* (Tucker) at about 50°C but ranged up to 70°C (Wallace, 1970a). Like *C. pachymela* this species of mite lives in regions with a Mediterranean type of climate : post-diapause development is favoured by relatively low temperatures of 5-20.5°C with the optimum at about 19°C (Wallace, 1970b). Other species in which diapause development proceeds under relatively high temperatures include : *Acheta commodus* (Walk.) with temperatures as high as 29.4°C (Hogan, 1960); *Sarcophaga argyrostoma* (R.-D.) and *S. bullata*

Parker with temperatures as high as 29°C (Fraenkel and Hsiao, 1968); *Diatraeagrandiosella* Dyar with 23-30°C (Chippendale and Reddy, 1973); *Ephestia elutella*(Hb.) with 25-30°C (Bell, 1976); *Locustana pardalina*(Walk.) with 35°C (Matthee, 1951); *Aedes atropalpus* (Coq.)with 30°C (Kalpage and Brust, 1974); *Chrysopa carnea* Stephens with 24°C (Tauber and Tauber, 1973); *Sminthurus viridis*(L.)with 30°C (Wallace, 1968).

Diapause in *C. pachymela* is an elegant adaptation to the environment in which the insect lives. By being in diapause the pupa escapes the rigours of a South Australian summer. At the same time development of the organism within the pupal cuticle is favoured by the high temperatures. The animal is not only brought to an advanced stage of development by such temperatures but diapause development is also favoured. By the end of the summer, the pharate adult is about ready to complete its final stage of development when temperatures start to fall. Since post-diapause morphogenesis is optimal at about 13°C or lower, the adult is prevented from emerging during an unfavourable time of the year, i.e. in summer or autumn. With the approach of winter, post-diapause morphogenesis is accelerated so that by mid-winter the adults are ready to emerge.

There is an alternative model to the one discussed above. This second model appears improbable because it does not resemble that of any species of insects studied so far. Nevertheless, the model fits the results of the experiments reported in Sections 4.3 and 4.5, and, because it does, its further testing by suitable experimentation may be of considerable importance to our

further understanding of diapause. The model proposes the same 4 processes as in the first model (Section 4.2), but it also includes the postulates : (1) diapause development in the pharate adult proceeds as rapidly at 13°C as at 25°C, and (2) morphogenesis of the post-diapause pharate adult proceeds rapidly at 13°C but very slowly, if at all, at 25°C. As a corollary of (1) and (2), diapause development and morphogenesis of the post-diapause pharate adult may proceed simultaneously at 13°C but the 2 processes cannot proceed simultaneously at 25°C. The fit of this model may be justified as follows :

(a) Adults did not emerge from the pupae when the pupae were kept continuously at 25°C (preliminary experiment) but they did emerge when the pupae were either kept at 13°C continuously or were given 2-16 weeks at 25°C and then placed at 13°C. So process 4 (post-diapause development) required an exposure to 13°C or some similar low temperature. The data of Experiment 3 indicate that 13°C was indeed near the optimum for the completion of process 4 and that - if postulate (2) is true - the process required about 9 weeks at 13°C (61.7 days in Table 4.2) for completion.

(b) From Experiment 1, two important inferences may be made. Firstly, the total number of days to emergence at each of the 25°C treatments was remarkably similar, and ranged from 168.9-183.2 days ($\bar{x}$=177.8) (see Table 4.1). Since the insects required 221.7 days at 13°C continuously, we may infer that an initial exposure to 25°C of anything between 2 and 16 weeks reduced the time subsequently required at 13°C by about 6 weeks (i.e. 221.7-177.8 = 43.9 days). This reduction can only be due to the rapid completion of processes 1 and 2 at 25°C.

Secondly an inference about the rate of completion of diapause development can be made by making comparisons of any pair of treatments that were initially at 25°C and were then moved to 13°C. Thus if we compare (i) 2 weeks at 25°C and (ii) 4 weeks at 25°C, treatment (ii) can be written as : 2 weeks at 25°C + 2 weeks at 25°C, and then kept at 13°C. Treatment (i) can be written as : 2 weeks at 25°C + 2 weeks at 13°C, and then kept at 13°C. And the 163.1 days at 13°C required for emergence in treatment (i) can be written as : 2 weeks at 13°C + another 163.1-14 days = 149.1 days.

So, in treatment (i) :

2 weeks at 25°C + 2 weeks at 25°C required another 153.8 days at 13°C

but, in treatment (ii):

2 weeks at 25°C + 2 weeks at 13°C required another 163.1-14 = 149.1 days at 13°C.

Since the first 2 weeks of each treatment were identical, the effects of the second 2 weeks can be compared. Seemingly, the second 2 weeks at 25°C was "equivalent" to 2 weeks at 13°C. Similarly, a comparison may thus be made between (i) 16 weeks at 25°C and (ii) 2 weeks at 25°C :

In (i) :

2 weeks at 25°C + 14 weeks at 25°C required another 71.2 days at 13°C

but, in (ii) :

2 weeks at 25°C + 14 weeks at 13°C required another 163.1-98 = 65.1 days at 13°C.

Seemingly again, the 14 weeks at 25°C was "equivalent" to the 14 weeks at 13°C. From these and other comparisons we may infer postulate (1), namely diapause development (process 3) proceeded at the same rate at 13°C as it did at 25°C. We may also infer that processes 1 and 2 require 2 weeks at 25°C.

(c) It may now be noticed that the pupae require 221.7 days (about 32 weeks) at 13°C for processes 1+2+3+4. But processes 1+2 required about 7 weeks at 13°C and process 4 (post-diapause morphogenesis) required 9 weeks at 13°C (see (a)); so process 3 (diapause development) required 16 weeks at either 25°C or 13°C.

(d) In Experiment 3, the pupae maintained at 13°C required 82.3 days (about 12 weeks) to emerge. So the experiment must have been started when the insects had about another 3 weeks of diapause development to complete. This amount of remaining diapause development, along with postulate (2), explains, as follows, the difference in the standard deviations of the 2 treatments, namely

(i) at 25°C for 40 days and then to 13°C and

(ii) at 13°C continuously.

The insect at (i) had, on average, another 3 weeks of diapause development to complete but they were exposed, instead, to another 40 days at 25°C. They would all, therefore, have completed their diapause development during these 40 days. But many would have completed it after 3-5 weeks and been unable - by postulate (2) - to start any post-diapause development. There would, therefore, have been an accumulation of those that had completed diapause development but could not develop any further. When they were all then placed at 13°C, they completed their post-diapause development with a smaller range in the emergence date than was

expected (and observed) in those kept continuously at 13°C. In this latter group, those that completed diapause development first could proceed at once with post-diapause development so that the population's genetic variability of duration of development was not reduced.

The same accumulation of pupae which had completed diapause development during the 40 days at 25°C also explains why, in Experiment 3, the total time to emergence at 40 days at 25°C before being transferred to 13°C was longer than at 13°C continuously - unlike the treatments at 25°C in Experiment 1 in which the longest exposure at 25°C was, fortuitously, about that required for the completion of diapause development.

Only further experimentation can determine which of the 2 models of diapause presented here better describes the total process.

CHAPTER 5

TROPHIC RELATIONS

5.1 Introduction

There have been various attempts to classify the components of environment in animal ecology (e.g. Andrewartha and Birch, 1954; Browning, 1962; Maelzer, 1965; Andrewartha, 1970). "Resources" is one of the components which has gained general acceptance, although what can be regarded as a resource is debatable (see for example, Andrewartha and Browning, 1961; Maelzer, 1965). There is, however, one resource which is recognised as important and universal to all animals - and this is food.

The degree of the importance of food is debatable, however. Nicholson (1933, 1954) and, to a certain extent, Uvarov (1931), both of whom have made extensive studies of the importance of food, have recognised that it is not uncommon for food to be critical for a population. Various other studies have demonstrated that food can indeed be a limiting resource bringing about the decline of insect populations (Morris, 1963; Readshaw, 1965; Dempster, 1968).

On the other hand there are many who hold the view that the numbers of phytophagous insects are rarely limited by a shortage of their plant food (Thompson, 1956; Imms, 1937; Milne, 1957; Pimentel, 1963). The consensus of opinion can be summarised by Wilson's (1968) conclusion that "Food is the ultimate sanction against population increase, but in the general opinion it is seldom invoked".

While the importance of food quantity has been the subject of much debate, the question of food quality has not been given its due attention in insect ecology (Huffaker, 1957; House, 1965b, 1969; Kimmins, 1971).

Before proceeding further it is useful to define the term "nutritional requirements" : in its broadest sense it includes the biochemical adequacy of the diet and all the conditions and factors necessary for successful feeding (Beck, 1956). House (1959) proposed that the term be restricted to the chemical factors essential to the adequacy of the diet. He further proposed that the term "chemical feeding requirements" should be restricted to the chemical factors important to normal feeding behaviour and the term "physical feeding requirements" should be restricted to the requirements in dietary texture, position, light intensities, and other physical factors that influence feeding behaviour. The following discussion is concerned with the "nutritional requirements" of insects as defined by House.

The subject of insect nutrition has been reviewed many times, more recently by House (1965a) and Dadd (1970, 1973). It will suffice here to state that insects not only require adequate quantities of the essential nutrients but also a proper balance of those nutrients in their food (Gordon, 1959; House, 1965b, 1969).

Deficiencies of food quality may produce one or more of the following effects in insects :

1. Reduced fecundity (Beckwith, 1970, 1976; Bailey, 1976; Maison et al., 1977; Hough and Pimentel, 1978; Webb and Moran, 1978; Wallner and Walton, 1979).

2. Decreased rate of growth and development (Andrewartha and Birch, 1954; Barbosa and Capinera, 1977; Webb and Moran, 1978).
3. Increased mortality (Beckwith, 1970; Bailey, 1976; Barbosa and Capinera, 1977; Hough and Pimentel, 1978; Wallner and Walton, 1979).
4. Smaller size and/or weight (Beckwith, 1970; Barbosa and Capinera, 1977; Hough and Pimentel, 1978).
5. Occurrence of nutritional diseases (House, 1961b, 1963).
6. Greater susceptibility to pathogens (Watanabe, 1971; David et al., 1972; Schmid, 1974; Tananda, 1976; David and Taylor, 1977).
7. Greater tendency to migrate or disperse (Linde, 1971; Capinera and Barbosa, 1976).
8. Lower tolerance to insecticides (Bass and Rawson, 1960; Gordon, 1961; Gaines and Mistric, 1960).
9. Increased number of moults (Wigglesworth, 1972; Leonard, 1970a,b; Beck, 1950).

The above classification is arbitrary and some of the effects are interrelated. For example, fecundity is often a function of body weight (Miller, 1957; Jacobson and Blakeley, 1958; Drooz, 1965; Jennings, 1974; Hough and Pimentel, 1978); and a greater susceptibility to pathogens can lead to a lower survival rate.

The adverse effects mentioned are manifested sooner or later during the life of the insect. In addition there is some evidence that maternal food quality can have a carry-over effect on the progeny. Among the reported effects of this kind are : a lower viability of eggs and difficulty of the first-instar larvae to become established on their food (Morris, 1967); reduced vagility

of young larvae (Capinera and Barbosa, 1976; Barbosa and Capinera, 1977); lower fecundity in the filial generation (Mason et al., 1977).

Deficiencies in food quality can therefore have a considerable influence on the ultimate number of survivors in a population. However, care must be exercised in attributing mortality to the food-related effects mentioned. These deleterious effects may not be widespread and be peculiar only to the species of insect concerned. Moreover, the relationship between poor food quality and observed adverse effects may not always be causal since feeding behaviour, the presence of toxic substances and other factors may be implicated (House, 1961a).

Fraenkel (1953) expressed the view that green leaves are excellent sources of all the food materials which insects require and that secondary plant substances determine the specificity of a food plant. On the contrary, Gordon (1961) and Schoonhoven (1969) are of the opinion that host plants are often nutritionally sub-optimal.

Shortage of protein or amino acids in the food plant appears to be a primary dietary problem amongst phytophagous insects. Eennah (1960) stated that the overriding factor in the nutrition of sucking phytophagous insects is normally the speed at which soluble nitrogenous compounds can be obtained and assimilated. Southwood (1973) pointed out that although successful synthetic diets normally contain from 25-40% dry weight of protein, many plant tissues are around the lower limit. White (1974) postulated that the numbers of phytophagous insects usually remain low because of a high mortality resulting from a relative shortage of nitrogenous food; on the occasions when the food plants become

an adequate source of nitrogen, outbreaks occur.

5.1.1 Pollen as a food for insects

Many insects other than bees feed on pollen. Among these insects are grasshoppers (Grinfeld, 1957), thrips (Andrewartha, 1935; Grinfeld, 1959), dipterans (Schneider, 1948, 1969; Downes, 1955; Barlow, 1961; Tsiropoulos, 1977), anthocorids (Carayon and Steffan, 1959), ichneumonids (Leius, 1961, 1963), beetles (Li and Larson, 1949; Pielou, 1950; Smith, 1961; Hagen, 1962), collembolans (Scott and Stojanovich, 1963), chrysopids (Sheldon and MacLeod, 1971), butterflies (Gilbert, 1972) and moths (Jaynes and Speers, 1949, Ebel, 1965; Rogers, 1978).

Pollen is rich in protein and amino acids (Titus, 1939; Vivino and Palmer, 1944); and, indeed all the essential amino acids are present in pollen (Stanley and Linskens, 1974). Inclusion of pollen in the diet of these insects confers various beneficial effects such as increased longevity and fecundity; but the constituents of pollen primarily responsible for these effects are not known.

The role of pollen in the population dynamics of the spruce budworm, *Choristoneura fumiferana* Clem., has received much attention. Pollen is known to be the preferred food of young larvae of this tortricid (Morris, 1951), and the occurrence of flowering balsam fir trees are correlated with outbreaks. However, the inclusion of pollen in the larval diet does not increase survival or fecundity (Jaynes and Speers, 1949; Blais, 1952; Greenbank, 1963); and although larval development is enhanced when larvae feed on staminate flowers (Blais, 1952; Greenbank, 1963), this effect is due to the warmer microclimate

present in staminate flowers as compared with vegetative buds or needles (Wellington, 1950).

5.1.2 Pollen as a food for *Chlenias pachymela*

Like other species of pine, the protein level of *P. radiata* pollen is low compared with that found in the pollens of other plant species (see Table in Spector, 1956). Indeed where pine pollens have been compared with other pollens in feeding trials with insects, the former were found to be nutritionally inferior (Leius, 1963; Tsiropoulos, 1977). But compared with other plant tissues on a fresh weight basis, pollen of *P. radiata* can be considered to be relatively rich in protein (see Table in Southwood, 1973).

No data appears to be available for the protein content in the foliage of *P. radiata*. The total nitrogen level, however, has been determined : the highest total nitrogen value of 1.38% of air dry weight was obtained for needles less than a year old sampled in New Zealand in December (Will, 1957). By multiplying this value by a factor of 6.25, a rough estimate of the crude protein content is derived (White et al., 1973). This calculation gives an overestimation because total nitrogen includes nonprotein as well as protein nitrogen (White et al., 1973). Even assuming that total nitrogen equals protein nitrogen, the maximum crude protein content in *P. radiata* needles as calculated from the figure of 1.38 given by Will (1957) is only 8.63% of dry weight. In comparison, pollen of *P. radiata* has a crude protein content of 13.4% of fresh weight (Spector, 1956) which works out to be 15.1% of dry weight. Therefore *P. radiata* pollen is considerably richer in protein than the needles.

First-instar larvae of *Chlenias pachymela* were seen feeding on the mature male strobili of *P. radiata* in the field. It was also observed that mortality was high when young larvae were fed washed vegetative shoots in the laboratory. I suspected that the absence of pollen was the cause. The aim of the following experiments was to investigate the influence of pollen as well as other natural food sources on the survival and growth of the early-instar larvae.

5.2 Laboratory experiments

5.2.1 Survival on 3 host species

Besides *P. radiata*, 2 other common hosts of the pine looper are the indigenous *Melaleuca armillaris* Sm. and the introduced *Cupressus macrocarpa* Hartw. This experiment compared the survival of neonate larvae (less than 24 hours old) on the shoots of these hosts. The word "shoot" is defined in Section 1.2.

The shoots were freed of adhering pollen by washing. The absence of pollen was ascertained by examining the shoots under a dissecting microscope and repeating the washing if necessary. The shoots were placed in a glass pomade jar (5 cm diameter, 9 cm deep) together with 10 larvae. Five such jars made up 1 replicate, and there were 6 replicates for each food type. The food was changed every other day. The experiment was conducted at 15°C. After 7 days, the number of survivors in each jar was recorded. The results are presented in Table 5.1.

An analysis of variance showed that the treatments were significantly different at P=0.01 (Appendix 5). Duncan's multiple range test was used to demarcate significant differences. The survival-rate of larvae was high when fed on shoots of either *Melaleuca* or *Cupressus*, but clearly pine shoots were inferior to

Table 5.1 The survival of first instar larvae of *Chlenias pachymela* when fed on shoots of 3 host species. The initial number of larvae in each replicate was 50. Means followed by the same letter are not significantly different at P=0.05 by Duncan's multiple range test.

Host species	Replicate No.						$\bar{x}$
	I	II	III	IV	V	VI	
Melaleuca armillaris	48	48	49	50	50	50	49.2a
Cupressus macrocarpa	43	40	45	47	50	49	45.7a
Pinus radiata	10	11	19	20	4	6	11.7

those of the other hosts and the survival-rate of larvae were low.

Between 1976 and 1978 shoots of *P. radiata* were abundant when the young larvae were present in the field. Such shoots are consumed by larvae in the field, but as the experiment has shown, they are a poor source of food that cause low survival of larvae.

5.2.2 Survival on diets of pine materials

The diets in this experiment were based on the parts of *P. radiata* that are available for consumption by young larvae in the field. The diets were as follows :

1. Mature foliage
2. Mature foliage and pollen
3. Shoots
4. Shoots and pollen
5. Mature male strobili

The terms "mature foliage", "shoots" and "male strobili" are defined in Section 1.2. The plant materials were freed of pollen as in the preceding experiment. Pollen was then added to the material where required by shaking both in a paper bag. Pollen was obtained from dehiscing male strobili collected from the field and kept in a deep freeze at -15°C until used. The test animals, the numbers used, and the conditions of rearing were the same as those in the preceding experiment.

The numbers of survivors on each diet are given in Table 5.2. An analysis of variance showed that treatments were significantly different at P=0.01 (Appendix 6). Duncan's multiple range test was used to demarcate significant differences.

Table 5.2 The survival of first instar larvae when fed on various diets of pine materials. The initial number of larvae in each replicate was 50. Means followed by the same letter are not significantly different at P=0.05 by Duncan's multiple range test.

Diet	Replicate No.						$\bar{x}$
	I	II	III	IV	V	VI	
Mature foliage	1	0	0	0	0	0	0.2a
Mature foliage	0	0	0	0	0	0	0.0a
Shoots	10	11	19	20	4	6	11.7
Shoots and pollen	17	24	39	40	45	30	32.5b
Mature male strobili	40	22	33	20	45	29	31.5b

The survival-rate was zero or near zero when larvae were fed either mature foliage or mature foliage with pollen. The highest survival-rates occurred on shoots with pollen and on mature male strobili. The survival-rate upon pine shoots alone was lower than that of larvae fed on either shoots with pollen or mature male strobili, but it was higher than that on mature needles either with or without pollen.

It may be inferred from these results that pine pollen enhances the survival of first-instar larvae of *C. pachymela* provided that the larvae have access to shoots. The role of this food source is probably supplementary and the availability of other suitable sources is essential for high rates of survival.

5.2.3 Rate of growth on various diets

Neonate larvae were fed on one of the following diets :

1. *M. armillaris* shoots
2. *C. macrocarpa* shoots
3. Pine shoots
4. Pine shoots and pollen
5. Pine male strobili

The rate of growth was determined by measuring the head capsule width of 20 larvae after 2 weeks on the diets. Other details of this experiment were the same as those in Sections 5.2.1 and 5.2.2.

The results are presented in Table 5.3. The mean head capsule widths were significantly different at P=0.01 (Appendix 7), and Duncan's multiple range test was used to compare individual treatment means.

Since the head capsule width is a criterion of growth, the growth of larvae was fastest when they were fed *Cupressus* and

Table 5.3 The mean head capsule width of young larvae fed on various diets for 2 weeks. Data in µm; 20 head capsules measured per treatment. Means followed by the same letter are not significantly different at P=0.05 by Duncan's multiple range test.

Diet	$\bar{x}$ ± S.E.
Melaleuca armillaris shoots	585.9 ± 5.7a
Cupressus macrocarpa shoots	579.3 ± 3.2a
Pine male strobili	460.5 ± 22.8b
Pine shoots and pollen	438.6 ± 22.2b
Pine shoots	380.4 ± 14.7

Melaleuca shoots, and it was slowest on pine shoots. Pine shoots with pollen and pine male strobili gave intermediate growth rates.

It can be concluded that the best of the *P. radiata* diets for larval growth was either pine shoots with pollen or pine male strobili, but both of these were inferior to the shoots of either *M. armillaris* or *C. macrocarpa*.

5.3 Field experiments on pine trees

Experiments were done to find out if the effects of various pine diets observed in the laboratory were applicable to larvae in the field. The treatments were :

1. Mature foliage
2. Mature foliage and pollen
3. Shoots
4. Shoots and pollen
5. Immature male strobili
6. Mature male strobili

Immature male strobili was a new treatment not included in the laboratory experiments because it was not available at the time.

To minimise pollen contamination of certain treatments, 2 separate experiments were carried out at different times. The first experiment was conducted at a time when very few male strobili had come into maturation, and the second just after the peak of pollen-shed. The treatment mature male strobili which was common to both experiments served as a standard.

5.3.1 Field Experiment I

The first experiment was set up on 21 July 1978. Neonate larvae were fed on one of the following diets :

1. Mature foliage
2. Shoots
3. Immature male strobili
4. Mature male strobili

The appropriate portion of a randomly selected tree was caged with 20 larvae. The cage was a sleeve of terylene voile braced from within by a cylinder, 12 cm diameter and 20 cm long, made of chicken mesh (Fig. 5.1). There were 5 replicates per treatment. The experiment was terminated after 2 weeks and the number of survivors recorded. All larvae were still in the first instar at the end of the experiment.

The results are given in Table 5.4. An analysis of variance showed significance at P=0.01 (Appendix 8). Duncan's multiple range test was used to compare individual treatment means.

The lowest number of survivors was recorded when larvae were fed on mature foliage. Highest survival-rate occurred on mature male strobili. There was no significant difference between the treatments shoots and immature male strobili; these diets lie between the 2 extremes in survival value.

5.3.2 Field Experiment II

The experiment was started on 19 August 1978 and terminated after 3 weeks. The larvae were fed on the following diets :

1. Mature foliage and pollen
2. Shoots and pollen
3. Mature male strobili

Fig. 5.1 A field cage made of an inner cylinder of chicken mesh enclosed by a sleeve of terylene voile.

Table 5.4 Survival of first-instar larvae of *Chlenias pachymela* in Field Experiment I (see text). The initial number of larvae in each replicate was 20. Means followed by the same letter are not significantly different at P=0.05 by Duncan's multiple range test.

Replicate No.	Diets			
	Mature Foliage	Shoots	Immature male strobili	Mature male strobili
I	0	4	0	8
II	0	4	12	6
III	0	3	3	2
IV	1	4	2	12
V	0	2	8	4
VI	0	9	1	19
VII	2	6	5	8
VIII	0	0	9	5
IX	0	0	3	13
X	0	11	9	13
$\bar{x}$	0.3	4.3a	5.2a	9.0

The pollen in the first 2 treatments drifted there naturally - no attempt was made to introduce additional pollen by hand. Other details of the experiment were the same as those given in Field Experiment I.

The results are given in Table 5.5. The treatment means were found to be significantly different at P=0.01 (Appendix 9). Duncan's multiple range test was used to compare individual treatment means.

The number of survivors on mature male strobili and on shoots with pollen did not differ significantly. The lowest survival-rate was on mature foliage with pollen.

This experiment lasted a week longer than Field Experiment I and permitted some larvae to undergo the first moult, thus enabling a comparison of the rate of development of larvae on the different diets. The percentage second-instar larvae after 3 weeks were as follows :

Diet	% second instars
Mature male strobili	44.0
Shoots and pollen	45.5
Mature foliage & pollen	0

5.4 The role of pollen in the population dynamics of *C. pachymela*

The laboratory and field experiments have shown that pollen may play an important role in influencing the survival and rate of growth of *C. pachymela*. But this is so only when the pollen is present either in mature male strobili or in association with shoots.

Table 5.5 : Survival of first-instar larvae of *Chlenias pachymela* in Field Experiment II (see text). The initial number of larvae in each replicate was 20. Means followed by the same letter are not significantly different at P=0.05 by Duncan's multiple range test.

Replicate No.	Diet		
	Mature foliage and pollen	Shoots and pollen	Mature male strobili
I	2	16	20
II	4	18	20
III	1	16	17
IV	4	12	16
V	1	18	19
VI	2	7	16
VII	3	19	19
VIII	1	19	19
IX	2	12	19
X	3	19	19
$\bar{x}$	2.3	15.6a	18.4a

The part of the young vegetative shoot that is fed upon by the young larvae is the green stem tissue. This food is available at the time of pollen-shed from the axes bearing the male sporangia as well as the elongating vegetative buds. It is therefore reasonable to discuss the role of pollen as if it is the only food source determining the survival of the young larvae.

Maximum survival of young larvae is ensured when the insect and host phenologies are in perfect synchrony, i.e. peak egg hatch occurs when mature male flowers of pine are most abundant. It is therefore appropriate to examine the insect and host phenologies and see how they relate to each other.

5.4.1 Host phenology

In a 5-year study at Mount Burr, the duration of pollen-shed of *P. radiata* was found to be between 30 and 68 days with the peak occurring about half-way through the period (Millett, 1944). For survival of the larvae of *C. pachymela* the peak period of pollen shed is more meaningful than the spread. During the peak period, the wind-distributed pollen is likely to be present in the larva's microhabitat in excess of its requirements. At Mount Burr the peak period of pollen shed in August and its duration is between 11 and 31 days (Fielding, 1947). My observations indicate that the bulk of the pollen is also released during the month of August at Noolook. This conclusion is corroborated by J. Chapman, the Chief Forester at Noolook for the last decade.

Trees at Canberra were found to shed their pollen some 7 weeks later than at Mount Burr and the duration of pollen shed lasted only about half as long (Millett, 1944). It appears that the variation in the time of flowering and the length of the flowering

period is far greater between localities than between years in a given locality. Spurr (1964) concluded, after examining phenological records of various tree species, that trees in general tend to flower on or about the same day in a given climate more or less independently of the weather at that particular time in a given year. Relative constancy in the time of flowering suggests that photoperiod is involved but other evidence indicates that pines, including *P. radiata*, are neutral plants with respect to photoperiod (Mirov, 1956; Mirov and Stanley, 1959).

5.4.2. Insect phenology

The phenology of adult emergence of *C. pachymela* at Noolook was studied in 1977 and 1978.

The number of adults ecloding into an emergence trap is probably the best indication of the time and pattern of adult emergence for any locality. Ideally, cages should be placed over soil in which larvae have pupated naturally. To avoid possible effects of handling the pupae or disturbing their microhabitat. It was not practicable to do this in 1977 because of the low pupal density, and pupae had to be dug up from elsewhere in the forest and placed under the emergence traps. Checks were made on the suitability of this method of measuring emergence by using 2 other indicators of adult emergence - the number of adults caught in a light trap and the number of egg masses laid in a given interval of time.

The method involving the use of emergence traps was as follows. Thirty pupae were placed on the soil surface at a

randomly selected site; the pupae were covered with 2 cm of soil and then by a layer of forest litter. A cage of 24 cm square and 34 cm height was placed over the pupae. There were 4 replicates. The cages were examined at weekly intervals and the number of adults counted and removed.

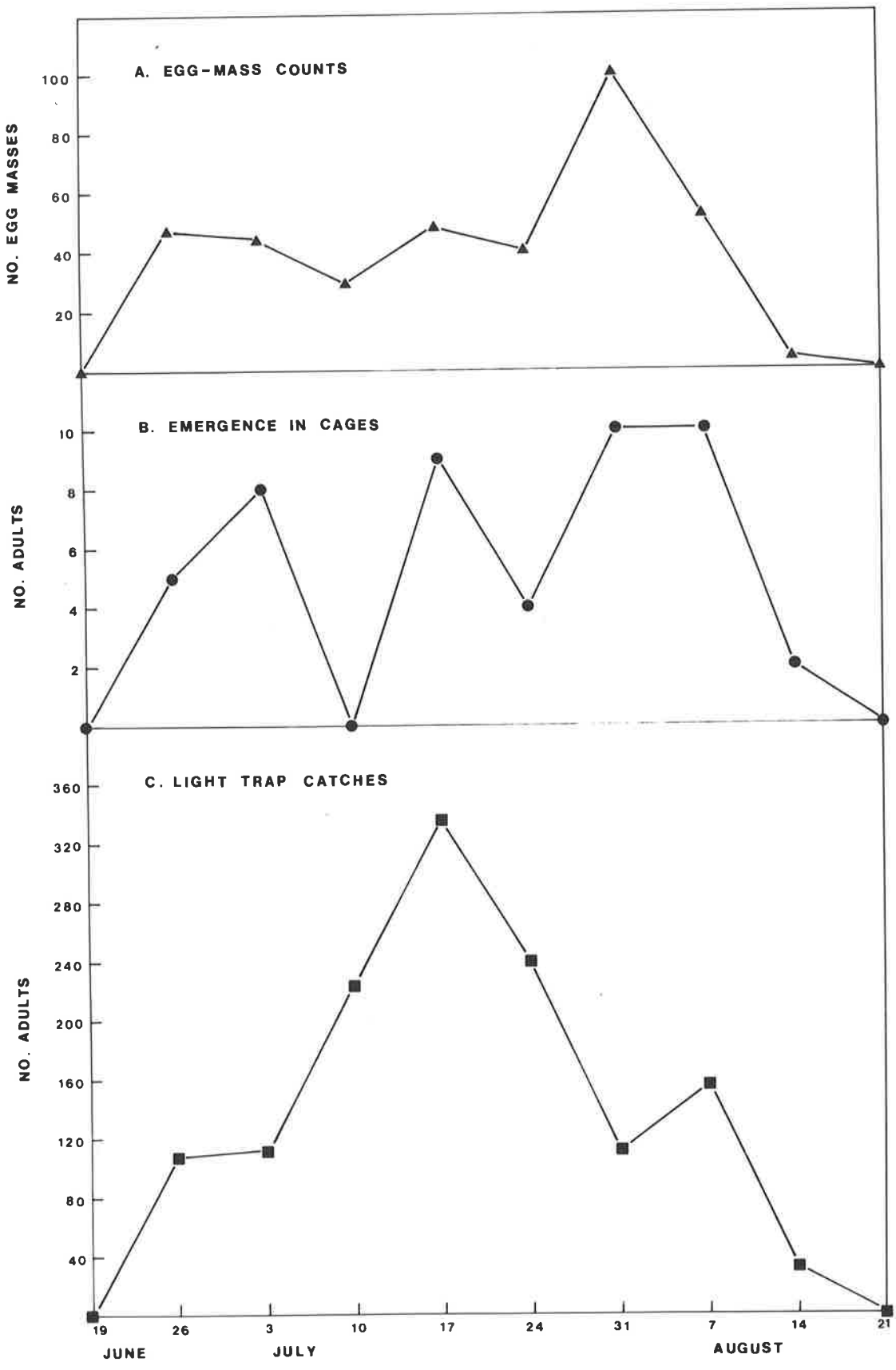
A weekly count of egg masses was obtained by walking along the northern and southern margins of Compartment 68 of the study area at Noolook and keeping a tally of recently laid egg masses found up to a height of 2.4 m. Recently laid eggs are easily recognisable by their pearly-green colour in contrast to the bronze colouration of eggs that have been laid for some time.

The materials and method for light trapping have been described in Section 2.3.

The results of the 3 methods are given in Fig. 5.2. The trend in the number of adults emerging within the cages approximated that of the number of egg masses found. This is not surprising considering that egg-laying in the laboratory begins within 2 days of female emergence. The trend in the number of adults caught in the light trap differed from that derived from either of the other 2 methods. A possible explanation for this anomaly is that local variations in the adult numbers were modified by immigration of males and females that had oviposited elsewhere.

The data indicate that the method using emergence traps seems to be a reasonable measure of local adult emergence. The method using egg-mass counts appears to be equally good; in addition it has several advantages, namely, (1) when pupal density is low egg-mass counts obviate the difficulty of finding sufficient numbers of pupae, (2) with the former method, there is always

Fig. 5.2 Pattern of adult emergence at weekly intervals in 1977 based on (A) egg-mass counts, (B) adult emergence in cages, and (C) adults caught in a light trap.


A. EGG-MASS COUNTS
NO. EGG MASSES
100
80
60
40
20
B. EMERGENCE IN CAGES
NO. ADULTS
10
8
6
4
2
C. LIGHT TRAP CATCHES
NO. ADULTS
360
320
280
240
200
160
120
80
40
19
26
3
10
17
24
31
7
14
21
JUNE
JULY
AUGUST

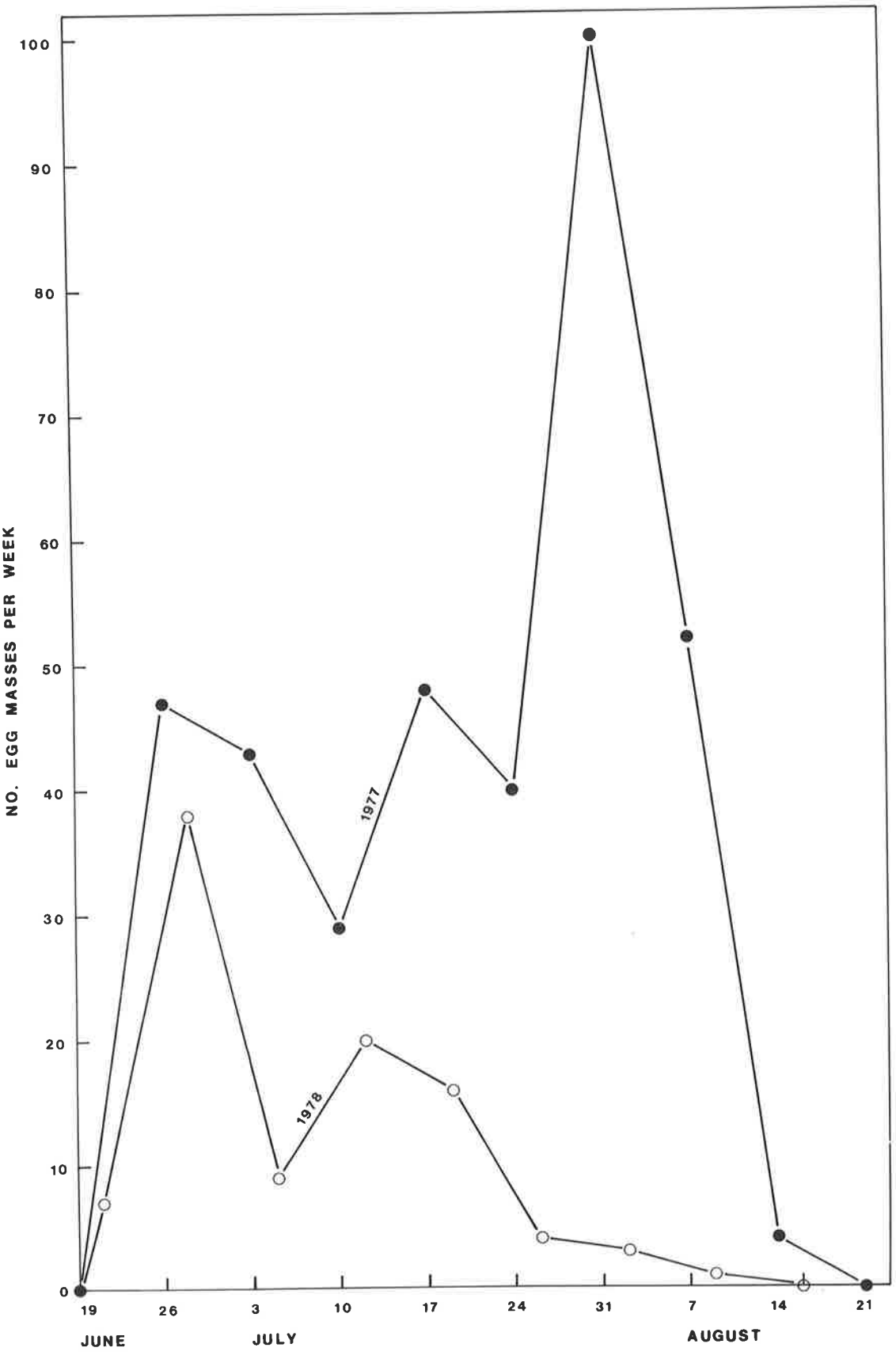
the danger that predators could get into the cage or that an outbreak of disease within a cage could kill off a high proportion of the pupae, (3) counting egg masses is not time consuming - it takes me about 2 hours to inspect 500 trees, (4) larger numbers are involved, and (5) a count of egg masses also provides an index of population density. One disadvantage with this method is that it can be conveniently used only when the lower branches have not been removed.

A count of egg masses was carried out again in 1978 and the results for 2 years are presented in Fig. 5.3. The graphs show that the density of egg masses was higher in 1977 than in 1978. However, the duration of the egg-laying period was about the same, from mid-June to late-August.

Previous observations by F.D. Morgan show that adult emergence can take place between mid-April and early September. An emergence cage placed over infested ground at Mount Burr in 1928 recorded emergence of the first moth on 25 May; on 4 June, 10 live and 6 dead moths were seen inside the cage (Woods and Forests Department of South Australia, unpublished report). I have found fourth to sixth instar larvae of *C. pachymela* on *Prostanthera ovalifolia*, *Melaleuca armillaris* and *Cupressus macrocarpa* in early August in 1977 and 1978 in the Adelaide area. This suggests that the phenology of the insect is earlier in the Central region than in the South-East region of South Australia.

Adult emergence takes place at the end of a long diapause. It was shown in Chapter 4 that the diapause processes are largely, if not solely, influenced by temperature. It is therefore to be expected that weather conditions can influence the time of adult emergence either to the detriment or benefit of the population.

Fig. 5.3 Number of egg masses counted at weekly intervals in 1977 and 1978 during the flight season of *Chlenias pachymela*.


NO. EGG MASSES PER WEEK
100
90
80
70
60
50
40
30
20
10
0
1977
1978
19
26
3
10
17
24
31
7
14
21
JUNE
JULY
AUGUST

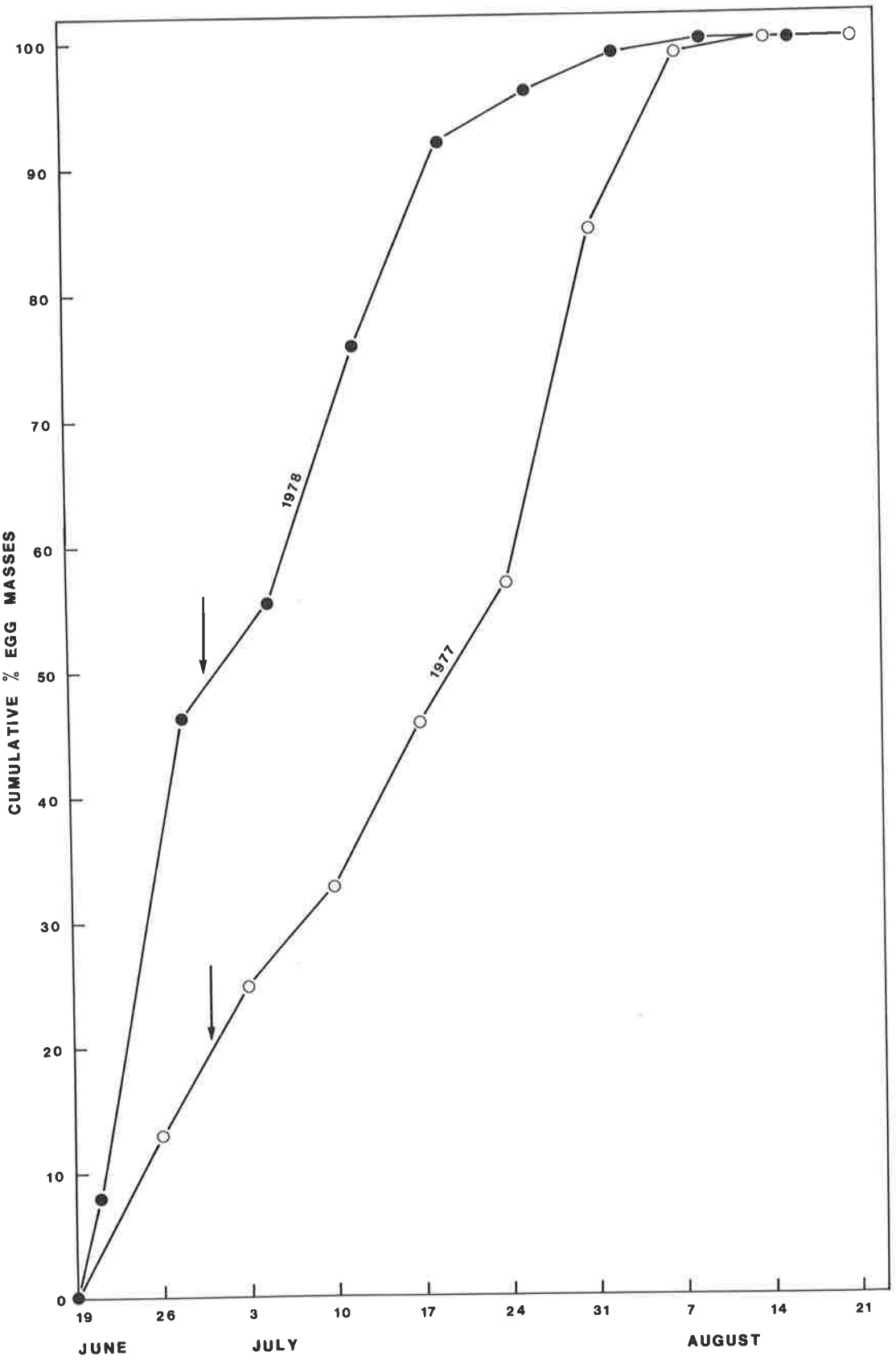
5.4.3. Insect-host phenological relations

It is known that the period of pollen shed in 1977 and 1978 occurred during the month of August. It is also known that the mean incubation period of eggs in both years was approximately 60 days. Thus only the larvae hatching from eggs laid during June would have benefitted most from the pollen. As can be seen in Fig. 5.4, in 1977 and 1978, the majority of larvae ecloded after the peak period of pollen-shed so that they would have hatched after the optimum period for feeding on pollen.

Larvae hatching after the period of pollen-shed are not totally deprived of pollen because pollen grains can be found lodged in the microhabitat of the larvae for some time. Nevertheless, the quantity of pollen available to the larvae must diminish with time due to its removal by wind and rain. Furthermore, it is possible that the nutritional content of the pollen will deteriorate considerably with age.

Morgan (unpublished report) remarked that the insect has not yet adapted to the growth cycle of *P. radiata* and as a result high mortality of first-instar larvae occurred in June and July. He attributed the mortality to a lack of soft needles to feed on. By implication, these larvae were observed much earlier at the time when he carried out his studies between 1960 and 1962 : during the period of my studies adults were just emerging and eggs were being laid in June and July. The fate that awaits larvae hatching too early in the season is just as bad, if not worse, than that which awaits larvae hatching too late. Early in the season the nutritional benefits that may be derived from residues of the previous year's pollen must be negligible; furthermore, the buds, both vegetative and staminate are protected by their enveloping scales and cannot be fed on.

Fig. 5.4 Cumulative frequency (%) curves of the number of egg masses counted at weekly intervals in 1977 and 1978. Arrows indicate the critical date for oviposition; eggs laid prior to this date would have hatched during the peak period of pollen shed.


CUMULATIVE % EGG MASSES
100
90
80
70
60
50
40
30
20
10
0
1978
1977
19
26
3
10
17
24
31
7
14
21
JUNE
JULY
AUGUST

CHAPTER 6

BIOTIC MORTALITY FACTORS

CHAPTER 6

BIOTIC MORTALITY FACTORS

6.1 Introduction

Solomon (1949), followed by Holling (1959), recognized two main responses of predators to changes in prey densities. A "functional response" is a relationship where the number of prey taken by one predator increases with increase in prey density. The predator shows a "numerical response" when its numbers increase in response to increasing prey density. Hassell (1966) pointed out that the numerical response of predators can be immediate, because of aggregation, as well as delayed, because of better survival and reproduction of the enemy as a result of improved food supply. He therefore proposed a new terminology :

1. The behavioural response. The behavioural response is shown by the predator species within one generation and may be classed as either "individual" or "aggregative". An individual response results from changes in the behaviour of individual predators which lead to changes in their efficiency. For example, an individual predator may take more prey as prey-density increases. An aggregative response occurs as a result of enemies concentrating on a particular prey when its numbers are high.

2. The intergenerational response. An increase in prey density may result in an increased number of predators in the next generation as a result of the improved survival or reproduction of the predator. Such a response may be (a) delayed and/or (b) directly or inversely proportional to prey density.

It is useful to discuss the relationship between *Chlenias* and its predators in terms of these responses. Thus far, the terms

"prey" and "predator" has been taken to cover "host" and "parasite" respectively as well; this has been done for the sake of brevity. In the sections below predators and parasites, as defined by Abercrombie et al. (1973), are discussed separately.

6.2 Parasites

Morgan (unpublished report) recorded 3 ichneumonid, 1 scelionid and 1 tachinid parasites. The 3 ichneumonid parasites were *Lissopimpla excelsa* (Costa), *Ophion* sp., and *Echthromorpha intricatoria* F.; the first he considered to be a prepupal parasite and the other 2, pupal parasites. The scelionid was reared from eggs and the tachinid from caterpillars; neither of these were named.

During the course of my studies, I recorded several parasites of *Chlenias* but only one of them, *L. excelsa*, attacks the pupal stage. The others are probably larval parasites. No egg parasites were recorded from numerous egg masses of various ages collected from Noolook and incubated in the laboratory.

Species of parasites found in the pine plantation at Noolook have not been found on *C. pachymela* inhabiting other host plants growing around Adelaide and vice-versa. For this reason the locality where each parasite species was found has been specified in the following sections. The difference in parasite species between the 2 localities may be attributed to differences in the habitats especially the influence of the variability in the respective plant communities. The study area at Noolook consists of monocultures of *P. radiata* with no close proximity to plants producing nectar, whereas around Adelaide, the hosts of *Chlenias* were growing among a varied flora. The availability of nectar or honeydew, the food resources of many Hymenoptera, have been shown to greatly influence parasite longevity (e.g. Hocking, 1967), and observations clearly indicate that such resources were common in the Adelaide areas and

not at Noolook. Habitat preferences and plant influences have been discussed also by Vinson (1976). Another explantation for the observed differences between the parasite fauna of *Chlenias* at Noolook and Adelaide may concern the greater variety of insect hosts available to polyphagous parasites in areas of greater floral diversity.

Mortality of *Chlenias* caused by parasites was low during the period of study - the percentage parasitism by any one species was below 5%.

Lissopimpla excelsa has been repeatedly mentioned in association with outbreaks of *Chlenias* and has been considered to have played a major role in terminating outbreaks (Woods and Forests Department of South Australia, unpublished reports). In view of its apparent importance, this species was selected for special investigation with the object of elucidating its ecological relationship with *Chlenias*.

6.2.1 *Lissopimpla excelsa* (Costa)

Family : Ichneumonidae

Subfamily : Pimplinae

Locality : Noolook

This ichneumonid is a common species in Australia and New Zealand but is probably native to the former (Parrott, 1952). The species is known by several other names, the most common of which is *Lissopimpla semipunctata* (Kirby). However, the name *L. excelsa* has precedence over the others (Parrott, 1952). A detailed description of the adults is given by Parrott (1952).

The species is known to have several hosts, all of which are Lepidoptera. In Australia the recorded hosts are *Spodoptera exempta*

(Walk.) (Weddel, 1936), *Tiracola plagiata* Walk. (Temperley, 1930), and *Phalaenoides glycine* Lewin (Cordingley, 1977). Hosts in New Zealand are *Oxycanus cervinata* Walk., *O. umbraculatus* Guen, *Orthoclydon praefectata* Walk., *Pseudaletia unipuncta* (Haw.), (Gourlay, 1930), and *Selidosema suavis* Butler (Rawlings, 1953). The last named, like *C. pachymela*, is also a geometrid defoliator of *P. radiata*.

Males of the species are noted for their peculiar habit of attempting to copulate with flowers of *Cryptostylis* spp. (Coleman, 1928, 1933, 1938). The flowers of these ground orchids are apparently able to mimic the female insect in some way so as to deceive the male into pollinating them.

In general, members of the Pimplinae oviposit into prepupae or into freshly formed pupae that may be entirely naked or enclosed in a dense cocoon; subterranean pupae or those well protected in burrows in twigs or weeds are not attacked (Townes, 1940). Species of the genus *Pimpla* are known occasionally to parasitize active larvae.

Lissopimpla is believed to parasitize the larval stage (Miller, 1919; Gourlay, 1930; Smith and Caldwell, 1947). It is not clear which stage of *S. exempta* was being parasitized when Weddell (1936) stated : "The adults of *Lissopimpla* were seen working over the caterpillars, and also over the ground in which mature caterpillars had burrowed for pupation". Cordingley (1977) referred to the species as a pupal parasite able to probe through wood and soil to oviposit its egg into the host, *Phalaenoides glycine* Lewin. She also mentioned that the adult emerged from the host pupa through a hole in the anterior end. On the other hand, Gourlay (1930) claimed that the

parasite larva emerged from the host larva to pupate.

In 1970, during a serious outbreak of *Chlenias* at Bundaleer, 5 emergence traps were placed over infested ground with the objective of assessing the proportion of pupal mortality due to *L. excelsa*. The traps were set up in July and by November a total of 5 specimens of an unidentified ichneumonid was found in the traps but none of *Lissopimpla* (Woods and Forests Department of South Australia, unpublished report).

Despite its commonness and frequent association with insect pests, the species has received little more than cursory attention and then largely from casual observation incidental to the study of its hosts.

6.2.1.1 Stock culture of *L. excelsa*

A stock culture of *L. excelsa* was maintained on *Heliothis punctigera* Wllgr. for laboratory experiments. The culture was started with adult parasites emerging from *C. pachymela* pupae collected at Noolook. Pupae of *H. punctigera*, rather than *C. pachymela*, were used because :

1. *H. punctigera* has a facultative diapause and a relatively short life cycle. In contrast, *C. pachymela* is univoltine with an obligate diapause.
2. The pupa of *C. pachymela* becomes heavily sclerotized and resistant to insertion by the parasite's ovipositor within a day of pupation (see Section 6.2.1.3). The pupa of *H. punctigera* is readily penetrable for the entire duration of the stage.
3. A high degree of superparasitism is necessary for successful parasitization of *C. pachymela* pupa (see Section 6.2.1.4) : with *H. punctigera* a single insertion of the ovipositor is sufficient.

H. punctigera, however, has not been recorded as a natural host of *L. excelsa*. An insect may be a suitable host in the laboratory but may not be parasitized in nature (Salt, 1976); with a laboratory host, the first stage of parasitization, host finding, is avoided.

Method : Prepupae of *H. punctigera* were allowed to pupate in 1 cm of fine vermiculite in a petri dish and were then exposed to female *Lissopimpla* for 8 hours in the insectary room. Each parasitized pupa was then incubated at 30°C in a vial (3.5 cm diameter by 8 cm deep) with a drop of honey smeared on the wall to provide food for the adult parasite when it emerges. Adult females emerged in 17-18 days and males in 14-16 days. The host pupa was exposed to mated or unmated females depending on the sex of the adult parasite desired. Unmated females always produced male progeny while mated females usually, but not always, produced female progeny.

Mating was readily achieved in the laboratory. When a female was introduced into a cage containing several males, most of the males would immediately attempt to mate with her simultaneously. Only one male would succeed and the others were rejected thereafter. Copulation lasted 15-30 seconds.

At emergence, adult parasites were transferred to the insectary room and maintained on a diet of honey. Some individuals were still alive and reproductive after 160 days when kept in this manner. The influence of food upon the longevity and activity of ichneumonids referred to above, however, emphasised the need to have test animals that were as similar to each other as possible

for experiments. Insects were therefore kept and fed for 1 month before being used in experiments.

6.2.1.2 Ovipositional behaviour

The antennae are held out in front and used to probe the substrate when the female is trying to locate her host. As soon as a suitable pupa has been located, the female unsheathes her ovipositor and proceeds to drill into the host. The pupa will wriggle and in doing so, often thwarts the effort of the parasite to penetrate its cuticle. The parasite may partially withdraw and insert her ovipositor and reposition herself several times. All this time the antennae are probing the host and the front legs are waving about in the air (Fig. 6.1). As soon as she succeeds in drilling through the cuticle she proceeds to lay her egg. This phase is signalled by the parasite remaining motionless except for a slight quivering of the abdomen and ovipositor. She then withdraws her ovipositor, sheathes it, usually cleans her antennae, and either walks away or attacks the same pupa again.

The behaviour signalling successful penetration is consistent and was confirmed by the presence of a puncture on each of numerous pupae.

The host is not paralysed at any time during oviposition. Paralysis sets in 2-4 days later (at a temperature of 30°C).

I have offered various stages of *C. pachymeta* and *H. punctigera* to the parasite but only pupae were attacked. The pupa must be within a cocoon : a naked pupa elicits no response. Cole (1959) pointed out that any feature of the lepidopteran pupa that makes the attacker's grip less secure or causes its ovipositor to slip is a potentially valuable defence.

Fig. 6.1 Female of *Lissopimpla excelsa* just about to insert her ovipositor into cocoon of *Chlenias pachymela*. Actual length of ovipositor sheath 8.3 mm.

He suggested that the cocoon may be a liability to the insect for it can provide an excellent foothold. My observations indicate that the female of *L. excelsa* needs to gain a firm foothold whilst attacking a host and this is so important that she has apparently adapted to respond only to a pupa within its cocoon.

6.2.1.3 Resistance of host cuticle to penetration

My first success in getting *L. excelsa* to parasitize a host in the laboratory was achieved with a *H. punctigera* pupa. When I attempted to repeat this with *C. pachymela* pupae which were collected from the field and were at least a month old, they were found to be readily attacked by the parasite but penetration was unsuccessful. It was clear that the host was still attractive but that its cuticle was too hard to penetrate. The period just after pupation would probably be the most vulnerable time for the host. The objective of the following experiment was to test this hypothesis and also to determine the length of time it takes the pupa to become sufficiently resistant to penetration.

Prepupae of *C. pachymela* were allowed to pupate in vermiculite 1 cm deep in a clear plastic container. The cocoon formed was adpressed to the bottom of the container and the progress of pupation could be observed. In this way pupae less than 24 hours and 2, 4, 8 and 16 days old were obtained.

Exposure to the parasite was arranged by making a small tear in an intact cocoon of *C. pachymela* collected from the field, the pupa within was discarded and one of known age (with its cocoon removed) inserted. Field-collected cocoons were used because the results obtained would be a better reflection of what happens in nature than if the cocoons had been formed in vermiculite and

stuck to the bottom of a container. Also, field-collected cocoons are more uniform in size : this is important because the space in which the pupa is free to move is likely to influence the ability of the parasite to oviposit into it. A minor problem was that in a few instances a pupa would slip out of the cocoon during the struggle that ensued when it was being attacked. Such a pupa would be re-inserted and the experiment repeated.

Female parasites used in the experiment had been given *H. punctigera* pupae to parasitize on at least 3 occasions. Each female was used only once in the experiment.

A clear polystyrene container of 7 cm diameter and 6.5 cm height served as the arena. The cocoon was buried in fine sand leaving only a small portion exposed. A female parasite was introduced. The time from first insertion of the ovipositor into the cocoon to its final withdrawal was recorded in those cases where penetration was successful. Only the initial attack was observed for an arbitrarily set time of 15 minutes or until the parasite gave up, whichever occurred first. All pupae were examined for puncture marks, and those without any were exposed to the parasite again and re-examined after 24 hours.

The results (Table 6.1) suggest that *C. pachymela* pupae were most vulnerable to penetration by *L. excelsa* during the first 24 hours of the pupal stage; and in pupae of this age, the duration of an attack ranged from 55 seconds to 3 minutes 10 seconds. The parasites had difficulty in piercing the host after the latter was more than 24 hours old; in the 3 pupae older than 24 hours in which penetration was achieved within 15 minutes, the times taken were 13 minutes 3 seconds (2-day old pupa),

Table 6.1 Number of *Lissopimpla* females successfully penetrating the cuticle of *Chlenias* pupae of various ages. Number of pupae tested per age group was 10.

Age of pupae	Number of pupae in which penetration :		
	was achieved <15 min	was achieved 15 min to 24 h	was not achieved
< 24 hours	10	0	0
2 days	2	7	1
4 days	1	8	1
8 days	0	1	9
16 days	0	0	10

6 minutes (2-day old pupa) and 4 minutes 24 seconds (4-day old pupa). It should be noticed, however, that pupae up to 8 days old were still vulnerable, this observation is mainly of theoretical interest because those parasites giving up after the initial attack were not allowed to leave as would probably happen in nature.

It is of interest to note that the cuticle of *H. punctigera*, unlike that of *C. pachymela* did not become increasingly resistant to being pierced by *L. excelsa* with time. Penetration was just as readily achieved with pupae containing the pharate adult, as it was with newly formed pupae.

The agility of the pupa and the hardness of its cuticle are properties considered useful in resisting the attack of a parasite (Askew, 1971). The pupa of *Chlenias* is capable of most movements of its abdomen during the first 24 hours of pupation. After a few days such movements are barely perceptible. In contrast, the pupa of *H. punctigera* during the entire stage wriggles violently when disturbed and this movement plus a smooth muscle cuticle, offers some resistance to an attacking parasite. The present observations suggest that the agility of a pupa within the confines of its cocoon does not appear to be as effective a defence as a tough cuticle.

6.2.1.4 Superparasitism

Females of many species of endoparasitic Hymenoptera are able to discriminate between parasitized and unparasitized hosts and, to a certain extent, to refrain from ovipositing in the former (Salt, 1961; Ullyett, 1936; Lloyd, 1940, 1956; Bosque and Rabinovich, 1979). However, multiple parasitism (or multi-parasitism) and superparasitism as defined by Smith (1916), are also common in the Hymenoptera. Obviously insects practising either of these modes of parasitism are unable to detect if the

host has been parasitized, or if they can, choose to ignore the message perceived.

Lissopimpla excelsa falls into the category of insects practising superparasitism. A previously parasitised pupa is readily attacked if it is presented to either the same female again or to another female. The pupa will be attacked even after it has become paralysed and a parasite larva is developing within. When pupae were exposed to parasites for several days the developmental period of the parasite was of the same duration as those in pupae that were exposed on the first day only. This indicated that the eggs laid subsequent to the first, died.

As many as 24 puncture marks have been counted on a single *H. punctigera* pupa. With *Chlenias* pupae, 1-8 such marks could be seen on a pupa, whether it was parasitized in the laboratory or in the field. It seemed to me at first that this habit of *L. excelsa* is exceedingly wasteful and must reduce its effectiveness as a parasite. However, there is some evidence that endoparasites are less liable to encapsulation by its host when there is a relatively high degree of parasitism (Puttler, 1967; Askew, 1968). The following observations seem to support this view.

When I collected pupae from the field and picked out those that were parasitized by *L. excelsa* on the basis of the presence of puncture marks, only a small proportion produced adult parasites. Dissection of parasitized pupae from which adult *L. excelsa* did not emerge showed that the host had died and the parasite along with it. Some of the parasites had died as fully mature larvae. A count of puncture marks revealed that the number present on a parasitized pupa from which no adult parasite emerged was between 1-5 (n=8); where adult parasites emerged successfully the number

was between 5-7 (n=5). Similar results were obtained with *C. pachymela* pupae parasitized in the laboratory. No attempt was made to determine the precise degree of superparasitism required for successful parasitism.

The results suggest that a certain degree of superparasitism is essential to enable the full development of a single adult parasite. Further experimentation is necessary before the number of punctures can be directly related to successful parasitization. To begin with the following questions have to be considered :

1. Is there a difference, as far as the host's defence reactions are concerned, between oviposition made, say, 3 times in quick succession and 5 times spread over several days?
2. It has been demonstrated that the haemocytic defence reactions of the host is weakest in a certain region and parasite development is favoured if the egg is placed there (Carton, 1978). Does such a region exist in *C. pachymela* pupae?
3. Does the presence of a puncture mark signify the successful placement of an egg, and if so, of only 1 egg?

Insects can make several cellular defence reactions to foreign bodies in their haemocoeles (Salt, 1970). Endophagous parasites in their turn have various means by which they can counteract the defence reactions of their usual hosts (Salt, 1968). One such means is by greatly weakening the host so that it is unable to react against them. Attrition of the host's defences can take several forms; Salt (1968) speculated that the gregarious habit of some endophagous parasites may be a means of protecting them against the defence reactions of their host.

Chlenias pupae from which *L. excelsa* adults had emerged were found to contain several similar-sized head capsules of parasite larva. The size of these mandibulate head capsules suggest that the supernumerary larvae would have been of considerable size before all but one of them died. The temporary presence of these supernumerary larvae would have an attrition effect of the kind envisaged by Salt (1968) although *L. excelsa* is not a gregarious parasite.

It has also been suggested that a high degree of superparasitism exhausts the host's limited powers of encapsulation (Askew, 1968; Puttler, 1967). It should be pointed out that both explanations - attrition of the host and exhaustion of the host's defences - are based on circumstantial evidence and have not been rigorously demonstrated for any parasite species.

6.2.1.5 Effect of adult feeding on longevity

The gravid female of *L. excelsa* is synovigenic - i.e. ovigenesis is not completed before oviposition begins but is more or less continuous throughout the life of the female. Compared with pro-ovigenic species (ovigenesis largely if not entirely completed before oviposition begins), synovigenic parasites are generally long-lived and are able to conserve reproductive material in relation to host density (Flanders, 1950). These are useful attributes in times of low host densities. Feeding is probably essential to the longevity of *L. excelsa* adults and an experiment was carried out to investigate whether this was so.

Newly-emerged adult parasites were used for this experiment. A single parasite was introduced into a lantern globe and supplied 1 of 4 treatments, namely, water, honey, honey and water, or nothing. Each treatment was replicated 12 times. The experiment

was conducted in an insectary room at a temperature of 20 ± 2°C. The longevity of each individual was noted. The experiment was terminated after 60 days.

The results are summarised in Table 6.2. Every individual fed with either honey or honey and water lived for more than 60 days. A t-test showed no significant difference between the mean longevity of adults fed on water and on nothing ($P>0.05$).

It may be inferred from these results that *L. excelsa* is able to live for a short period without food or water. The provision of water does not extend this period although the adults are able to mate and the females to oviposit normally. Clearly, the adults do hold some food reserves to carry them through early post-emergence. Food becomes imperative after this period; the longevity of *L excelsa* adults and therefore their effectiveness as parasites, depends on it.

Ichneumonid species obtain food and moisture from feeding on nectar, honeydew and upon hosts (Townes, 1958). In nature nectar and honeydew are probably important sources of nutrients to *L. excelsa* adults, but host-feeding has not been observed in this species. The parasite is known to feed on the sticky exudate that is produced when *Paspalum dilatatum* Poir., a subtropical pasture grass, is infected by the fungus *Claviceps paspali* Stev. and Hall (Langdon and Champ, 1954).

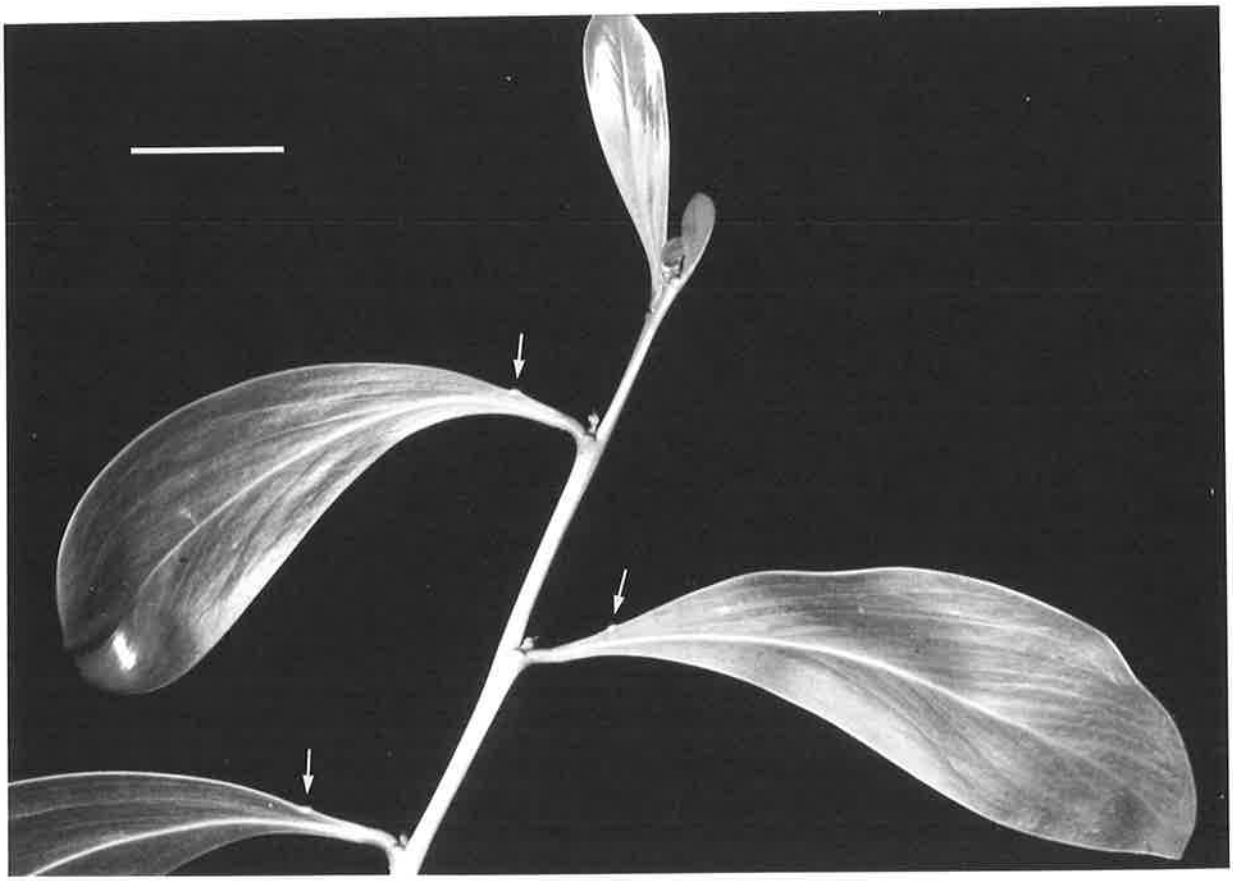
I have seen 2 *L. excelsa* individuals obtaining their food and water from the extrafloral nectaries present in the phyllodes of *Acacia pycnantha* Benth. A single nectary is present near the proximal end of each phyllode (Fig. 6.2). Extrafloral nectaries are common in the genus *Acacia* (Carne, 1913).

Table 6.2 Influence of food on the longevity of *Lissopimpla* adults.
(n = 12 per treatment; temperature 20 ± 2°C)

Food	Longevity (days)
Honey and water	>60
Honey	>60
Water	7 - 11
Nothing	6 - 10

Fig. 6.2 Phyllodes of *Acacia pycnantha*. A single extrafloral nectary (arrow) is present in each phyllode.

Scale represents 22 mm.



An interesting review of extrafloral nectaries and their adaptive significance is found in Bentley (1977). Her account is largely confined to ants because these are by far the most frequent visitors to extrafloral nectaries. But she noted that the literature does suggest that nectar can be extremely important in the nutrition and local distribution of Hymenoptera which parasitize phytophagous insects.

As can be expected, in monocultural plantings, trees of other species are rare. Acacia trees are few in a *P. radiata* plantation and are therefore unlikely to be an important source of nectar. Probably a more important source of nutriments to adults of *L. excelsa* is the honeydew produced by *Pineus pini* (Macq.). This insect belonging to the family Adelgidae is widespread in Australian radiata pine plantations (Neumann, 1979).

6.2.1.6 Thermal requirements

An experiment was carried out to determine the developmental thresholds and the thermal constants of the pre-imaginal stages of *L. excelsa*. *H. punctigera*, rather than *C. pachymela* pupae were used as hosts for the reasons mentioned in Section 6.2.1.1. The pupae, which were 2-3 days old, were exposed to female parasites for 8 hours and then incubated at constant temperatures of 15, 19, 25 and 30°C until adult emergence. The total developmental time of the pre-imaginal stages (from oviposition to adult emergence) was recorded for each individual.

The median developmental times at each constant temperature for both males and females are given in Table 6.3. The theoretical threshold temperature for development (t) and the thermal constant in day degrees (K), were estimated using the method outlined in Section 2.2.1. For males, t=9.9°C and K=303 D°; for females, t=9.7°C and K=339 D°.

Table 6.3 Developmental times of pre-imaginal stages of *Lissopimpla excelsa* at various temperatures

Sex	Temperature	n	Median (days)	Range (days)
Male	15	13	57	49-73
	19	12	34	34-36
	25	10	20	18-22
	30	11	15	14-16
Female	15	17	63	57-79
	19	10	38	35-40
	25	10	21	20-23
	30	15	17	16-18

It has been shown that the thermal constant (oviposition to adult emergence), but not the threshold temperature, varies according to the host or diet on which the insect is feeding (Bonnemaison, 1951; Gutierrez et al., 1971; Markkula, 1953). For this reason the thermal constants estimated for *L. excelsa* on *H. punctigera* may not be applicable to the parasite on *C. pachymela*.

In 3 instances where adult parasites successfully emerged at 25°C from pupae of *C. pachymela* parasitized in the laboratory, the times to adult emergence were 24 (male), 26 (female) and 27 days (female) which are somewhat longer than those on *H. punctigera*. It seems reasonable to conclude that the developmental time for *L. excelsa* on *C. pachymela* in the field would be fairly short because of the high (mid-summer) temperatures prevailing. This tentative conclusion was confirmed by field data (Section 6.2.1.7).

It is perhaps appropriate here to make some comments regarding diapause, or rather the lack of it, in *L. excelsa*. It should be to the parasite's advantage if it is able to diapause because the host is available for only a brief period each year and the parasite has a short developmental time. In many parasites, diapause is effected through the host's hormonal system (see reviews in Askew, 1971 and Fisher, 1971). There was no indication that this is so in *L. excelsa* because adult parasites emerged from both diapausing and non-diapausing pupae of *H. punctigera* at various temperatures within the normal range of time for the particular temperature. This happened even when the host was parasitized either early or late in the pupal stage. Parasites within field-parasitized pupae of *C. pachymela* showed no indication of diapause when kept in the laboratory.

Parrott (1952) used data attached to specimens in various collections as well as data from his personal collecting to construct a graph of the seasonal abundance of adult *L. excelsa* in New Zealand. The graph shows that *L. excelsa* was active throughout the year except during the months of January, August, September and October. It is possible that the adults were quiescent then and development of the immature stages slowed down during the cooler months of August to October. It is difficult to explain the lack of adult activity in January as indicated by Parrott's data.

6.2.1.7 Host-parasite phenological relationship

My own observations and past reports (Woods and Forests Department of South Australia, unpublished reports) show that *L. excelsa* was active from the month of December, but that none could be seen by February. Pupal sampling, carried out at intervals over the period that pupae were present in the field show that parasitized pupae could be found only during January and February (Table 6.4). The phenological relationship between the parasite and its host can now be put together based on this information and the results found in the preceding sections.

C. pachymela starts to pupate in early December and the parasite population starts to build up. A much larger sample than was actually taken in December would probably have detected the presence of the parasite. By January at least 1 generation of parasites emerges from the current host population owing to the short developmental period of the parasite and the high summer temperatures. However, the number of newly formed pupae of *C. pachymela* is on the decline at this time. Hence, female parasites will find easily penetrable hosts becoming scarce.

Table 6.4 Percentage *Chlenias* pupae parasitised by *Lissopimpla* at Noolook.

Date sampled	No. pupae sampled	% parasitised pupae
14.12.77	23	0
11.1.78	41	4.9
15.2.78	297	3.0
27.3.78	311	0
26.4.78	192	0
18.5.78	186	0

By the beginning of February no new pupae are being formed and therefore no fresh parasitism takes place. The parasitized pupae that may be found at this time are the products of oviposition made in January. The adult parasite emerging now will have to find an alternative host either within or outside the pine forest.

In terms of the types of parasite-host responses defined by Hassell (1966), an increase in *Chlenias* pupal density will lead to *L. excelsa* responding as follows :

1. Individual behaviour response. Less time is spent by the parasite in searching for its host and therefore more pupae are likely to be parasitized within the limited time when they are vulnerable.
2. Intergeneration response. Since the parasite has a short generation time relative to the host, there will be a direct, rather than a delayed density-dependent response to an increase in host density. This response, however, can only occur within a short period in each host generation. If the mean percentage host mortality caused by *L. excelsa* were to be plotted against the mean host density over several consecutive generations of the host, no obvious relationship would be observed. This is because the mean host mortality is influenced not only by the host density, but also by the density of alternative hosts available to *L. excelsa* for the greater part of each year.

The overall effect of the above 2 responses of the parasite to an increased host density probably accounts for the increased sightings of *L. excelsa* during past outbreaks of *C. pachymela*.

6.2.1.8 Conclusion

It seems unlikely that *L. excelsa* has much effect on the numbers of *C. pachymela* because of the following factors :

1. Superparasitic habit of *L. excelsa*. Superparasitism is apparently necessary to overcome the host's defences. Nevertheless the habit is considered to reduce a parasite's effectiveness through wastage of eggs (Stary, 1970; Askew, 1971). In this case the time wasted may also be important.
2. Asynchrony of parasite and host. The latter undergoes a lengthy diapause while no diapause is apparent in the former.
3. Effective cuticular protection of the host. Only the pupal stage is attacked by the parasite and this period is further reduced by the host being able to invest itself in an impenetrable cuticle within a short time.

These difficulties notwithstanding, *L. excelsa* could contribute to the collapse of outbreaks following an initial decline of the host population through the action of other factors, e.g. starvation. From this viewpoint, the parasite has one characteristic that weighs in its favour - it is able to make limited but positive aggregative behavioural and intergenerational responses to an increased host density.

6.2.2 Notes on other parasites

6.2.2.1. *Macrocentrus rubromaculatus* (Cameron)

Family : Braconidae

Subfamily : Macrocentrinae

Locality : Noolook

Members of the Macrocentrinae are solitary or gregarious endoparasites of Lepidoptera larvae (Askew, 1971); the gregarious forms seem to be polyembryonic (Muesebeck et al., 1951). In at

least one species, *Macrocentrus ancylivorus* Rohwer, the parasite is polyembryonic and practices superparasitism and yet only one adult finally issues from a single host (Daniel, 1932). This paradox lends further support to Puttler's (1967) and Askew's (1968) contention that several parasite bodies within the host may exhaust the host's defence reactions.

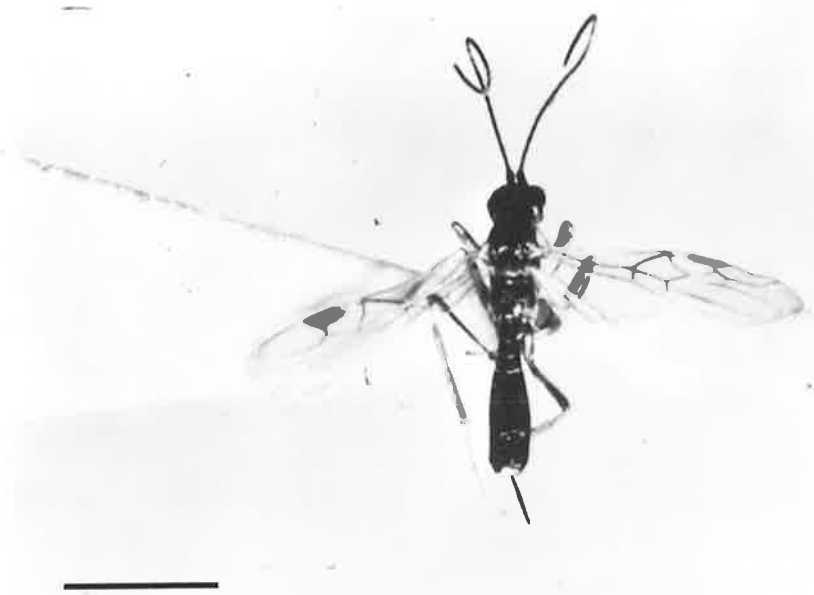
In *M. rubromaculatus* a number of cocoons of the parasite can be found packed within a single host cocoon. Of 8 host cocoons examined, the number of parasite cocoons ranged from 43-123, and these were arranged so that their longitudinal axes were parallel and their anterior ends were all pointing in the same direction. The entire mass of cocoons was covered by a layer of silk which in turn was enveloped by the host cocoon (Fig. 6.3).

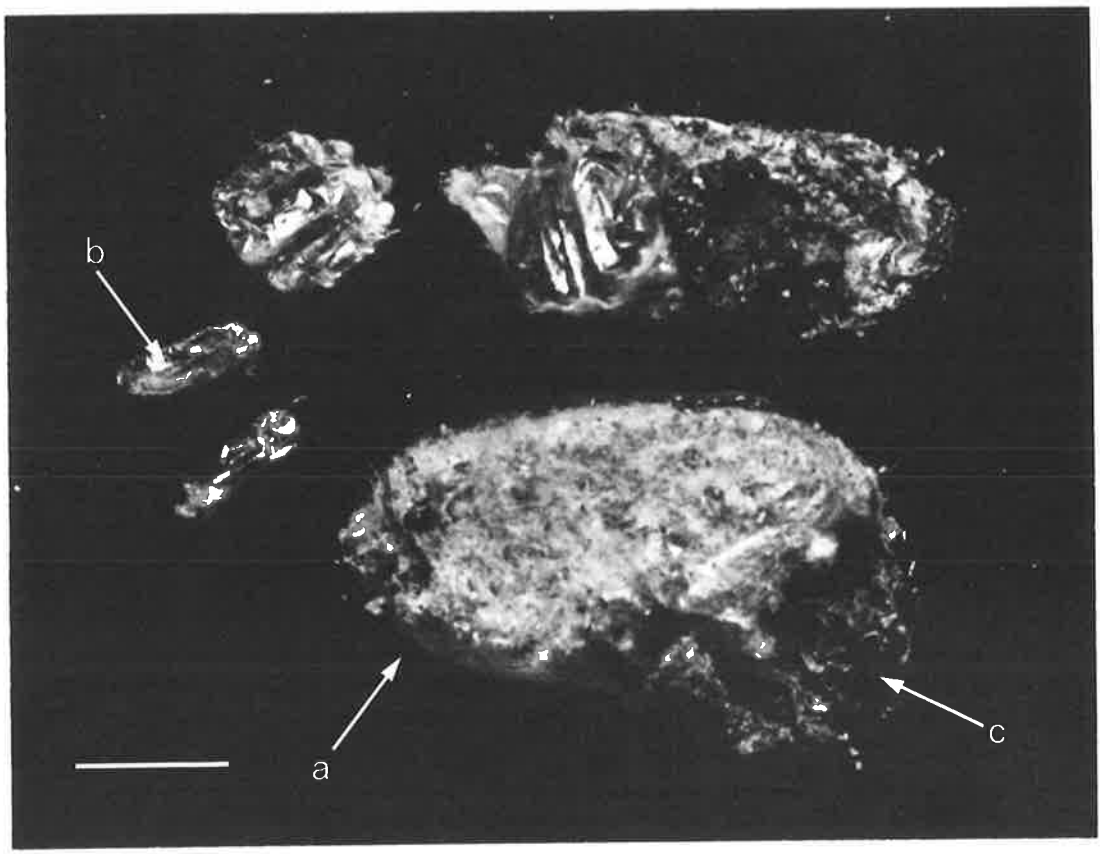
The presence of the exuvium of the sixth instar larva of *Chlenias* within the cocoon is evidence that the host died in the prepupal stage after having spun its cocoon. The host is probably oviposited into during the larval stage. This has been shown to be so in the related *M. gifuensis* Ashmead (Parker, 1931) and *M. ancylivorus* (Daniel, 1932). In the latter species, the larval frass or webbing is apparently necessary to elicit the ovipositional response.

Parasitized cocoons of *C. pachymela* collected in March were found to contain parasites in an advanced stage of development - adults could be seen within their cocoons. All adults had emerged by early May when kept at 20°C.

The adults emerging from a host cocoon were made up of either macropterous females (Fig. 6.3) and males, or macropterous

Fig. 6.3 *Macrocentrus rubromaculatus* showing the macropterous female (top), and 2 masses of cocoons (bottom) 1 of which has been broken up. The labels indicate (a) an intact mass of cocoons, (b) a single cocoon, and (c) remains of the sixth larval instar of *Chlenias*. Scales represent 1.7 mm (top) and 2.6 mm (bottom).




b
a
c

females and males and brachypterous males. No brachypterous females were found. The adults kept in the insectary room lived for 10-17 days when fed with honey and water.

If *M. rubromaculatus* parasitizes the larval stage of its host, then the phenology of the parasite is probably not synchronised with that of its host. Preliminary observations suggest indeed that the parasite adults emerge while the host is still in its pupal stage and the parasites probably do not live long enough to be able to attack the larvae. *M. rubromaculatus* is therefore unlikely to play a significant role in the regulation of the abundance of its host.

6.2.2.2 *Enicospilus* sp.

Family : Ichneumonidae

Subfamily : Ophioninae

Locality : Noolook

Members of the Ophioninae are endoparasites of lepidopterous larvae. Adults (Fig.6.4) are mostly nocturnal (Askew, 1971). At least the second part of this statement may be true of *Enicospilus* sp. as suggested by the presence of 2 male adults in light traps on 2 separate occasions in August at Noolook.

The cocoon of *Enicospilus* sp. is an elliptical, hard, leathery structure. The dimensions are summarised in Table 6.5. It is generally dark coloured but may have a brown transverse band. The cocoon is found within the cocoon of *C. pachymela* in the soil together with the remains of the latter's sixth instar larva. This suggests that the host is killed when it has formed its cocoon and the parasite larva then emerges to pupate.

Fig. 6.4 *Enicospilus* sp., male.

Scale represents 5 mm.

Table 6.5 Dimensions (in mm) of cocoons of *Enicospilus* sp. (n = 12)

	Length	Maximum diameter
Mean	13.5	6.2
Range	12.6-14.7	5.6-6.6
S.E.	0.2	0.1

An experiment was carried out to obtain some preliminary data concerning the thermal and moisture requirements of the parasite while in its cocoon. Cocoons of *Enicospilus* sp. were collected at Noolook on 24 March, 1978 and held in the laboratory (temperature 18-24°C). Eleven days later 4 cocoons were placed at each of the following constant temperatures : 13, 20 and 30°C; at each temperature 2 cocoons were covered with moist vermiculite and 2 with dry.

Only 4 adults emerged. Their times to emergence and the treatments they were at, are given in Table 6.6. The other cocoons were dead either because of the treatments or because they were already dead when collected. The small sample involved does not allow firm conclusions to be drawn, but the data may be of use to initiate future experiments. In particular, the extremely long time it took the adults to emerge from cocoons at 13°C - compared with 20°C - indicate the possibility of a pupal diapause. A pupal diapause has been demonstrated in a related species, *E. sakaguchii* (Nagatomi, 1972). If *Enicospilus* sp. diapauses, it may be able to synchronise with its host and account for a higher percentage parasitism than *Lissopimpla excelsa*. Its potential has not been recognised because the adults are probably nocturnal and its activity not conspicuous.

Adults lived between 29-98 days on a diet of honey and water.

6.2.2.3 Unidentified larval parasite

Order : Hymenoptera

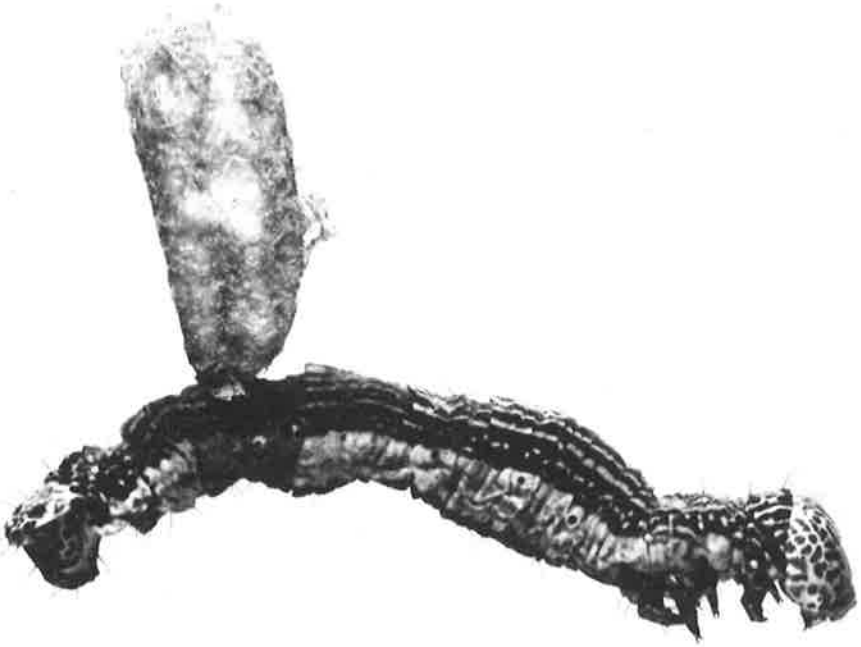
Locality : Noolook

This is an endoparasite but emerges from its host to form a cocoon on the dorsal side (Fig. 6.5). The cocoon, which is yellow

Table 6.6 Incubation period of cocoons of *Enicospilus* sp.

Temperature (°C)	Moist or dry	Days to emergence (from 24 . 5. 78)	Sex
20	Moist	70	Male
13	Moist	342	Male
13	Dry	355	Female
13	Moist	402	Female

Fig. 6.5 Unidentified larval parasite of *Chlenias pachymela*.
Parasite cocoon attached to dorsal aspect of fifth instar larva of host.
Scale represents 1.7 mm.



to orange in colour, may detach from its host soon after formation or may remain on the host and is carried around for several days before the latter dies. Parasitized caterpillars died while in their fifth instar. I was unable to induce emergence of the parasite adult.

6.2.2.4 *Chaetophthalmus* sp.

Family : Tachinidae

Locality : Urrbrae, Adelaide

Food plant of host : *Prostanthera ovalifolia*

This tachinid (Fig. 6.6) is a larval endoparasite. It emerges from its host to form a puparium when the host is in its prepupal stage and has formed its cocoon.

A single newly formed puparium was placed in moist vermiculite and held at 20°C; the adult tachinid ecloded 24 days later.

6.2.2.5 *Netelia* sp.

Family : Ichneumonidae

Subfamily : Tryphoninae

Locality : Waite Institute, Adelaide

Food plant of host : *Melaleuca armillaris*

The following account is based on observations made on 6 parasitized caterpillars.

The glossy black egg of *Netelia* sp. is firmly attached to the integument of the caterpillar by a pedicel. Parasite eggs were found only on sixth instar larvae and hatched after the host had become a prepupa and formed its cocoon. The larvae emerged through a longitudinal split in the ovoid egg. The posterior end of the larva remains between the 2 halves of the egg case. The

anterior end is free to move and from this position the larva proceeds to feed upon the host which remains alive for several days.

Near maturity the parasite larva detaches itself from the egg case but continues to feed upon the dead caterpillar until all that remains of the latter is the shrivelled integument. Then the larva begins to spin its cocoon. The cocoon is a hard, leathery, elliptical structure resembling that of *Enicospilus* sp. but is more elongated.

When a host prepupa was not allowed to form its cocoon, the development of the parasite proceeded normally until it reached maturity. The larva then spun its silk in the form of an irregular mat around itself and continued to do so until it was debilitated and died. This behaviour has also been observed in other parasites (Parker, 1931; Nagatomi, 1972).

Of the 6 caterpillars, 2 carried 2 parasite eggs each, while the rest had 1 each. Where 2 eggs were laid on a single caterpillar the parasite larva ecloding first developed normally, while development of the larva ecloding later was somehow suppressed. It is not certain how this was achieved. Physical attack can be ruled out as the eggs were sufficiently far apart to make this an impossibility at this stage. It is possible that the feeding activity of the first larva altered the host in such a way that it led to physiological suppression of the second larva when it ecloded and started to feed. Details concerning physiological suppression can be found in Salt (1961) and Fisher (1961).

6.2.2.6 Unidentified Dipteran parasite

Order : Diptera

Locality : Waite Institute, Adelaide

Food plant of host : *Melaleuca armillaris*

The parasite emerged from the dead caterpillar to form a puparium. Parasites were reared from host larvae collected while they were in their fourth to sixth instars Attempts to induce emergence of the adult parasite were unsuccessful.

6.3 Predators

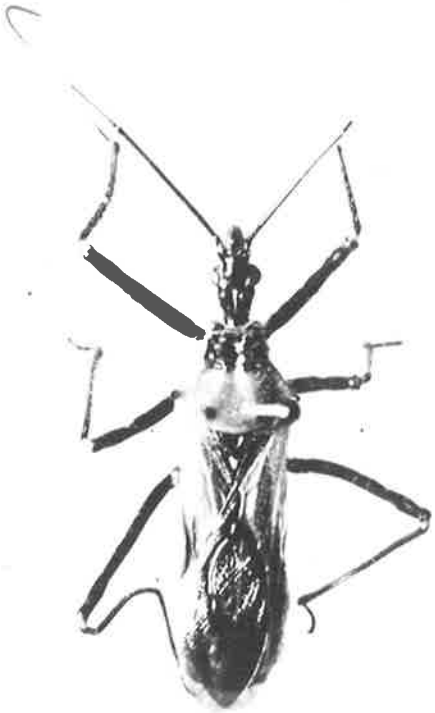
Predators, especially birds and spiders, may play an important role in the population dynamics of *C. pachymela* but no attempts were made to evaluate their importance in the present studies, mainly because the population of *C. pachymela* was decreasing throughout the period of my study.

6.3.1 Arthropod predators

Spiders were seen preying upon the various larval instars in the field. A single bug belonging to the family Reduviidae was seen feeding upon a fifth instar caterpillar (Fig. 6.6).

An unusual predator of eggs of *C. pachymela* was the larva of *Lepidoscia* sp. which belongs to the family Psychidae. The larva was seen feeding upon an egg mass in the field. The species is probably normally phytophagous as larvae have been successfully reared on *P. radiata* foliage in the laboratory. There has been at least one other record of a facultatively predaceous psychid : Plank and Cressman (1934) observed extensive feeding by the larvae of *Platoeceticus gloverii* Pack. upon the camphor scale, *Pseudaonidia duplex* Ckll. This psychid species is also

Fig. 6.6 *Chaetophthalmus* sp. (top), a tachinid parasite; and an unidentified reduviid predator (bottom) of *Chlenias pachemyla*.



normally a plant feeder, yet in 1932 in Louisiana it was estimated that well over 90% of the scales in a heavy infestation were destroyed by it.

The adult female of *Lepidoscia* sp. is wingless while the adult male is winged (Fig. 6.7).

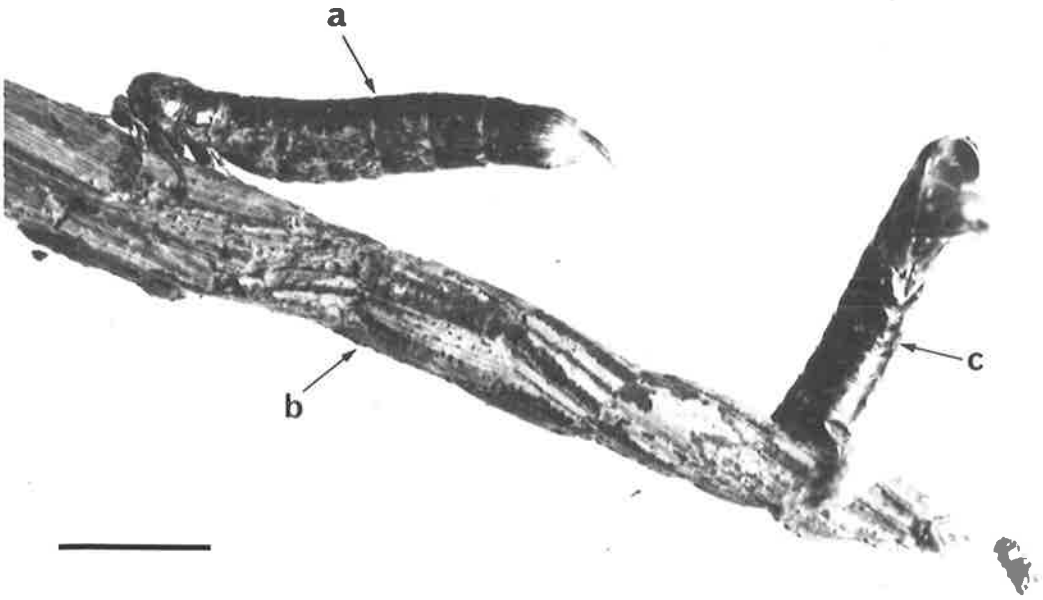
6.3.2 Vertebrate predators

Remains of *C. pachymela* larvae were found among the gut contents of a female shingleback lizard, *Trachydosaurus rugosus* Gray, caught in the forest in December 1976. This lizard is not an arboreal animal and therefore the larvae consumed must have fallen from the trees.

Birds and mammals are potentially important forest insect predators because they are homoiothermic and operate at relatively high metabolic levels (Buckner, 1966). Mice and several avian species are suspected to be predators of *C. pachymela* in South Australian pine plantations (Woods and Forests Department of South Australia, unpublished reports): unfortunately such reports have not been verified.

Superficial disturbances of the forest litter have been ascribed by foresters to the red fox, *Vulpes vulpes* L., searching for *Chlenias* pupae. Three scats belonging to this mammal were found at Noolook in April 1976. Examination of the scats showed the presence of hair and feathers (suggesting mammalian and avian prey) and the remains of carabid beetles and cockroaches but none of *Chlenias*. Pine needles were also found but these could have been accidentally swallowed along with the prey. A larger sample of fresh scats collected at different times of the year would have to be examined before *Chlenias* can be ruled out as a food item in the fox's diet. Nevertheless it is possible that

Fig. 6.7 *Lepidoscia* sp., a facultative psychid predator of eggs of *Chlenias pachymela* : adult male (top); (a) wingless adult female resting on (b) larval case at the posterior end of which is (c) the pupal case. Scales represent 2.5 mm (top) and 2.4 mm (bottom).


a
b
c

at least some of the superficial scratchings on the forest floor were caused by the fox searching for carabid beetles and cockroaches rather than *C. pachymela* pupae.

Aggregative behavioural response caused by movements of bird populations have been reported by various workers (Blais and Parks, 1964; Buckner and Turnock, 1965; Hudleston, 1958; Smith and Popov, 1953). Movements of this kind are usually much more spectacular than increases in resident breeding birds. Birds are especially well adapted to respond to population movement because of their great mobility and because territorial behaviour is usually minimal when such movements occur (Buckner, 1966).

During the 1928 outbreak of *C. pachymela* at Mount Burr forest, a huge flock of wood swallow (*Artamus* sp.) moved in and is believed to have been responsible for terminating the outbreak (Woods and Forests Department of South Australia, unpublished report). The flock was estimated to have numbered a million at its peak. The reliability of this estimate is open to doubt, but the flock must have been large and would have severely reduced the population of pine loopers. The birds were probably not the only important mortality factor operating during this particular outbreak - ichneumonids (species not specified) and starvation were significant too (Woods and Forests Department of South Australia, unpublished report).

Thirty five bird species were regularly seen in plantations of radiata pine in north-eastern Victoria (Suckling et al., 1976). Of these, 9 species obtained a significant part of their food and shelter from the pine canopy. Birds were observed attacking pupae and adults in an outbreak of *Chlenias* sp. on *P. radiata* in Tasmania

(Madden and Bashford, 1977b). At Noolook, there is a bird population comprising several species, and this may have been responsible for at least some mortality of *Chlenias* adults as suggested by the presence of wings of these moths on the forest floor.

6.4 Pathogens

It has not been possible to give estimates of mortality due to pathogens for life table purposes. A substantial proportion (<30%) of all larvae collected from the field died when reared in the laboratory and death could not be ascribed to any known mortality factor. Elements of this "unknown" mortality possibly were (1) mechanical injury caused by handling, and (2) stress imposed when larvae were transferred from the field to the confines of rearing jars in the laboratory. Death could have occurred owing to the direct effect of these elements, or the vigour of the larvae could have been reduced by these elements to the extent that they succumbed to microorganisms which would otherwise have been tolerated.

Of the 2 contributory factors to the unknown mortality, probably stress was the more important since larvae continued to die despite utmost care in handling. The part played by stressors in disease development has been discussed by many workers (Wallis, 1957; Steinhaus, 1958a, 1958b; Steinhaus and Dineen, 1960; Jaques, 1961; Neilson, 1963; Vago, 1963; Tanada, 1965).

Conditions in the field were probably sub-optimal too and larvae would have been subjected to various adverse factors although these might have been of a different kind from those found in the laboratory. Possible stressors in the field could have been

high temperatures, excessive moisture and poor food quality.

Above were some of the difficulties in relating mortality from diseases and unknown causes in the laboratory to existing field conditions. Neilson (1963) attempted to measure the role of the complex of diseases and their interaction with other factors in the epidemiology of the spruce budworm, *Choristoneura fumiferana* Clem. The difficulties outlined by him are also relevant here.

Morgan (personal communication) found the following fungal pathogens of *Chlenias* : *Entomophthora aphrophorae* Rostrup, *E. sphaerosperma* Fres., *Isaria* sp., and *Beauveria bassiana* (Bals.) Vuill. *Isaria* is, however, a doubtful genus and many fungi placed in *Isaria* may go in *Beauveria* (Kendrick and Carmichael, 1973) and *Paecilomyces* (Brown and Smith, 1957).

Larvae attacked by *E. aphrophorae* and *E.sphaerosperma* develop dark spots in the mid-abdomen and become stiff after about 48 hours. *Isaria* sp. and *B. bassiana* can be seen as a white felt of fungal mycelium on the pupa and prepupa.

In addition, 2 other pathogens have been identified during the course of these studies. They were *Paecilomyces* sp. and *Adelina* sp.

6.4.1 *Paecilomyces* sp. (Deuteromycotina: Hyphomycetes)

Paecilomyces sp. was found growing on pupae and prepupae placed at 13°C in moist vermiculite. The hosts were collected as larvae from Noolook and infection might possibly have occurred from the gut. A related fungus, *P. farinosus* (Dicks ex Fr.) Brown and Smith, is also believed to originate from the gut of the host although infection of the pupa via either the spiracles or intersegmental membrane is considered possible (Alma, 1975).

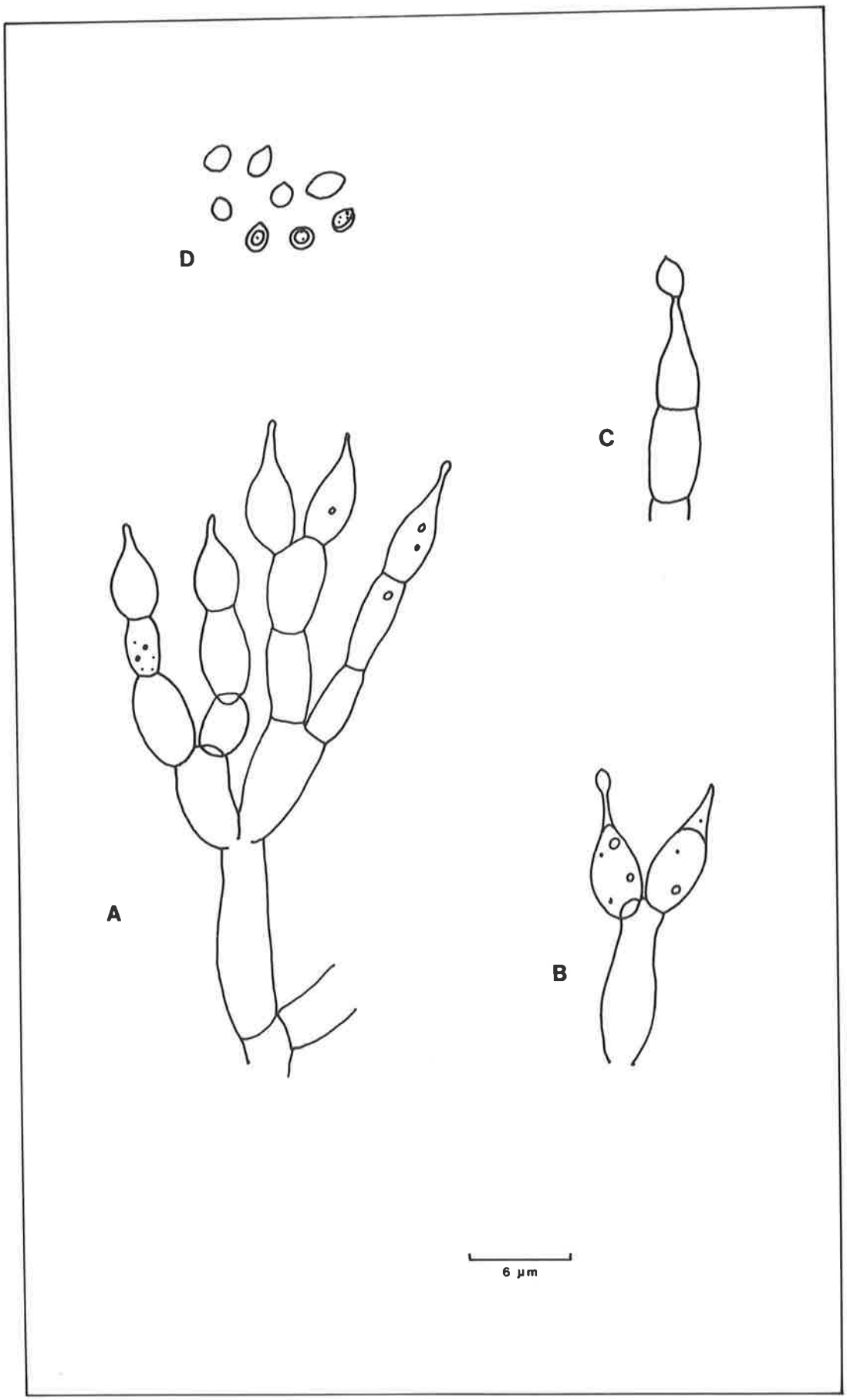
The host in this case is *Heliothis armigera* Hub., a defoliator of *Pinus radiata* in New Zealand.

Paecilomyces sp. enveloped the pupa of *C. pachymela* in a thin sheet of white mycelium. The fungus reproduced asexually by forming elongated, vertical spore-bearing structures or synnemata. Synnemata were generally white in colour but yellow at the base. The spores or conidia were extruded in chains from small bottle-shaped structures called phialides (Fig. 6.8). Phialides occurred singly or in groups on the aerial mycelium. Spores were smooth, oval or elliptical, and greenish-yellow to hyaline.

6.4.2 *Adelina* sp. (Protozoa : Coccidida)

Adelina sp. was found infecting caterpillars collected from Noolook. The coccidian parasite was identified on the basis of its characteristic oocysts within each of which were several spherical sporocysts.

Fig. 6.8 *Paecilomyces* sp.: A, conidiophores; B, phialides with conidia forming; C, phialide with mature conidia; D, conidia.


D
C
A
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6 µm

CHAPTER 7

POPULATION DYNAMICS

CHAPTER 7

POPULATION DYNAMICS

7.1 Introduction

By far the best way of understanding the population dynamics of a species is through the construction and analysis of life tables (Dempster, 1975). Much has been written about population dynamics in general and life tables in particular; among the recent reviews are those by Varley and Gradwell (1970), Pottinger and LeRoux (1971), Varley et al., (1973), Dempster (1975) and Southwood (1978).

Life table studies were carried out on *C. pachymela* infesting a stand of radiata pines at Noolook. Three population trend indices (I's) were obtained from estimates of egg numbers in 4 generations; and survival-rates for eggs, larvae and pupae were estimated in each of 3 generations by estimating the numbers in each of the following stages :

Year	Numbers estimated for stages:				I determined as:
1976	pupae	eggs	larval instars I-VI	pupae	
1977	pupae	eggs	larval instars I-VI	pupae	eggs in 1977/eggs in 1976
1978	pupae	eggs	larval instars I-VI	pupae	eggs in 1978/eggs in 1977
1979	pupae	eggs			eggs in 1979/eggs in 1978

Densities of the different stages were expressed as mean numbers per tree. The methods of estimation of the numbers of the different stages were as given below.

7.2 Methods

7.2.1 Population area

Compartment 68 at Noolook forest was chosen as the population area. The compartment was on flat land and was 20.7 ha in area. It was rectangular in shape with the breadth of the rectangle running in a north-south direction. The trees were planted in 1969. A summary of the dimensions of these trees in 1976, 1977 and 1978 is given in Table 7.1.

No other vegetation grew within the compartment except where the trees were sufficiently far apart e.g. in areas where there were outcrops of limestone. The forest floor was covered with a litter of pine needles. The soil was a loose sandy loam.

There were approximately 200 rows each of about 140 trees in the compartment which was arbitrarily divided into 10 blocks so that each block was made up of 50 rows 70 trees deep. A tree was selected for sampling by drawing random numbers for the block, the row within the block and the tree within the row. The first 2 rows of trees at the perimeter of the compartment were not considered as part of the sampling universe.

7.2.2 Sampling eggs

As egg shells remained on the trees until at least the larvae had pupated, sampling for eggs could be carried out at any time before the end of December. The progress of oviposition and egg development were monitored by observing egg masses along the margins of the experimental plot (see Section 5.4.2).

In 1976, sampling was carried out near the end of the egg-laying period and so may have given a slight underestimate of the

Table 7.1 Dimensions (cm) of trees in compartment 68 in 1976, 1977 and 1978. D.B.H. = diameter at breast height (1.25 m above ground).

	1976		1977		1978	
	D.B.H.	Height	D.B.H.	Height	D.B.H.	Height
No. of trees	14	14	26	26	30	30
$\bar{x}$	13.1	904.3	15.1	1072.3	15.6	1147.8
Range	8	690	12	915	11	820
	-17	-1200	-19	-1345	-20	-1408
S.E.	0.68	44.3	0.35	23.3	0.48	25.4

egg population; but it was done then in an attempt to estimate the proportion of egg parasitism. No egg parasites were found, so in subsequent years egg sampling was done after the egg-laying period was over.

The sampling unit was a randomly selected tree. The entire tree was systematically searched for egg masses. The number of individual eggs in each egg mass was counted in the laboratory using the method described in Section 2.4. Seven sampling units were examined on each occasion.

7.2.3 Sampling larvae

From a tree chosen at random, 1 out of every 3 whorls of branches was randomly selected. The branches in the selected whorl were numbered in a clockwise direction, with branch number 1 at the northern aspect. One of these branches was selected at random and cut and lowered to the ground to be examined for larvae. Near the top where the trunk was too slender to be climbed, the entire crown was cut and lowered to the ground to be examined for larvae. The trunk was also inspected for larvae. This last procedure was especially important when temperatures were high and larvae had a tendency to stay on the trunk rather than on the branches (see Section 2.3.1).

The sampling unit was a branch. The number of sampling units taken per tree varied because the number of whorls per tree varied from tree to tree. The number of trees sampled on each occasion is as shown in Tables 7.2, 7.3 and 7.4.

In 1976 a sample of larvae had to be taken in a hurry and it was uncertain how many branches from how many trees were required for a good sample. So on this occasion the larvae on all the branches from the 1 tree were counted. From this data and from a subsequent sampling experiment on eggs (Maelzer, Morgan and Khoo, unpublished data), it was determined that an optimal number of trees to be sampled was about 4; this sample size resulted in errors which were within the 10-20% limits usually acceptable for population studies.

Pupal sampling was carried out in January soon after pupation, and again in late April to early June before adult emergence.

7.2.4 Sampling pupae

Since the pupae were found in the ground, the pupal density was expressed as the mean number occupying an area circumscribed by a circle of 1 m radius with the base of the tree at the centre of the circle. The distance between rows and between trees within row was approximately 2 m; therefore the estimated number of pupae in each circle can be considered to "belong" to the tree. This method probably underestimated the pupal numbers per tree since the interstitial spaces between adjoining circles were not included in the estimation. But this source of error was probably negligible compared with other sampling errors.

Pupal sampling was done by digging and sieving the soil. The sampling unit was a quadrat 20 cm square and 6 cm deep. At a

randomly selected tree, 2 cardinal directions relative to the base of the tree were chosen at random. In each of the two directions, 5 consecutive sampling units were taken with the first unit next to the base of the tree.

The soil sample was passed through a 7 mm mesh sieve. Pupae within their cocoons remained in the sieve but the occasional naked pupae did pass through. However, the latter were easily spotted because their maroon colouration stood out against the orange-coloured soil.

7.2.5 Sampling adults

Attempts were made on 2 occasions during the flight season of the adult moth to estimate the adult population by the capture-recapture method (Southwood, 1978). Adults caught in light traps (see Section 2.3) were dusted with a fluorescent powder and released on the same night. Unfortunately, the marked moths remained near where they were released. Furthermore, they did not fly into the light trap on the following night. It is probable that those adults which were attracted to the light trap were old moths (see also Section 3.5). The procedure was obviously unsatisfactory as a means of estimating moth numbers and was abandoned.

7.3 Analysis of the life table data

The method of analysis of the life table data was essentially the same as that of Morris and Miller (1954). Analysis of the data was based on a model similar to that used by Morris (1963) and Harcourt (1963) :

$$I = S_E \cdot S_{L1} \cdot S_{L2} \cdot S_{L3} \cdot S_{L4} \cdot S_{L5} \cdot S_{L6} \cdot S_P \cdot S_A \cdot P_{♀} \cdot F \cdot P_F$$

Definitions of the symbols follow :

I = population trend index in a given generation

S_E = survival-rate of eggs to eclosion

S_{L1}-S_{L6} = survival-rate of each of the larval instars I-VI

S_P = survival-rate of pupae

S_A = survival-rate of adults

$P_{♀}$ = the proportion of adults that are females

F = mean potential fecundity per female

P_F = proportion of F that can be achieved by the female of a given population.

The method of calculating the survival-rate for each of the different stages is given below.

7.3.1 Eggs

S_E was assumed to be 1.0 because the proportion that did not hatch or was killed by parasites and predators was negligible.

7.3.2 Larval instars I-VI

Since both the number of eggs and the number of pupae could be estimated by taking a sample when all the insects were in the one stage, the survival-rate of the larvae over all 6 instars could be estimated as :

$$S_{L1} \cdot S_{L2} \cdot S_{L3} \cdot S_{L4} \cdot S_{L5} \cdot S_{L6} = \frac{\text{No. of pupae}}{\text{No. of eggs}}$$

Similar estimates of the numbers of larvae entering any one larval stage could not, of course, be obtained because the eggs hatched at different times so that at any one sampling time various numbers of larvae of different instars were observed. The survival-

rates of each larval instar from I-V were therefore obtained by Manly's (1976) modification of Kiritani and Nakasuji's (1967) method in which the number of larvae entering any one particular stadium are calculated as a function of the area under the curve of observed numbers of that instar. This procedure was not followed for larval instar VI because of the unreliability of Manly's method for estimation of the last survival-rate in a series (Maelzer, personal communication), and the survival-rate of instar VI was obtained instead by substitution of the other estimates in the above equation, i.e. :

$$S_{L6} = \frac{\text{No. of pupae}}{S_{L1}.S_{L2}.S_{L3}.S_{L4}.S_{L5}.\text{No of eggs}}$$

7.3.3 Pupae

This was based on the ratio of number of pupae at the beginning of the pupal period to the number at the end of the pupal period.

7.3.4 Adult properties

As in Morris (1963) and Harcourt (1963), corrections were made for sex ratio and adult mortality. However, a correction was not necessary for mean fecundity.

1. Sex ratio. The sex ratios (in percentages) were based on the sex ratio of the pupae.
2. Adult survival. Adult survival was calculated from :

$$\frac{\text{actual No. of eggs}}{\text{expected No. of eggs}}$$

The expected number of eggs was estimated from :

No. of pupae at the end of the pupal period x proportion of these pupae that were females x mean potential fecundity of moths.

3. Mean fecundity. The mean (potential) fecundity of moths was estimated in the laboratory by dissection (see Section 3.5) and was found to be 1245 eggs per female. Considering that females caught in light traps were found to have oviposited almost all their eggs (see Section 3.5), the potential fecundity was likely to be attained unless the moth died prematurely.

Since the weight of female pupae of *C. pachymela* was correlated with potential fecundity, and since the weights of female pupae did not differ significantly in the 4 years (see Section 3.4), it was not necessary to make a correction for reduction in fecundity of adults as was done by Miller (1963) and Harcourt (1963).

7.4 Results

The mean number per tree for each of the different stages in each of the 3 years, 1976-77, 1977-78, and 1978-79, are shown in Tables 7.2, 7.3 and 7.4.

The estimated survival-rates of the various stages for the 3 generations are shown in Table 7.5. The population trend index (calculated using the equation given in Section 7.3) for each generation is also included in the table. The reliability of the survival-rates is discussed in Section 7.5.

7.5 Discussion

There are several methods available to identify the key factor(s) influencing the population trend (see Southwood, 1978). However, none of these methods are suitable here because life tables were constructed for only 3 generations. The determination of the stage(s) which have a strong influence on the survival of the

Table 7.2 Summary of the population estimates of *Chlenias pachymela* in compartment 68 at Ncolook in 1976-1977. Estimates expressed as mean number per tree.

Sampling date	No. trees sampled	Pupa	Egg	Larva I	Larva II	Larva III	Larva IV	Larva V	Larva VI	Pupa
3.6.76	27	54.4								
3.8.76	7		4457.9	0	0	0				
15.9.76	1			707.0	63.0	14.0				
29.9.76	2			2708.3	280.0	38.8	0	0		
26.10.76	4			14.6	348.8	243.4	114.7	13.0	0	
30.11.76	4			0	0	21.3	45.6	90.0	100.2	
21.12.76	3					0	1.0	5.2	14.0	
24.1.77	10						0	0	0	27.0

Table 7.3 Summary of the population estimates of *Chlenias pachymela* in compartment 68 at Noolook in 1977-1978. Estimates expressed as mean number per tree. The word "survey" refers to the method used to determine when the eggs started to hatch (see Section 7.3.1.1).

Sampling date	No. trees sampled	Pupa	Egg	Larva I	Larva II	Larve III	Larva IV	Larva V	Larva VI	Pupa
26.5.77	10	20.7								
24.8.77	7		603.6							
19.8.77	Survey			0	0					
7.9.77	4			165.8	48.3	0	0			
25.9.77	4			146.6	112.3	27.9	1.6	0		
12.10.77	4			14.1	74.3	126.4	20.4	2.8	0	
2.11.77	4			0	0	18.8	71.9	60.1	10.9	
23.11.77	5					0	11.2	24.4	20.0	
13.12.77	5						0	0	17.5	
11.1.78	10								0	6.7

Table 7.4 Summary of the population estimates of *Chlenias pachymela* in compartment 68 at Noolook in 1978-1979. Estimates expressed as mean number per tree. The word "survey" refers to the method used to determine when the eggs started to hatch (see Section 7.3.1.1).

Sampling date	No. trees sampled	Pupa	Egg	Larva I	Larva II	Larva III	Larva IV	Larva V	Larva VI	Pupa
27.4.78	20	2.8								
16.9.78	7		519.6							
4.8.78	Survey			0	0					
5.9.78	5			151.9	19.5	0				
28.9.78	5			24.3	78.6	44.3	0	0		
17.10.78	5			5.2	16.9	52.2	22.2	4.6	0	
9.11.78	5			0	0	2.8	4.3	40.8	18.2	
27.11.78	5					0	0	18.5	18.7	
18.12.78	5							2.6	1.2	
15.1.79	20							0	0	4.3
19.5.79	12	4.0								
13.9.79	7		205.3							

Table 7.5 Survival-rates and population trend indices for 3 generations of *Chlenias pachymela*. For explanation of symbols see Section 7.3.2.

Stage survival-rate	1976-77	1977-78	1978-79
S_E	1.000	1.000	1.000
S_{L1}	0.344	0.693	0.605
S_{L2}	0.513	0.666	0.651
S_{L3}	0.545	0.594	0.565
S_{L4}	0.562	0.571	0.799
S_{L5}	0.512	0.375	0.356
S_{L6}	0.219	0.189	0.131
S_P	0.763	0.418	0.930
$P_{♀}$	0.140	0.400	0.300
S_A	0.167	0.373	0.137
F	1245	1245	1245
I (Population trend index)	0.135	0.861	0.395

population was consequently done by visual inspection of the survival-rates in Table 6.6, and the conclusions thus drawn must be considered to be only tentative. In general it may be inferred that the survival-rates that were most important were those which varied considerably between the 3 generations for any one stage.

The population trend indices suggest that the population was on the decline in each of the 3 generations studied. The lowest value for I occurred in the 1976-1977 generation. Therefore the stage within this generation which showed a markedly low survival-rate compared with the other 2 generations may be considered to be the stage at which the key factor was operating. The values of the survival-rates, S_{L1} and $P_{♀}$, in the 1976-1977 generation were considered unusually low.

It was concluded that a key factor operated in the L_1 stage and another (or the same) key factor influenced the sex ratio. Another key factor may operate in the adult stage. These possible key factors are discussed below, along with the possibility that food is the key factor.

A key factor in the L_1 stage?

The major mortality factors operating on the first-instar larvae were considered to be , (1) dispersal losses (2) poor food quality, and (3) rain. Of the 3 factors, only food quality has been closely examined (Chapter 5).

The tendency of neonate larvae to disperse has been briefly discussed in Section 3.3.1. Variations in dispersal losses may be related to poor food quality although this has not been conclusively demonstrated.

Frequent and intense rains, which are not unusual at the time of the year when larvae are hatching, may kill larvae either

directly by drowning or indirectly by favouring the development of diseases. However, rain may only be regarded as a key factor if it can be demonstrated that it causes a variable mortality between years and that this mortality is inversely proportional to the population trend index.

A key factor affecting sex ratio?

It is uncertain what caused the abnormally low proportion of female pupae in the 1976-1977 generation. The factors or processes known to cause a greater mortality among females than males of some species of insects are adverse temperatures and humidities (Brandt, 1938), crowding (Titschack, 1937), starvation (Brandt, 1938; Graham, 1939) and poor food quality (Goldsmith, 1932). In *Chlenias* it may well be that the nutritional requirements of the female larva are different from that of the male and the detrimental effects of poor food quality are felt more strongly by the female. Also, since the female larva takes a longer time to develop than the male (see Table 3.6), it is exposed that much longer to predators, parasites and diseases. Polyhedrosis virus and other unknown factors were shown to kill more female than male larvae of *Colias philodice eurytheme* Boisduval because of the slower rate of development of the female larvae (Stern and Smith, 1960). It is very likely that far more females than males are killed by *Lissopimpla excelsa* because the parasite density is at its peak later in the season when *Chlenias* females are pupating (see Section 6.2.1.7). Other parasites of *Chlenias* may also have a similar effect.

Low S_A values

It is necessary to comment on the surprisingly low values of S_A in each of the years. The agents probably responsible were

dispersal, mating failure and predators, especially birds. Other possible agents were misadventure and adverse weather conditions. I was unable to make a proper appraisal of the status of these agents and the following remarks must be considered conjectural.

A nett loss of females from the population area is a possibility to be considered. Since fully gravid females do not disperse (see Section 3.5), dispersal is probably done after the moths have oviposited at least some of their eggs. Mating failure is another possibility; although infertile eggs were rarely found in the field, "adult mortality" caused by mating failure may not be detected because such females retain almost all their eggs till they die (see Section 3.5). As mentioned in Section 6.3.2, there was evidence of moth mortality caused by bird predation. The sum effect of these agents plus other agents like misadventure and adverse weather conditions may account for the low values of S_A.

Is food the key factor?

Of the 3 major causes of mortality of the first-instar larvae, food was probably the most important and is likely to be the key factor in the population dynamics of *Chlenias*. This conclusion is consistent with the results obtained from other aspects of the study (see Chapter 8).

Reliability of estimates

Finally, one of the major difficulties in the preparation of life tables has been the estimation of the numbers entering a stage or age class (l_x). The difficulty arises because there is normally an overlap in time of successive stages of a cohort. An ideal situation for ease of estimating l_x would be one where all the individuals of any one stage are in perfect synchrony. Since

such a situation does not exist in nature, various means have been devised to estimate l_x. For example, Morris and Miller (1954) estimated l_x for larval instars III-VI of *Choristoneura fumiferana* by a direct population sampling when instar III was the prevalent instar in the field. Harcourt (1963) divided the larval stage into periods 1, 2 and 3. Larval period 2, for example, was from the middle of the fourth-instar to cocoon formation, and l_x was estimated by direct population sampling of larvae at the middle of the fourth-instar. It is obvious that considerable errors in the estimates are unavoidable with such methods.

Manly (1976) modified Kiritani and Nakasuji's (1967) method to enable estimation of the survival-rate for any stage for samples taken at irregular intervals. Manly's method was used here for the estimation of survival-rates for larval instars I-V of *Chlenias* but not for larval instar VI, the survival-rate of which was estimated differently (see Section 7.3.2). If, for example, Harcourt's method has been used here instead, the variability in the survival of larval instar I would not have been detected. A problem with using Manly's method is that it is based on the estimation of the area under the frequency trend curve; and the area under the curve is likely to be extremely variable unless based on very frequent observations. Therefore, some of the estimates of the survival-rates of the larvae of *Chlenias* may be crude because they were based on a small number of observations.

Densities of pupae, eggs and early larval instars were high in 1976. But the numbers declined sharply and remained low for the rest of the study. Hence, estimates for the later stages of

each generation, in particular the pupal stage, may also not be reliable.

In this study it was too expensive in terms of time and travel costs to sample more frequently than was done, and Manly's method of estimating survival-rates has been used mainly to illustrate its potential in life table analysis.

CHAPTER 8

GENERAL DISCUSSION

CHAPTER 8

GENERAL DISCUSSION

Pinus radiata has been grown on a plantation scale in South Australia for 103 years. The recorded history of the association of the indigenous *C. pachymela* with this introduced host dates back 52 years. There have been numerous reports of outbreaks of this insect, and some of these outbreaks were so severe that insecticides had to be applied.

The geographical distribution of the outbreaks in South Australia is interesting. With the possible exception of Bundaleer*, all the outbreaks have occurred in the Lower South-East region and yet the polyphagous *C. pachymela* is found in other areas of the state. In these other areas they occasionally appear in epidemic proportions on various host species but not on *P. radiata*.

Life table studies suggest that the key factors are those which (1) operate on the first-instar larvae, and (2) have a differential effect on the sexes, i.e. the deleterious effect is more severe on the female than on the male. No satisfactory explanation can presently be offered for the differential mortality of the sexes although poor food quality and parasites may be causal factors. The probable factor responsible for significant and variable mortality in the first-instar larvae is discussed below.

The role of parasites and predators in the population dynamics of *C. pachymela* has not been fully evaluated. But in view of the low proportion of mortality caused by these enemies

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* The species here was probably not *Chlenias pachymela* (Morgan, personal communication).

their role cannot be major. There were certainly no important parasites and predators of the first-instar larvae.

Significant reductions in the rate of growth and survival of first-instar larvae were observed when pollen was not included in the diet of these larvae. The following argument will show how pollen can be a critical factor influencing the survival of the population.

An insect such as *Chlenias* that depends on temperature to regulate its diapause processes can be expected to show some variation in its seasonality. Indeed, past observations have provided evidence that *C. pachymela* does vary in the time of adult emergence. Pollen shed in *P. radiata*, on the other hand, seems to be a regular phenomenon.

Morris (1957) has stated that "... variation is the important attribute of mortality, and that low but variable mortalities may therefore have more influence on population trend than high but relatively constant mortalities". The influence of variable mortalities on population changes are considered to be important whether they are density-dependent or density-independent (LeRoux et al., 1963). Such mortalities are called "key factors" by Morris (1959) which according to him mean "simply that changes in population from generation to generation are closely related to the degree of mortality caused by this factor, which therefore has predictive value".

The unavailability of pollen to feed on may be considered to be a key factor in the population dynamics of *C. pachymela*. The hypothetical relationships between pollen and pine looper densities are as follows :

1. Negligible insect densities if the period of larval hatch is completely out of phase with the pollen shed period.
2. Low to medium insect densities when the period of larval hatch partially overlaps the period of pollen shed.
3. High insect densities when the peak period of larval hatch coincides with the peak period of pollen shed.

The first relationship probably exists in the Central region of South Australia. Around Adelaide, adult emergence takes place much earlier than at Noolook and larval eclosion occurs before the pollen shed period of *P. radiata*. Hence high mortality occurs and most of the population fails to establish.

The second relationship was observed in 1977 and 1978 at Noolook. A similar relationship would probably be found in the forests of the Lower South-East where larvae are present, but in low numbers in most years.

The third relationship would have been the cause of outbreaks of the insect observed in the Lower South-East. In this region, fortuitous deviations in temperature from that of "normal" years (i.e. years in which no outbreaks occurred), could result in synchrony of peak larval emergence and peak pollen shed. Given the high reproductive potential of *C. pachymela*, the endemic population in a plantation could reach epidemic proportions within a single generation as has been observed by foresters in the past.

The hypothesis that pollen is a key factor in the population dynamics of *C. pachymela* therefore provides an explanation for both the distribution and abundance of the insect in South Australia.

The study carried out did not seek to define the beneficial effect of pollen. But the role of pollen may reasonably be assumed to be nutritional. Pine pollen is rich in various nutriments and is certainly much richer in nitrogen than pine foliage (see Section 5.1.2). Increased nitrogen levels has important implications in the population dynamics of many species of insects (White, 1969, 1974, 1976; Clark and Dallwitz, 1974, 1975).

Food quality has a number of effects on an insect (see Section 5.1) but only 2 - survival and growth - have been investigated. So the unavailability of pollen for larvae to feed on may actually have far wider implications for *C. pachymela* than is presently known. This study seems to support a general principle spelled out by Webb and Moran (1978) for the population dynamics of the many phytophagous insects which remain at endemic levels of abundance for long periods - that it is the host plant which plays a critical role in determining their numbers.

Assuming that pollen is the key factor affecting *C. pachymela*, several possibilities may be considered for its future control without the use of insecticides. Alteration of tree phenology is one way of achieving this. Eidt and Little (1968) and Holliday (1977) have considered this approach. Eidt and Little (1970) actually attempted to induce host-insect asynchrony by applying growth retardants on balsam fir, *Abies balsamea* (L.) Mill., but were not successful. It does seem that the practical difficulties involved in altering the host phenology are too great. Even if some chemical can be found to achieve this, it would have to compare favourably in cost to insecticides. Of course the use of insecticides should be avoided because of their undesirable

side-effects; but as has been practised in past outbreaks of *C. pachymela* on *P. radiata*, the judicious and infrequent use of insecticides would have minimal impact on the environment. There is perhaps a better alternative to alteration of the tree phenology to control *Chlenias*.

Fielding (1960) has measured the production of cones, pollen and pollen-bearing material by *P. radiata*. He estimated the dry weight of these materials to be equivalent to 16% of the mean annual increment of the plantations. This estimate of the amount of growth energy annually expended on sexual reproduction would be even higher if one takes into consideration the fact that seed and pollen are richer than wood in nutrients. Fielding suggested that : "Selection against profuse flowering may possibly result in diverting a greater proportion of the material elaborated by the tree into wood production, thus increasing the yield of the forest". This suggestion, if adopted, would not only result in increased yield, but would probably prevent or at least reduce the severity of outbreaks of *C. pachymela*.

Perhaps Fielding's suggestion should be carried to one extreme and stands of trees that are completely female, i.e. they do not produce any male strobili, should be planted. Such trees already exist in plantations and can be propagated by cuttings (Fielding, 1960). This measure should prevent the development of outbreaks of *Chlenias* in *P. radiata* plantations.

Southwood (1973) has stated that " ... pollen feeding often seems to represent 'the first step' (in the evolutionary path of the phytophagous insect) and feeding in or on foliage, 'full success'". Others have also discussed the possibility that insects may evolve to overcome the resistance of host plants (Beck, 1974; Knight and Alston, 1974). It may well be that

C. pachymela is in the process of overcoming the resistance, i.e. the nutritional barrier of the foliage, of *P. radiata*. Although the foliage of species of *Pinus* is known to be poor in nitrogen, various insect species are known to have adapted to this source of food and even thrive on it. In Europe, 4 species of lepidopterous defoliators of pines occasionally cause serious damage (Schwerdtfeger, 1935, 1941; Klomp, 1968) and in none of these is pollen known to be a critical factor in the survival of the larvae. One of these 4 species, *Bupalus piniarius* L., is a geometrid like *C. pachymela*, and defoliates *Pinus sylvestris* L. (Klomp, 1966); the total nitrogen present in the needles of *P. sylvestris* is low (maximum value 1.5% of dry weight) like other *Pinus* species (Wright and Will, 1958) and yet the larvae of *B. piniarius* seem to thrive on this food resource.

The planting of male-sterile radiata pines may eliminate the possibility of *Chlenias* evolving to thrive on *P. radiata* alone. On the other hand, such plantations may exert selective pressure that might hasten the evolution of *Chlenias* towards a form capable of surviving on foliage alone. This last possibility may be obviated by retaining large tracts of native forests within plantations of male-sterile radiata pines : this step would remove the selection pressure on the polyphagous insect to adapt to pine foliage. The retention of areas of native forests within pine plantations has other benefits which are discussed below.

It is widely accepted that unevenaged and ecologically complex forests with substantial floral and faunal diversity are less seriously affected by insect pests than those of more homogeneous structure (Graham, 1963; Matthews, 1976; U.S. Dept. Agric., 1977). Friend (1978) advocated that plantation management should be directed towards the establishment of a mosaic of pine stand and interconnecting areas of retained native forest. This proposition is aimed at conservation of wildlife : Friend found that blocks of native forest retained within plantations enabled many of the species of mammals and birds dependent on the native forest to exist within the plantation. Birds and mammals are, of course, potential predators of *C. pachymela* and their presence in the plantation is to be encouraged.

It has been found in this and other studies (e.g. Hocking, 1967) that the longevity of parasites are dependent on nectar and honeydew to feed on. Such food resources are scarce in a pine plantation and Friend's proposition should increase parasite activity here. Moreover, those polyphagous parasites unable to synchronise with *Chlenias*, e.g. *Lissopimpla excelsa*, would also benefit from a mixed forest by having alternative hosts.

Friend's proposition would not entail radical changes in current silvicultural practices. Already significant areas of native vegetation are retained on plantation boundaries, along permanent streams and on steep slopes (Neumann, 1979).

All that requires to be done is to retain larger areas of native forests adequately dispersed within pine plantations, which is presently not being practised.

It will be noted that the above recommendations were not made with the sole aim of controlling the pine looper. Far from this, the other benefits (i.e. increased yield of pine timber and improved conservation of wildlife) that would accrue if these recommendations are implemented would complement the benefits resulting from the control of an insect.

APPENDICES

Appendix 1 Means of daily air temperatures (°C) recorded at Noolook forest in 1976, 1977 and 1978.

Month	Maximum			Minimum			½(Max + Min)		
	1976	1977	1978	1976	1977	1978	1976	1977	1978
January	23.7	24.6	22.9	11.9	11.9	10.5	17.5	18.3	16.7
February	27.0	25.4	23.1	12.5	11.6	10.5	19.8	18.5	16.8
March	21.8	21.9	23.5	10.7	11.0	11.0	16.3	16.5	17.3
April	19.9	18.1	19.7	10.1	8.7	8.4	15.0	13.4	14.1
May	16.0	16.3	17.2	8.4	7.1	7.5	12.2	11.7	12.4
June	14.3	14.2	14.3	6.8	7.0	5.5	10.6	10.6	9.9
July	13.9	13.8	13.3	5.0	4.0	6.5	9.5	8.9	9.9
August	14.4	15.9	13.5	6.0	5.4	3.8	10.2	10.7	8.7
September	15.4	15.7	16.0	7.0	5.4	5.8	11.2	10.6	10.9
October	16.3	19.3	18.3	6.7	7.3	5.9	11.5	13.3	12.1
November	21.1	20.2	19.3	9.1	8.7	10.6	15.1	14.5	15.0
December	22.2	22.5	21.9	12.0	12.3	11.7	17.1	17.4	16.8
Year	18.8	19.0	18.6	8.9	8.4	8.1	13.8	13.7	13.4

Appendix 2 Monthly rainfall (mm) at Noolook forest.

Month	1976	1977	1978
January	13.4	38.0	32.4
February	45.2	11.2	10.4
March	6.8	48.6	14.6
April	40.8	23.6	32.0
May	45.8	82.8	51.6
June	80.4	112.4	86.8
July	64.6	49.8	131.4
August	64.6	39.4	87.2
September	86.4	36.4	69.2
October	30.6	52.8	30.6
November	39.8	99.8	46.6
December	55.2	9.8	22.8
Year	573.6	604.6	615.6

Appendix 3 Analyses of variance of weights of pupae of *Chlenias pachymela* collected from Noolook at various times during the pupal period in 1978 (see Section 3.4).

Male pupae

Source	d.f.	S.S.	M.S.	F	P
Treatment	4	6,767.00	1,691.75	1.92	>0.05
Error	95	83,740.17	881.48		
Total	99	90,507.17			

Female pupae

Source	d.f.	S.S.	M.S.	F	P
Treatment	4	39,490.97	9,872.74	2.39	>0.05
Error	86	355,723.58	4,136.32		
Total	90	395,214.55			

Appendix 4 Analyses of variance of weights of pupae of *Chlenias pachymela* collected fron Noolook in 1976, 1977, 1978 and 1979 (see Section 3.4).

Male pupae

Source	d.f.	S.S.	M.S.	F	P
Treatment	3	5,550.47	1,850.16	1.05	>0.05
Error	76	133,371.71	1,754.89		
Total	79	138,922.18			

Female pupae

Source	d.f.	S.S.	M.S.	F	P
Treatment	3	4,584.49	1,528.16	0.46	>0.05
Error	67	221,741.58	3,309.58		
Total	70	226,326.07			

Appendix 5 Analysis of variance of survival data of Table 5.1 (see Section 5.2.1).

Source	d.f.	S.S.	M.S.	F	P
Replicate	5	349.78	69.96	2.33	>0.05
Treatment	2	926.78	463.39	15.45	<0.01
Error	10	299.88	29.99		
Total	17	1,576.44			

Appendix 6 Analysis of variance for survival data of Table 5.2 (see Section 5.2.2).

Source	d.f.	S.S.	M.S.	F	P
Replicate	5	222.17	44.43	0.84	>0.05
Treatment	4	6,207.00	1,551.75	29.42	<0.01
Error	20	1,054.95	52.75		
Total	29	7,484.12			

Appendix 7 Analysis of variance of head capsule widths of young larvae fed on various diets for 2 weeks (see Section 5.2.3).

Source	d.f.	S.S.	M.S.	F	P
Treatment	4	653,801.04	163,450.26	32.15	<0.01
Error	95	482,970.60	5,083.90		
Total	99	1,136,771.64			

Appendix 8 Analysis of variance of Field Experiment I (see Section 5.3.1).

Source	d.f.	S.S.	M.S.	F	P
Replicate	9	134.40	14.93	1.08	>0.05
Treatment	3	382.60	127.53	9.22	<0.01
Error	27	373.40	13.83		
Total	39	890.40			

Appendix 9 Analysis of variance of Field Experiment II (see Section 5.3.2).

Source	d.f.	S.S.	M.S.	F	P
Replicate	4	19.60	4.90	0.33	>0.05
Treatment	2	712.93	356.47	24.09	<0.01
Error	8	118.40	14.80		
Total	14	850.93			

BIBLIOGRAPHY

Abercrombie, M., Hickman, C.J. and Johnson, M.L. (1973). A Dictionary of Biology. Penguin, Harmondsworth (England), 311 pp.

Alma, P.J. (1975). Infection of pupae of *Heliothis armigera* by *Paecilomyces farinosus*. N.Z.J. for Sci., 5 : 42-44.

Andrewartha, H.G. (1935). Thrips investigation No. 7. On the effect of temperature and food upon egg production and the length of adult life of *Thrips imaginis*, Bagnall. J. Counc. scient. indust. Res. Aust., 8 : 281-288.

Andrewartha, H.G. (1952). Diapause in relation to the ecology of insects. Biol. Rev., 27 : 50-107.

Andrewartha, H.G. (1970). Introduction to the Study of Animals. Chapman and Hall, London, 283 pp.

Andrewartha, H.G. and Birch, L.C. (1954). The Distribution and Abundance of Animals. University of Chicago Press, Chicago, 782 pp.

Andrewartha, H.G. and Browning, T.O. (1961). An analysis of the idea of "resources" in animal ecology. J. Theoret. Biol., 1 : 83-97.

Askew, R.R. (1968). A survey of leaf-miners and their parasites on laburnum. Trans. R. ent. Soc. Lond., 120 : 1-37.

Askew, R.R. (1971). Parasitic Insects. Heinemann, London, 316 pp.

Bailey, C.G. (1976). A quantitative study of consumption and utilisation of various diets in the bertha armyworm, *Mamestra configurata* (Lepidoptera : Noctuidae). Can. Ent., 108, 1319-1326.

Baker, R.R. (1968). A possible method of evolution of the migratory habit in butterflies. Phil . Trans. Roy. Soc. Lond. (B), 253 : 309-341.

Barbosa, P. and Capinera, J.L. (1977). The influence of food on developmental characteristics of the gypsy moth *Lymantria dispar* (L.). Can. J. Zool., 55 : 1424-1429.

Barlow, C.A. (1961). On the biology and reproductive capacity of *Syrphus corollae* Fab. (Syrphidae) in the laboratory. Entomologia exp. appl., 4 : 91-100.

Bass, M.J. and Rawson, J.W. (1960). Some effects of age, pre-imaginal habitat and adult food on susceptibility of boll weevil to certain insecticides. J. econ. Ent., 53 : 534-536.

Beck, S.D. (1950). Nutrition of the European corn borer, *Pyrausta nubilalis* (Hbn.) II. Some effects of diet on larval growth characteristics. Physiol. Zool., 23 : 353-361.

Beck, S.D. (1956). The European corn borer, *Pyrausta nubilalis* (Hbn.) and its principal host plant. II. The influence of nutritional factors on larval establishment and development on the corn plant. Ann. ent. Soc. Am., 49 : 582-588.

Beck, S.D. (1974). Theoretical aspects of host plant specificity in insects. Proceedings of the Summer Institute on Biological Control of Plant Insects and Diseases (Ed. F.G. Maxwell and F.A. Harris), pp. 290-311. University Press of Mississippi, Jackson.

Beckwith, R.C. (1970). Influence of host on larval survival and adult fecundity of *Choristoneura conflictana* (Lepidoptera : Tortricidae). Can. Ent., 102 : 1474-1480.

Beckwith, R.C. (1976). Influence of host foliage on the Douglas-fir tussock moth. Environ. Entomol., 5 : 73-77.

Bednall, B.H. (1962). Annual Report 1960-1961. Woods and Forests Department, South Australia.

Bell, C.H. (1976). Factors influencing the duration and termination of diapause in the warehouse moth, *Ephestia elutella* Physiol. Ent., 1 : 169-178.

Bentley, B.L. (1977). Extrafloral nectaries and protection by pugnacious bodyguards. A. Rev. Ecol. Syst., 8 : 407-427.

Blais, J.R. (1952). The relationship of the spruce budworm *Choristoneura fumiferana* (Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). Can. J. Zool., 30 : 1-29.

Blais, J.R. and Parks, C.H. (1964). Interaction of evening grosbeaks (*Hesperiphona vespertina*) and the spruce budworm *Choristoneura fumiferana* (Clem.) in a localised budworm outbreak treated with DDT in Quebec. Can. J. Zool., 42 : 1017-1024.

Bodnaryk, R.P. (1977). Stages of diapause development in the pupa of *Mamestra configurata* based on the β-ecdysone sensitivity index. J. Insect Physiol., 23 : 537-542.

Bonnemaison, L. (1951). Contribution à l'étude des facteurs provoquant l'apparition des formes ailées et sexuées chez les Aphidinae. Annls. Épiphyties, 2 : 1-380.

Bosque, C. and Rabinovich, J.E. (1979). Population dynamics of *Telenomus fariai* (Hymenoptera : Scelionidae), a parasite of Chagas' disease vectors. VII. Oviposition behaviour and host discrimination. Can. Ent., 111 : 171-180.

Brandt, H. (1938). Untersuchungen über die Änderung des Geschlechtverhältnisses bei der Nonne (Lymantria monacha L.) und ihre Ursachen. Z. angew. Ent., 24 : 87-94.

Brown, A.H.S. and Smith, G. (1957). The genus *Paecilomyces* Bainer and its perfect stage *Byssochlamys* Westling. Trans. Br. mycol. Soc., 40 : 17-89.

Browning, T.O. (1962). The environments of animals and plants. J. theoret. Biol., 2 : 63-68.

Buckner, C.H. (1966). The role of vertebrate predators in the biological control of forest insects. A. Rev. Ent., 11 : 449-70.

Buckner, C.H. and Turnock, W.J. (1965). Avian predation on the larch sawfly, *Pristiphora erichsonii* (Htg.), (Hymenoptera : Tenthredinidae). Ecology, 46 : 223-236.

Burns, J.M. (1968). Mating frequency in natural populations of skippers and butterflies as determined by spermatophore counts. Proc. natn. Acad. Sci. U,S.A., 61 : 852-859.

Buxton, P.A. (1932). Terrestrial insects and the humidity of the environment. Biol. Rev., 7 : 275-320.

Campbell, A., Frazer, B.D., Gilbert, N., Guttierrez, A.P. and Mackauer (1974). Temperature requirements of some aphids and their parasites. J. appl. Ecol., 11 : 431-438.

Capinera, J.L. (1979). Zebra caterpillar (Lepidoptera : Noctuidae): foliage consumption and development of larvae on sugarbeet. Can. Ent., 111 : 905-909.

Capinera, J.L. and Barbosa, P. (1976). Dispersal of the first-instar gypsy moth larvae in relation to population quality. Oecologia, 26 : 53-60.

Carayon, J. and Steffan, J.R. (1959). Observations sur le régime alimentaire de *Orius* et particulierement d' *Orius pallidicornis* (Reut.). Cabiers des Naturalistes, Bull. N.P., n.s. 15:53-64.

Carne, W.M. (1913). The secretion of nectar by extrafloral glands in the genus *Acacia* (wattles). Aust. Nat., 2 : 198-199.

Carton, Y. (1978). Biologie de *Pimpla instigator* (Hym : Ichneumonidae). IV. Modalités du development larvaire en fonction du site de ponte; role des réactions hémocytaires de l'hôte. Entomophaga, 23 : 249-259.

Chippendale, G.M. and Reddy, A.S. (1973). Temperature and photoperiodic regulation of diapause of the southwestern corn borer, *Diatraea grandiosella*. J. Insect Physiol., 19 : 1397-1408.

Clark, L.R. and Dallwitz, M.J. (1974). On the relative abundance of some Australian Psyllidae that coexist on *Eucalyptus blakeyi*. Aust. J. Zool., 22 : 387-415.

Clark, L.R. and Dalliwitz, M.J. (1975). The life system of *Cardiaspina albitextura* (Psyllidae) 1950-74. Aust. J. Zool., 23 : 523-561.

Cobbinah, J.R. (1978). The biology and food preferences of the gum leaf skeletonizer, *Uraba lugens* (Walk.). PhD thesis, University of Adelaide.

Cole, L.R. (1959). On the defences of lepidopterous pupae in relation to the oviposition behaviour of certain Ichneumonidae. J. Lepid. Soc., 13 : 1-10.

Coleman, E. (1928). Pollination of an Australian orchid by the male Ichneumonid *Lissopimpla semipunctata*, Kirby. Trans. Ent. Soc. Lond., 76 : 533-539.

Coleman, E. (1933). Further notes on the pollination of *Cryptostylis subulata* (Labill.) Reichb. Victorian Nat., 50 : 41-44.

Coleman, E. (1938). Further observations on the pseudo-copulation of the male *Lissopimpla semipunctata* Kirby (Hymenoptera parasitica) with the Australian orchid, *Cryptostylis leptochila* F.v.M. Proc. R. ent. Soc. Lond. (A), 13 : 82-83.

Cordingley, C.L. (L977). The ecology of the grape vine moth *Phalaenoides glycine* Lewin. PhD thesis, University of Adelaide.

Dadd, R.H. (1970). Arthropod nutrition. In Chemical Zoology, (Ed. M. Florkin, B.T. Scheer), 5 : 35-95. Academic Press, New York.

Dadd, R.H. (1973). Insect nutrition : current developments and metabolic implications. A. Rev. Ento., 18 : 381-420.

Daniel, D.M. (1932). *Macrocentrus ancylivorus* Rohwer a polyembryonic braconid parasite of the oriental fruit moth. Tech. Bull. N.Y. St. agric. Exp. Stn. No. 187.

Danilevsky, A.S., Goryshin, N.I. and Tyshchenko, V.P. (1970). Biological rhythms in terrestrial arthropods. A. Rev. Ent., 15 : 201-244.

David, W.A.L., Ellaby, S. and Taylor, G. (1972). The effect of reducing the content of certain ingredients in a semisynthetic diet on the incidence of granulosis virus disease in *Pieris brassicae*. J. Invertebr. Pathol., 20 : 332-340.

David, W.A.L. and Taylor, C.E. (1977). The effect of sucrose content of diets on susceptibility to granulosis virus disease in *Pieris brassicae*. J. Invertebr. Pathol., 30 : 117-118.

Dempster, J.P. (1968). Intra-specific competition and dispersal : as exemplified by a psyllid and its anthocorid predator. In Insect Abundance (Ed. T.R.E. Southwood) pp. 8-17. Blackwell Scientific Publications, Oxford.

Dempster, J.P. (1975). Animal Population Ecology. Academic Press, London. 155 pp.

Dickson, R. (1976). A lepidopterist's handbook. The Amateur Entomologists' Society, Hanworth, Middlesex. 138 pp.

Downes, J.A. (1955). The food habits and description of *Atrichopogon pollinivorus* sp. n. (Diptera : Ceratopogonidae). Trans. R. ent. Soc. Lond., 106 : 439-453.

Drooz, A.T. (1965). Some relationships between host, egg potential and pupal weight of the elm spanworm, *Ennomos subsignarius* (Lepidoptera : Geometridae). Ann. ent. Soc. Am., 58 : 243-245.

Ebel, B.H. (1965). The *Dioryctria* coneworms of north Florida pines (Lepidoptera : Phycitidae). Ann. ent. Soc. Am., 58 : 623-630.

Edney, E.B. (1977). Water Balance in Land Arthropods. Springer-Verlag, Berlin. 282 pp.

Eidt, D.C. and Little, C.H.A. (1968). Insect control by artificially prolonging plant dormancy - a new approach. Can. Ent., 100 : 1278-1279.

Eidt, D.C. and Little, C.H.A. (1970). Insect control through induced host-insect asynchrony : a progress report. J. econ. Entomol., 63 : 1966-1968.

Fielding, J.M. (1947). The seeding and natural regeneration of Monterey pine in South Australia. Bull. Commonw. For. Timb. Bur. Aust., No. 29.

Fielding, J.M. (1953). Variations in Monterey pine. Bull. Commonw. For. Timb. Bur. Aust., No. 31.

Fielding, J.M. (1955). The seasonal and daily elongation of the

shoots of Monterey pine and the daily elongation of the roots. Leafl. Commonw. For. Timb. Bur., Canberra, No. 75.

Fielding, J.M. (1957). The introduction of Monterey pine into Australia. Aust. For., 21 : 15-16.

Fielding, J.M. (1960). Branching and flowering characteristics of Monterey pine. Bull. Commonw. For. Timb. Bur. Aust., No. 37.

Fisher, R.C. (1961). A study in insect multiparasitism. II. The mechanism and control of competition for possession of the host. J. exp. Biol. 38 : 605-628.

Fisher, R.C. (1971). Aspects of the physiology of endoparasitic Hymenoptera. Biol. Rev. 46 : 243-278.

Flanders, S.E. (1950). Regulation of ovulation and egg disposal in the parasitic Hymenoptera. Can. Ent., 82: 134-140.

Fraenkel, G. (1953). The nutritional value of green plants for insects. Trans. 9th Int. Congr. Ent., Amsterdam 1951, 2 : 90-160.

Fraenkel, G, and Hsiao, C. (1968). Manifestations of a pupal diapause in two species of flies, *Sarcophaga argyrostoma* and *S. bullata*. J. Insect Physiol., 14 : 689-705.

Friend, G. (1978). A comparative study of the flora and fauna of exotic pine plantations and adjacent, indigenous eucalypt forests in Gippsland, Victoria. PhD thesis, University of Melbourne.

Gaines, J.C. and Mistric, W.J. (1960). Factors affecting insects during exposure to insecticides. In Methods of Testing Chemicals on Insects (Ed. H.H. Shepard), Vol. 2, pp. 10-18. Burgess, Minneapolis, Minnesota.

Gilbert, L.E. (1972). Pollen feeding and reproductive biology of *Heliconius* butterflies. Proc. natn. Acad. Sci. U.S.A., 69 : 1403-1407.

Goldsmith, M. (1932). La proportion des sexes chez *Galleria mellonella*. C.R. Acad. Sci., Paris, 194 : 797-798.

Gordon, H.T. (1959). Minimal nutritional requirements of the German Roach, *Blatella germanica* L. Ann. N.Y. Acad. Sci., 77 : 290-351.

Gordon, H.T. (1961). Nutritional factors in insect resistance to chemicals. A. Rev. Ent., 6 : 27-54.

Gourlay, E.S. (1930). Preliminary host list of the entomophagous insects in New Zealand. Bull. N.Z. Dep. scient. ind. Res., No. 22.

Graham, K. (1963). Concepts of Forest Entomology. Reinhold Publ. Corp;., New York. 388 pp.

Graham, S.A. (1939). Forest insect populations. Ecol. Monogr. 9 : 301-310.

Greenbank, D.O. (1963). Staminate flowers and the spruce budworm. In The Dynamics of Epidemic Spruce Budworm Populations (Ed. R.F. Morris), pp. 202-218. Mem. ent. Soc. Can., No. 31.

Grinfeld, E.K. (1957). The feeding of grasshoppers (Orthoptera : Tettigoniodea) on pollen of flowers and their possible role in the origin of Entomophily of plants (Translated). Entomol. Obozr., 36 : 620-624.

Grinfeld, E.K. (1959). The feeding of thrips (Thysanoptera) on pollen of flowers and the origin of asymmetry in their mouthparts (Translated). Entomol. Obozr., 38 : 798-804.

Guest , E. (1886). A classified list of geometrina found round Balhannah, with notes on species. Trans. R. Soc. S. Aust., 9 : 126-141.

Gutierrez, A.P., Morgan, D.J. and Havenstein, D.E. (1971). The ecology of *Aphis craccivora* and subterranean clover stunt virus. I. The phenology of aphid populations and the epidemiology of virus in pastures in south-east Australia.

Hagen, K.S. (1962). Biology and ecology of predaceous Coccinellidae. A. Rev. Ento., 7 : 289-326.

Harcourt, D.G. (1963). Major mortality factors in the population dynamics of the diamond back moth *Plutella maculipennis* (Curt.) (Lepidoptera : Plutellidae). In Population Dynamics of Agricultural and Forest Insect Pests, (Ed. E.J. LeRoux,), Mem. ent. Soc. Can., 32 : 55-66.

Harker, J.E. (1961). Diurnal rhythms. A. Rev. Ent., 6 : 131-146.

Hassell, M.P. (1966). Evaluation of parasite or predator responses. J. Anim. Ecol., 35 : 65-75.

Hinton, H.E. (1973). Neglected phases in metamorphosis : a reply to V.B. Wigglesworth. J. Ent. (A), 48 : 57-68.

Hirai, Y. (1977). The biological clock. In Adaptation and Speciation in the Fall Webworm, (Ed. T. Hidaka), pp. 61-79. Kodansha, Tokyo.

Hocking, H. (1967). The influence of food on longevity and oviposition in *Rhyssa persuasoria* (L.) (Hymenoptera : Ichneumonidae). J. Aust. ent. Soc., 6 : 83-88.

Hogan, T.W. (1960). The onset and duration of diapause in eggs of *Acheta commodus* (Walk.) Aust. J. biol. Sci., 13 : 14-29.

Holliday, N.J. (1977). Population ecology of winter moth *(Operophtera brumata)* on apple in relation to larval dispersal and time of bud burst. J. appl. Ecol., 14 : 803-813.

Holling, C.S. (1959). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Ent., 91 : 293-320.

Hough, J.A. and Pimentel, D. (1978). Influence of host foliage on development, survival, and fecundity of the gypsy moth. Environ. Entomol., 7 : 97-102.

House, H.L. (1959). Nutrition of the parasitoid *Pseudosarcophaga affinis* (Fall.) and of other insects. Ann. N.Y. Acad. Sci., 77 : 394-405.

House, H.L. (1961a). Insect nutrition. A. Rev. Ent., 6 : 13-26.

House, H.L. (1961b). Insect diseases resulting from malnutrition. Proc. ent. Soc. Ontario, 91 : 13-22.

House, H.L. (1963). Nutritional diseases. In Insect Pathology, An Advanced Treatise, (Ed. E.A. Steinhaus), 1 :133-160. Academic Press, New York.

House, H.L. (1965a). Insect nutrition. In The Physiology of Insects, (Ed. M. Rockstein), 2 : 769-813. Academic Press, New York.

House, H.L. (1965b). Effects of low levels of the nutrient content of a food and of nutrient imbalance on the feeding and the nutrition of a phytophagous larva, *Celerio euphorbiae* (Linnaeus) (Lepidoptera : Sphingidae). Can. Ent., 97 : 62-68.

House, H.L. (1969). Effects of different proportions of nutrients on insects. Entomologia exp. appl., 12 : 651-669.

Hudleston, J.A. (1958). Some notes on the effects of bird predators on hopper bands of the Desert Locust (*Schistocerca gregaria* Forsk.) Entomologist's mon. Mag., 94 : 210-214.

Huffaker, C.B. (1957). Fundamentals of biological control of weeds. Hilgardia, 27 : 101-157.

Imms, A.D. (1937). Recent Advances in Entomology. J. and A. Churchill, London. 431 pp.

Jacobson, L.A. and Blakeley, P.E. (1958). Development, mortality from starvation and oviposition of the pale western cutworm *Agrotis orthogonia* Morr. (Lepidoptera : Noctuidae), when fed on various food plants. Can. Ent., 90 : 650-653.

Jaques, R.P. (1961). The influence of physical stress on growth and nuclear polyhedrosis of *Trichoplusia ni* (Hübner). J. Insect Pathol., 3 : 47-54.

Jaynes, H.A. and Speers, C.F. (1949). Biological and ecological studies of the spruce budworm. J. econ. Ent., 42 : 221-225.

Jennings, D.T. (1974) Potential fecundity of *Rhyacionia neomexicana* (Fyar) (Olethreutidae) related to pupal size. J. Lepid. Soc., 28 : 131-136.

Kalpage, K.S.P. and Brust, R.A. (1974). Studies on diapause and female fecundity in *Aedes atropalpus*. Environ. Entomol., 3 : 139-145.

Kendrick, W.B. and Carmichael, J.W. (1973). Hyphomycetes. In The Fungi Vol. IV A, A Taxonomic Review with Keys : Ascomycetes and Fungi Imperfecti (Ed. G.C. Ainsworth, F.K. Sparrow and A.S. Sussman). Academic Press, New York.

Kimmins, J.P. (1971). Variations in the foliar amino acid composition of flowering and non-flowering balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss) in relation to outbreaks of the spruce budworm (*Choristoneura fumiferana* (Clem)). Can. J. Zool., 49 : 1005-1011.

Kiritani, K. and Nakasuji, F. (1967). Estimation of the stage-specific survival rate in the insect population with overlapping stages. Res. Popul. Ecol., 9 : 143-152.

Klomp, H. (1966). The dynamics of a field population of the pine looper, *Bupalus piniarius* L. (Lep., Geom.). Adv. Ecol. Res., 3 : 207-305.

Klomp, H. (1968). A seventeen-year study of the abundance of the pine looper *Bupalus piniarius* L. (Lepidoptera : Geometridae). In Insect Abundance (Ed. T.R.E. Southwood), pp. 98-108. Blackwell Scientific Publications, Oxford.

Knight, R.L. and Alston, F.H. (1974). Pest resistance in fruit breeding. In Biology in Pest and Disease Control (Ed. D. Price Jones and M.E. Solomon), pp. 73-86. Blackwell Scientific Publications, Oxford.

Langdon, R.F.N. and Champ, B.R. (1954). The insect vectors of *Claviceps paspali* in Queensland. J. Aust. Inst. agric. Sci., 20 : 115-118.

Lees, A.D. (1956). The physiology and biochemistry of diapause. A. Rev. Ent., 1 : 1-16.

Leius, K. (1961). Influence of food on fecundity and longevity of adults of *Itoplectis conquisitor* (Say) (Hymenoptera : Ichneumonidae). Can. Ent., 93 : 771-780.

Leius, K. (1963). Effect of pollen on fecundity and longevity of adult *Scambus buolianae* (Htg.) (Hymenoptera : Ichneumonidae). Can. Ent., 95 : 202-207.

Leonard, B.E. (1978). South Australian Year Book No. 13, 1978. Australian Bureau of Statistics, South Australian Office.

Leonard, D.E. (1970a). Effects of starvation on behaviour, number of larval instars and developmental rate of *Porthetria dispar*. J. Insect Physiol., 16 : 25-31.

Leonard, D.E. (1970b). Intrinsic factors causing qualitative changes in populations of *Porthetria dispar* (Lepidoptera : Lymantriidae). Can. Ent., 102 : 239-249.

LeRoux, E.J., Paradis, R.O. and Hudson, M. (1963). Major mortality factors in the population dynamics of the eye-spotted bud moth, the pistol casebearer, the fruit-tree leaf roller, and the

European corn borer in Quebec. In Population Dynamics of Agricultural and Forest Insect Pests (Ed. E.J. LeRoux,), Mem. ent. Soc. Can., 32 : 67-82.

Lewis, N.B. (1975). A hundred years of state forestry in South Australia : 1875-1975. Bull. Woods Forests Dep. S. Aust., No.22.

Li Peng-Fi and Larson, R.E. (1949). *Meligethes aeneus* as a factor in the musk melon breeding program in Pennsylvania. J. econ. Ent., 42 : 399.

Linde, R.J., Van Der (1971). The sailing flight of the caterpillars of the gypsy moth *(Lymantria dispar* L.) and the effect of the food plant on this phenomenon. Z. angew. Ent., 67 : 316-324.

Lloyd, D.C. (1940). Host selection by Hymenopterous parasites of the moth *Plutella maculipennis*. Proc. R. Soc.(B), 128 : 451-484.

Lloyd, D.C. (1956). Studies on parasite oviposition behaviour I. *Mastrus carpocapsae* Cushman (Hymenoptera : Ichneumonidae). Can. Ent., 88 : 80-89.

Lower, O.B. (1893). New Australian Lepidoptera. Trans. R. Soc. S. Aust., 17 : 146-185.

Madden, J.L. and Bashford, R. (1977a). The life history and behaviour of *Chlenias* sp., a geometrid defoliator of radiata pine in Tasmania. J. Aust. ent. Soc., 16 : 371-378.

Madden, J.L. and Bashford, R. (1977b). Population biology of *Chlenias* sp. a geometrid defoliator of *Pinus radiata* in Tasmania. J. Aust. ent. Soc., 16 : 379-388.

Maelzer, D.A. (1965). A discussion of components of environment in ecology. J. Theoret. Biol., 8 : 141-162.

Manly, B.F.J. (1976). Extensions to Kiritani and Nakasuji's method for analysing insect stage-frequency data. Res. Popul. Ecol., 17 : 191-199.

Markkula, M. (1953). Biologisch-okologische Untersuchungen uber die Kohlblattlaus, *Brevicoryne brassicae* (L.) (Hem., Aphididae). Suomal. elain -ja kasvit. Seur. van. kasvit. Julk., 15 : 1-113.

Mason, R.R., Beckwith, R.C. and Paul, H.G. (1977) Fecundity reduction during collapse of a Douglas-fir tussock moth outbreak in northeast Oregon. Environ. Entomol., 6 : 623-626.

Matthée, J.J. (1951) The structure and physiology of the egg of *Locustana pardalina* (Walk). Bull. Dep. Agric. Un. S. Afr., No. 316.

Matthews, E.G. (1976) Insect Ecology. Univ. Queensl. Press, St. Lucia. 226 pp.

Messenger, P.S. and Flitters, N.E. (1958) Effect of constant temperature environments on the egg stage of three species of Hawaiian fruit flies. Ann. ent. Soc. Am., 51 : 109-119.

Meyrick, E. (1891) Revision of Australian Lepidoptera. Proc. Linn. Soc. N.S.W., (2nd series), 6 : 581-678.

Miller, C.A. (1957) A technique for estimating the fecundity of natural populations of the spruce budworm. Can. J. Zool., 35 : 1-13.

Miller, D. (1919) The economic bearing of hymenopterous insects. N.Z.J. Agric., 19 : 201-208.

Miller, C.A. (1963). The analysis of female proportion in the unsprayed area. In The Dynamics of Epidemic Spruce Budworm Populations (Ed. R.F. Morris), Mem. ent. Soc. Can., 31 : 70-75.

Millett, M.R.O. (1944) Pollen shed of Monterey pine. Leafl. Commonw. For. Timb. Bur., Canberra, No. 59.

Milne, A. (1957) The natural control of insect populations. Can. Ent., 89 : 193-213.

Minko, G. (1965). Injurious insects affecting *Pinus radiata* (D. Don) in Ovens Plantation. Dip. For. Thesis, Vic. Board For. Educn.

Mirov, N.T. (1956). Photoperiod and flowering of pines. For. Sci., 2 : 328-332.

Mirov, N.T. and Stanley, R.G. (1959). The pine tree. A. Rev. Plant Physiol., 10 : 223-238.

Monro, J. (1972). 3. Terminal diapause in geometrid pupae - a new link in the endocrine chain? Insect Endocrines III, Academia Praha. (Reference as given in reprint).

Morgan, F.D. and Cobbinah, J.R. (1977). Oviposition and establishment of *Uraba lugens* (Walker), the gum leaf skeletoniser. Aust. For., 40 : 44-45.

Morris, R.F. (1951). The effects of flowering on the foliage production and growth of balsam fir. For. Chron., 27 : 40-57.

Morris, R.F. (1957). The interpretation of mortality data in studies on population dynamics. Can. Ent., 89 : 49-69.

Morris, R.F. (1959). Single-factor analysis in population dynamics Ecology, 40 : 580-588.

Morris, R.F. (1963). The development of a population model for the spruce budworm through the analysis of survival rates. In The Dynamics of Epidemic Spruce Budworm Populations (Ed. R.F. Morris), Mem. ent. Soc. Can., 31 : 30-32.

Morris, R.F. (1967). Influence of parental food quality on the survival of *Hyphantria cunea*. Can. Ent., 99 : 24-33.

Morris, R.F. and Miller, C.A. (1954). The development of life tables for the spruce budworm. Can. J. Zool., 32 : 283-301.

Muesebeck, C.F.W., Krombein, K.V., Townes, H.K., et al. (1951). Hymenoptera of America north of Mexico. U.S. Dep. Agric., Agric. Monogr. No. 2.

Nagatomi, A. (1972). Parasites of *Sesamia inferens* Walker at sugar cane field in Kagoshima Pref., Japan (Lep., Noctuidae). Mushi, 46 : 81-105.

Neilson, M.M. (1963). Disease and the spruce budworm. In The Dynamics of Epidemic Spruce Budworm Populations (Ed. R.F. Morris), Mem. ent. Soc. Can., 31 : 272-287.

Neumann, F.G. (1979). Insect pest management in Australian radiata pine plantations. Aust. For., 42 : 30-38.

Nicholson, A.J. (1933). The balance of animal populations. J. Anim. Ecol., 2 : 132-178.

Nicholson, A.J. (1954). An outline of the dynamics of animal populations. Aust. J. Zool., 2 : 9-65.

Obrycki, J.J. and Tauber, M.J. (1978) Thermal requirements for development of *Coleomegilla maculata* (Coleoptera : Coccinellidae) and its parasite *Perilitus coccinellae* (Hymenoptera : Braconidae). Can. Ent., 110 : 407-412.

Parker, H.L. (1931). *Macrocentrus gifuensis* Ashmead, a poly-embryonic braconid parasite in the European corn borer. Tech. Bull. U.S. Dep. Agric., No. 230.

Parrott, A.W. (1952). New Zealand Ichneumonidae. II Tribe Echthromorphini (Pimplinae). Trans. R. Soc. N.Z., 80 : 155-170.

Pielou, D.P. (1950). The effect of insecticide applications on the insect fauna and seed yield of alsike clover in Southern Ontario. Can. Ent., 82 : 141-160.

Pimentel, D. (1963). Natural population regulation and inter-species evolution. Int. Congr. Zool. XVI (Washington) 3 : 329-336.

Plank, H.K. and Cressman, A.W. (1934). Some predatory habits of the orange bagworm *Platoeceticus gloverii* Packard. Mon. Bull. Calif. Dep. Agric., 23 : 207-209.

Pottinger, R.P. and LeRoux, E.J. (1971). The biology and dynamics of *Lithocolletis blancardella* (Lepidoptera : Gracillariidae) on apple in Quebec. Mem. ent. Soc. Can., No. 77.

Puttler, B. (1967). Interrelationships of *Hypera postica* (Coleoptera : Curculionidae) and *Bathyplectes curculionis* (Hymenoptera : Ichneumonidae) in the eastern United States with particular reference to encapsulation of the parasite eggs by the weevil larvae. Ann. ent. Soc. Am., 60 : 1031-1038.

Rawlings, G.B. (1953). Insects of *Pinus radiata* forests in New Zealand. N.Z. For. Res. Notes, 1 : 1-19.

Readshaw, J.L. (1965). A theory of phasmatid outbreak release. Aust. J. Zool., 13 : 475:490.

Rogers, C.E. (1978). Sunflower moth : feeding behavior of the larva. Environ. Entomol., 7 : 763-765.

Salt, G. (1961). Competition among insect parasitoids. Symp. Soc. exp. Biol., 15 : 96-119.

Salt, G. (1968). The resistance of insect parasitoids to the defence reactions of their hosts. Biol. Rev., 43 : 200-232.

Salt, G. (1970). The Cellular Defence Reactions of Insects. Cambridge University Press. 118 pp.

Salt, G. (1976). The hosts of *Nemeritis canescens*, a problem in the host specificity of insect parasitoids. Ecol. Ent., 1 : 63-67.

Schmid, A. (1974). Untersuchungen zur Trans-ovum-Uebertragung des Granulosisvirus des Grauen Laerchenwicklers, *Zeiraphera diniana* (Lep. : Tortricidae) und Ausloesung der akuten Virose durch stressfaktoren. Entomophaga, 19 : 279-292.

Schneider, F. (1948). Beitrag zur Kenntnis der generations - verhältnisse und diapause rauberischer schwebefliegen (Syrphidae : Diptera). Mitt. schweiz. ent. Ges., 21 : 249-285.

Schneider, F. (1969). Bionomics and physiology of aphidophagous Syrphidae. A. Rev. Ent., 14 : 103-124.

Schoonhoven, L.M. (1969). Gustation and food-plant selection in some lepidopterous larvae. Ent. exp. appl., 12 : 555-564.

Schwerdtfeger, F. (1935). Studien über den Massenwechsel einiger Forstschädlinge. Z. Fort. -u. Jagdw., 67 : 15-38, 85-104, 449-482, 513-540.

Schwerdtfeger, F. (1941). Über die Ursachen des Massenwechsels der Insekten. Z. angew. Ent., 28 : 254-303.

Scott, C.W. (1960). *Pinus radiata*. F.A.O., Rome. 328 pp.

Scott, H.G. and Stojanovich, C.J. (1963). Digestion of juniper pollen by Collembola. Fla Ent., 46 : 189-191.

Sheldon, J.K. and Macleod, E.G. (1971). Studies on the biology of the Chrysopidae II. The feeding behavior of adult *Chrysopa carnea*. Psyche, 78 : 107-121.

Smith, B.C. (1961). Results of rearing some coccinellid larvae on various pollens. Proc. ent. Soc. Ont., 91 : 270-271.

Smith, H.S. (1916). An attempt to redefine the host relationships exhibited by entomophagous insects. J. econ. Ent., 9 : 477-486.

Smith, J.H. and Caldwell, N.E.H. (1947). Army worm and other noctuid outbreaks during 1946-47. Qd agric. J., 65 : 396-401.

Smith, K.D. and Popov., G.B. (1953). On birds attacking desert locust swarms in Eritrea. Entomologist, 86 : 3-7.

Solomon, M.E. (1949). The natural control of animal populations. J. anim. Ecol., 18 : 1-35.

South, P.M. (1978). Annual report 1976-1977. Woods and Forests Dep., South Australia.

Southwood, T.R.E. (1973). The insect/plant relationship - an evolutionary perspective. In Insect/Plant Relationships (Ed. H.F. Van Emden), pp. 3-30. Blackwell Scientific Publications, Oxford.

Southwood, T.R.E. (1978). Ecological Methods. Chapman and Hall, London. 524 pp.

Spector, W.S.(ed.) (1956). Handbook of Biological Data. Saunders, Philadelphia, 584 pp.

Spurr, S.H. (1964). Forest Ecology. Ronald Press, New York, 352 pp.

Stanley, R.G. and Linskens, H.F. (1974). Pollen : Biology, Biochemistry, Management. Springer-Verlag, Berlin, 307 pp.

Stary, P. (1970). Biology of Aphid Parasites. Junk, The Hague, 643 pp.

Steinhaus, E.A. (1958a). Stress as a factor in insect disease. Proc. X Intern. Congr. Ent. Montreal, 1956, 4 : 725-730.

Steinhaus, E.A. (1958b). Crowding as a possible stress factor in insect disease. Ecology, 39 : 503-514.

Steinhaus, E.A. and Dineen, J.P. (1960). Observations on the role of stress in agranulosis of the variegated cutworm. J. Insect Pathol., 2 : 55-65.

Stern, V.M. and Smith, R.F. (1960). Factors affecting egg production and oviposition in populations of *Colias philodice eurytheme* Boisduval (Lepidoptera : Pieridae). Hilgardia, 29 : 411-454.

Suckling, G.C., Backen, E., Heislers, A. and Neumann, F.G. (1976). The flora and fauna of radiata pine plantations in north-eastern Victoria. For. Comm. Vic. Bull. No. 24.

Sullivan, C.R. and Wellington, W.G. (1953). The light reactions of larvae of the tent caterpillars, *Malacosoma disstria* Hbn., *M. americanum* (Fab.), and *M. pluviae* (Dyar) (Lepidoptera : Lasiocampidae). Can. Ent., 85 : 297-310.

Tanada, Y. (1965). Factors affecting the susceptibility of insects to viruses. Entomophaga, 10 : 139-150.

Tanada, Y. (1976). Ecology of insect viruses. In Perspectives in Forest Entomology (Ed. J.F. Anderson and H.K. Kaya), pp. 265-283. Academic Press, New York.

Tauber, M.J. and Tauber, C.A. (1973). Seasonal regulation of dormancy in *Chrysopa carnea*. J. Insect Physiol., 19 : 1455-1463.

Temperley, M.E. (1930). Life history notes on the banana fruit-eating caterpillars (*Tiracola plagiata* Walk.). Qd agric. J. 33 : 251-261.

Thomas, J. (1971). Annual report 1969-1970. Woods and Forests Dep., South Australia.

Thompson, W.R. (1956). The fundamental theory of natural and biological control. A. Rev. Ent., 1 : 379-402.

Tindale, N.B. (1928). Species of pine-attacking *Chlenias* (Lepidoptera, family Boarmiidae). Rec. S. Aust. Mus., 4 : 43-48.

Titschack, E. (1937). Experimentelle Untersuchungen uber den Einfluss der Massenzucht auf das Einzettier. Z. angew. Ent., 23 : 1-64.

Titus, H. (1939). Practical feeding of poultry. U.S.D.A. Yearbook, pp. 839-843.

Townes, H. (1958). Some biological characteristics of the Ichneumonidae (Hymenoptera) in relation to biological control. J. econ. Ent., 51 : 650-652.

Townes, H.K. (1940). A revision of the Pimplini of eastern North America. Ann. ent. Soc. Am., 33 : 283-323.

Tsiropoulos, G.J. (1977). Reproduction and survival of the adult *Dacus oleae* feeding on pollens and honeydews. Environ. Entomol., 6 : 390-392.

Twine, P.H. (1971). Cannibalistic behaviour of *Heliothis armigera* (Hübn.). Qd J. Agric. Anim. Sci., 28 : 153-157.

Ullyett, G.C. (1936). Host selection by *Microplectron fuscipennis* Zett. (Chalcid. Hym.). Proc. R. Soc. (B), 120 : 253-291.

United States Department of Agriculture (1977). Western Forest Insects. Miscel. Publ. No. 1339.

Uvarov, B.P. (1931). Insects and climates. Trans. ent. Soc. Lond., 79 : 1-247.

Vago, C. (1963). Predispositions and interrelations in insect diseases. In Insect Pathology, An Advanced Treatise (Ed. E.A. Steinhaus), 1 : 339-379. Academic Press, New York.

Varley, G.C. and Gradwell, G.R. (1970). Recent advances in insect population dynamics. A. Rev. Ent., 15 : 1-24.

Varley, G.C., Gradwell, G.R. and Hassell, M.P. (1973). Insect Population Ecology. Blackwell Scientific Publications, Oxford, 212 pp.

Vinson, S.B. (1976). Host selection by insect parasitoids. A. Rev. Ent., 21 : 109-133.

Vivino, A.E. and Palmer, L.S. (1944). The chemical composition and nutritional value of pollen collected by bees. Arch. Biochem., 4 : 129-136.

Wallace, M.M.H. (1968). The ecology of *Sminthurus viridis* (Collembola). II. Diapause in the aestivating egg. Aust. J. Zool., 16 : 871-183.

Wallace, M.M.H. (1970a). Diapause in the aestivating egg of *Halotydeus destructor* (Acan : Eupodidae). Aust. J. Zool., 18 : 295-313.

Wallace, M.M.H. (1970b). The influence of temperature on post-diapause development and survival in the aestivating eggs of *Halotydeus destructor* (Acari : Eupodidae). Aust. J. Zool., 18 : 315-329.

Wallis, R.C. (1957). Incidence of polyhedrosis of gypsy-moth larvae and the influence of relative humidity. J. econ. Ent., 50 : 580-583.

Wallner, W.E. and Walton, G.S. (1979). Host defoliation: a possible determinant of gypsy moth population quality. Ann. ent. Soc. Am., 72 : 62-67.

Watanabe, H. (1971). Resistance of the silkworm to cytoplasmic-polyhedrosis Virus. In The Cytoplasmic-Polyhedrosis Virus of the Silkworm (Ed. H. Aruga and Y. Tanada,), 169-184. Univ. Tokyo Press, Tokyo.

Webb, J.W. and Moran, V.C. (1978). The influence of the host plant on the population dynamics of *Acizzia russellae* (Homoptera : Psyllidae). Ecol. Ent., 3 : 313-321.

Weddell, J.A. (1936). A recent army worm outbreak. Qd agric. J., 45 : 449-460.

Wellington, W.G. (1950). Effects of radiation on the temperatures of insectan habitats. Scient. Agr., 30 : 209-234.

Wellington, W.G. and Henson, W.R. (1947). Notes on the effects of physical factors on the spruce budworm *Choristoneura fumiferana* (Clem.). Can. Ent., 79 : 168-170, 195.

White, A., Handler, P. and Smith, E.L. (1973). Principles of Biochemistry. McGraw-Hill, New York. 1296 pp.

White, T.C.R. (1969). An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecology, 50 : 905-909.

White, T. C. R. (1974). A hypothesis to explain outbreaks of looper caterpillars with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand.Oecologia, 16 : 279-301.

White, T.C.R. (1976). Weather, food and plagues of locusts. Oecologia, 22 : 119-134.

Wigglesworth, V.B. (1972). The Principles of Insect Physiology. Chapman and Hall, London, 827 pp.

Will, G.M. (1957). Variations in the mineral content of radiata pine needles with age and position in tree crown. N.Z. J. Sci. Tech.(B), 38 : 699-706.

Wilson, F. (1968). Insect abundance : prospect. In Insect Abundance (Ed. T.R.E. Southwood), pp. 143-158. Blackwell Scientific Publications, Oxford.

Winston, P.W. and Bates, D.H. (1960). Saturated solutions for the control of humidity in biological research. Ecology, 41 : 232-237.

Wright, J.P., Marks, G.C. and Minko, G. (1967). The incidence of defect and its effect on merchantable volume in radiata pine (*Pinus radiata* D. Don). For. tech. Pap., For. Comm. Vic., 19 : 25-43.

Wright, T.W. and Will, G.M. (1958). The nutrient content of Scots and Corsican pines growing on sand dunes. Forestry, 31 : 13-25.