THE ECOLOGY OF THE GRAPE VINE MOTH

Phalaenoides glycine Lewin.

by

Charlma L. Cordingley B.Sc.Hons. (La Trobe)

A thesis submitted for the Degree of Doctor of Philosophy in the Faculty of Agricultural Science at the University of Adelaide.

Department of Entomology,
Waite Agricultural Research Institute,
University of Adelaide.

March 1977.

TABLE OF CONTENTS

SUMMARY

The Grape-Vine Moth, Phalaenoides glycine is a native Australian insect. It originally fed on native foodplants but is now a pest on the introduced grape vine.

Adults of the first generation emerged in spring. This generation was completed by December. The second generation began in mid-January and lasted through until March. Numbers in the second generation were always much higher than in the first generation. It is suggested that this was due to pupae remaining in diapause from one second generation to the next.

The sex ratio was male dominated at the beginning of the season but changed to female dominated at the end of the season. Overall the sex ratio was 1:1 but it differed both in time and space.

The distribution of eggs and larvae in the vineyard was patchy - at least in the second generation when population numbers were high. In the first generation numbers were always low and the distribution did not differ from random.

There was usually a pre-oviposition period of 1-2 days but this was not necessary for the production of fertile eggs. On emergence no eggs in the ovaries were mature. Maturation continued throughout the life of the moth. The rate of oviposition was greatest on the second day of oviposition.

The female reproductive tract and the reproductive states of moths of different ages were examined and used to determine the mated state of live and dead females in the field. Dead females realized most of their reproductive potential. The mean fecundity of moths was approximately 1100 eggs but rarely was this number laid. The optimum temperature for oviposition was approximately 25^{o}C. Food (adult) influenced fecundity

because it influenced longevity. In general heavier moths were more fecund. All eggs examined in the field were fertile and all female moths collected had mated.

Female moths do not oviposit at random. Most eggs were found on canes that trailed on the ground. Shelter was the main factor determining choice of oviposition site. Wind speed affected moth flight and thus, indirectly, oviposition. Moths flew at wind speeds of up to 11.0 km/hr.

The most important predator of Phalaenoides glycine was Oechalia schellenbergii. Bug population numbers fluctuated in a similar manner to those of larvae but the peak in bug numbers occurred approximately 3 weeks after the peak in larval numbers. Other predators included birds, spiders and robberflies.

The most important parasites were Tachinid flies. These attacked late instar larvae and in some seasons the rate of parasitism was as high as 64%. Other parasites were a small Eulophid wasp, Euplectrus agaristae, parasitic on the larval stages of P. glycine; Lissopimpla semipunctata and Ecthromorpha intricatoria, two Ichneumonids and Eurytoma sp., a Eurytomid, all pupal parasites.

Disease (a granulosis virus), flooding of the vineyard in winter, temperature, ploughing and fertility were not considered important causes of death.

In the egg stage there was considerable mortality due to failure of the eggs to hatch.

Phalaenoides glycine is an unusual insect in that it is a native insect which has seemingly deserted its native hosts and become a pest on the introduced grape vine. P. glycine larvae will survive on Hibbertia scandens (a native of New South Wales) but not on Hibbertia sp. native to South Australia. Adult moths which fed on vines as larvae "preferred"

vines for oviposition but would oviposit on Hibbertia if no vines were present. No native populations of P. glycine have been found in S. Aust. A possible explanation for this is that there are two races of P. glycine - one which still exists in eastern Australia on its native foodplants and another which became established on grape vines when they were introduced and has since spread to other parts of Australia with the vines.

Phalaenoides glycine has 2 generations per season at Langhorne Creek and a partial third generation in Adelaide. This difference in the number of generations per season can be explained by differences in temperature between the two localities.

Prepupae wander for some time before pupating. During this phase they are attracted to upstanding objects of different sizes over different distances. The effect of temperature on wandering prepupae and the speed of travel was investigated.

Phalaenoides glycine has a facultative diapause in the pupal stage. The intensity of diapause is very variable, some pupae taking little more than 30 days and others well over 100 days to emerge as adults. Diapause is induced in the early larval stages (by the 3rd instar). It is induced by low temperatures. Daylength and food by themselves have no effect on induction but they may reinforce the temperature stimulus.

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, contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

Charlma L. Cordingley.

March 1977.

ACKNOWLEDGEMENTS

I am grateful to my supervisors, Professor T.O. Browning and Dr. R. Laughlin, for their advice, criticism and encouragement throughout the thesis.

I am particularly grateful to Mr. Len Potts for permission to work on his vineyard at Langhorne Creek and for giving me a 'free hand' to do whatever I wanted there.

I would like to thank all my friends who helped with field work and who were forever collecting 'caterpillars' for me.

I am grateful to members of the Entomology Department who assisted with various aspects of the work and who helped to make my stay in Adelaide such a pleasant one.

My thanks also to Mr. B. Palk for preparing the figures and to Mrs. Pam Anderson for typing the thesis.

Finally my thanks to Brian for his help with proof-reading and for encouraging me to 'keep at it', especially during the final writing up period.

CHAPTER I

INTRODUCTION

The grape vine moth, Phalaenoides glycine, is native to Australia. It was previously known as Agarista glycinae and was first described by Lewin in 1822. At that time it was common in all the settled areas of Australia. Originally the larval stages fed on several species of native plants (see later) but spread to the grape vine when it was introduced into Australia.

Phalaenoides glycine is an interesting species to study ecologically because it is a native insect that has become a pest. It seems to have completely abandoned its original host plants since becoming established on grape vines.

This study was carried out to examine Phalaenoides glycine in the field and to investigate its relationships with the environment. Laboratory studies were made to aid the interpretation of field studies.

1.1 Pest Status

Phalaenoides glycine has been regarded as a pest since the 1880's. McCoy (1885) states that it was a pest in vineyards in Victoria and was responsible for extensive damage to the vines. French (1916) stated that it was a very common pest in Victoria and was present wherever there were vines. It was also regarded as a pest in New Zealand (Miller, 1940). Today it is widespread over most of Australia, wherever vines are grown (McLachlan, 1968; Fenner, 1961).

Much has been written about the voracious feeding of the larvae and their destruction of vine leaves, also young grape bunches (Anon., 1934, 1938, 1943, 1952, 1965, 1966; Fenner, 1961; McKeown, 1942; French, 1893; Zeck, 1955). It is also a pest in home gardens (Anon.,

1965; de Castella, 1927; Jones, 1967; Williams, 1946).

At Langhorne Creek, during the three years of this study, damage was always below the economic threshold, though some vines were completely stripped of leaves. This occurred only in late summer and early autumn, during the second generation of larvae, when population numbers were high. In the first generation numbers were always low with very little damage occurring to the vines. Damage becomes important only if it occurs early in the season or early in the second generation i.e. January - February and into March, when the grape bunches are forming. If the vines are defoliated at this stage they will produce new leaves rather than grapes. If, as usually happened, the damage occurs later in the season when the grapes are formed, the damage is not so important; however larvae may move into the bunches to feed if the foliage is depleted.

1.2 Phalaenoides glycine - The Insect

1.2.1 Adults : Most of the literature concerning Phalaenoides glycine includes a description of the adult and larval stages. These descriptions are often very brief, (Anon., 1934-1967; French, 1893; McKeown, 1942; Smith, 1938; Zeck, 1955), however detailed descriptions are given by Lewin (1822), McCoy (1885) and Miller (1940). Perhaps the most detailed is that of McCoy who describes in detail the colouring and pattern of the wings and body of both males and females.

The adults (Figure 1.1) are day-flying, gregarious moths with a lifespan of 2-3 weeks. They feed on nectar. They are mainly black in colour with white or yellowish markings on the wings (yellow in newly emerged moths fading to white in older moths). The abdomen is black with orange horizontal stripes and with an orange tuft on the tip.

Both Lewin (1822) and McCoy (1885) describe the male as having a

Figure 1.1 *Phalaenoides glycine* - adult.

yellow spot in the middle of the upper surface of the hindwing. They say that this spot is absent in the female. Miller (1940) states there are no spots or bands on the hindwings. However in this study it was found that many male moths did not have a yellow spot on the hindwings (although many did) and that many females (though not all) did have yellow spots. Further, some moths, both males and females, had very indistinct spots (Figure 1.2). Thus there is a gradation in both males and females from no spot to a very well defined spot on the upper surface of the hindwings.

Males and females can be distinguished only by examination of the tip of the abdomen. In general the tip is squarish in males and tapered in females.

Phalaenoides glycine moths have a characteristic fluttering flight. They do not glide. They are capable of flying to a height of 25 metres or more, often straight up. When disturbed they immediately fly on an erratic zig-zag course. This makes them difficult to catch.

On the abdomen of male moths a tuft of brush-like hairs, attached internally to a glandular body, was found. There was a tuft situated on each side of the fused 1st and 2nd abdominal segments (Figure 1.3). These tufts or hair pencils were normally retracted into the body but were extended prior to mating and when the moth was handled. Such structures have been found in many species of moths and butterflies (see Jacobson, 1974), for example in Danaid butterflies such as Danaus gilippus berenice (Pliske and Eisner, 1969; Schneider, 1975) and Lycorea ceres ceres (Meinwald et al., 1966) and in Noctuid moths such as Leucania sp. (Aplin & Birch, 1968), Phlogophora meticulosa (Birch, 1970; Eltringham, 1925) and Xylophasia monoglypha (Eltringham, 1925).

Hairpencils function in courtship to stimulate the female by the

Figure 1.2 Variations in hindwing markings

a = no spot

b = indistinct spot

c = well defined spot.

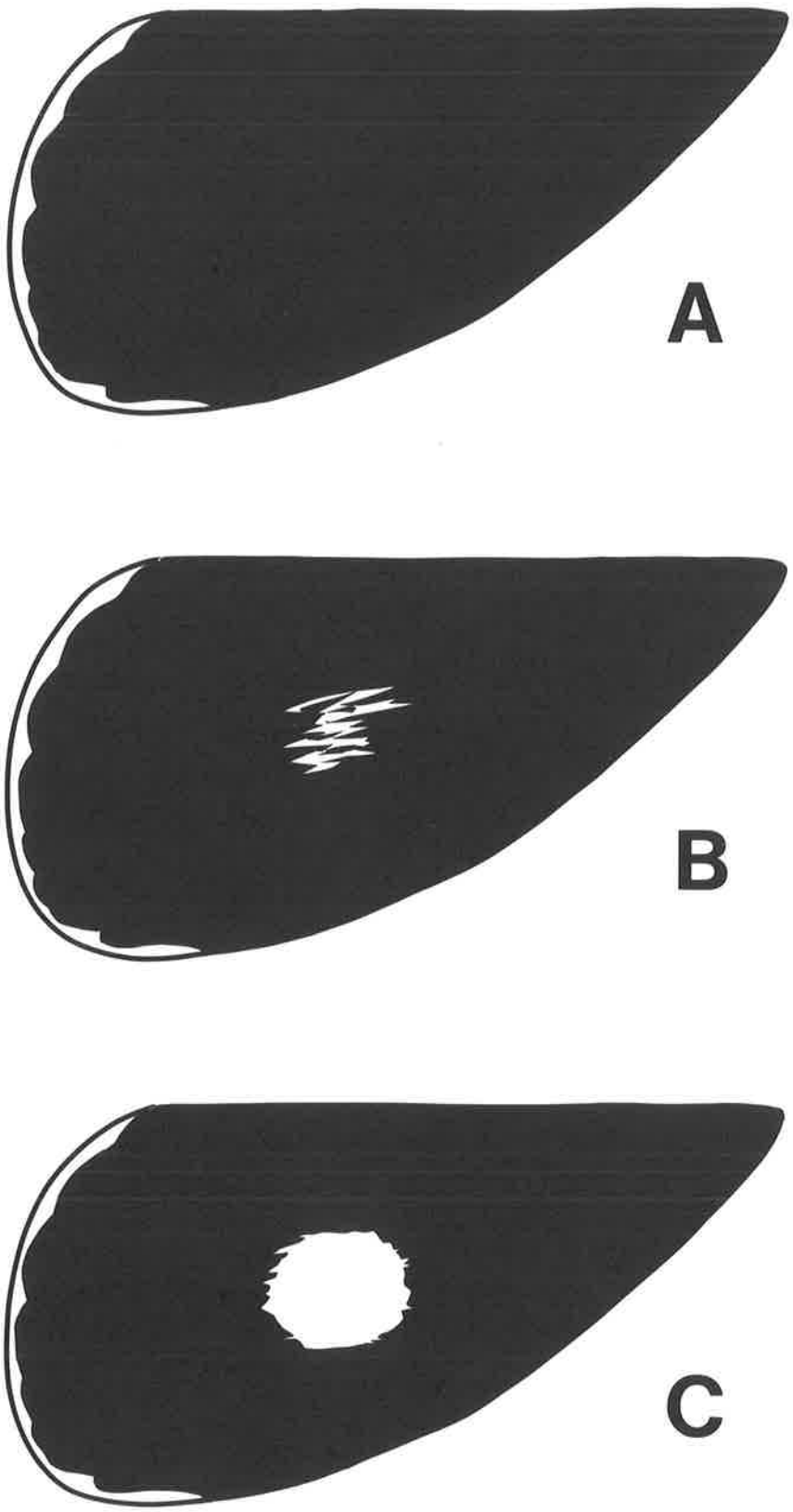
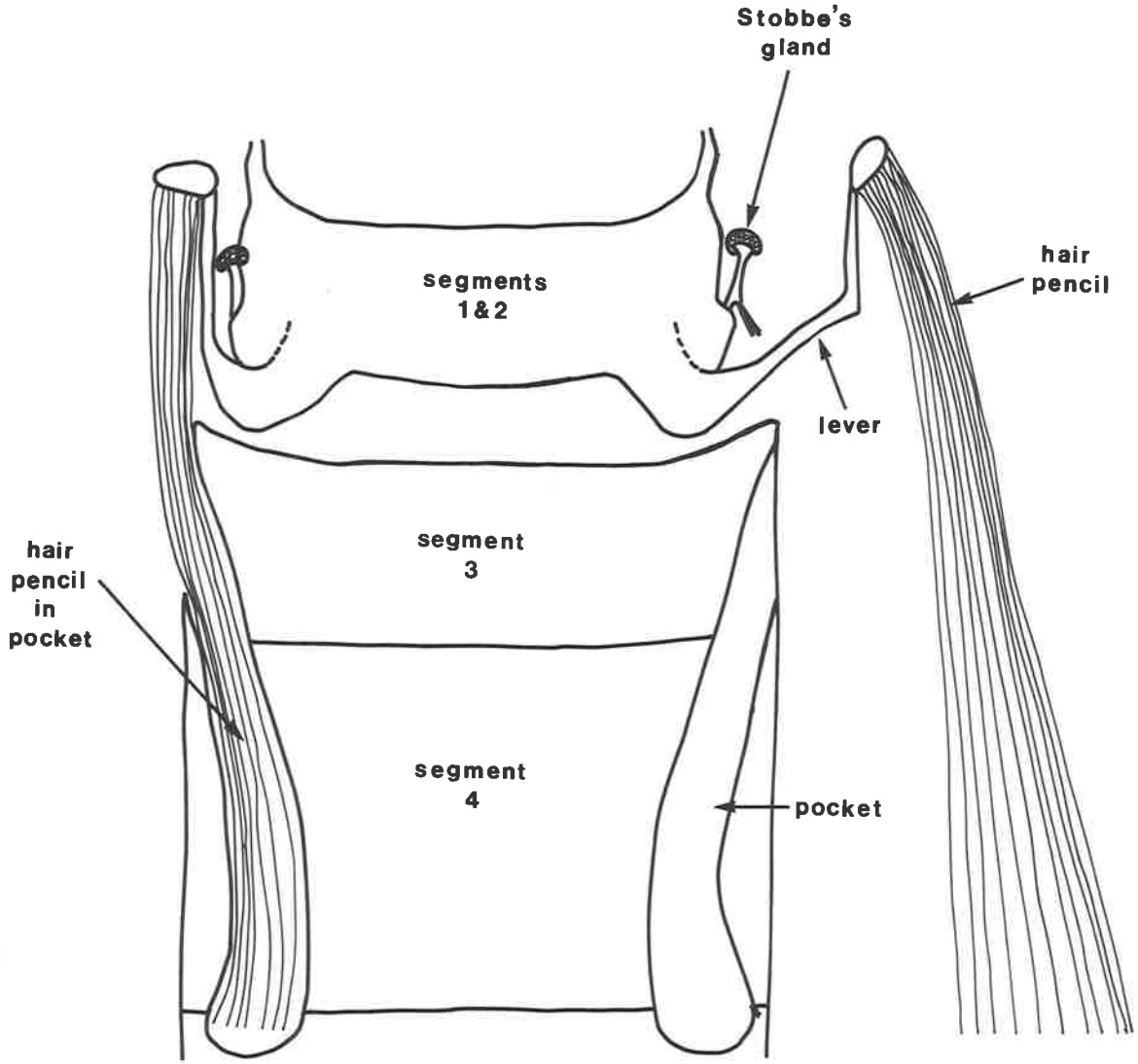

A
B
C

Figure 1.3 Diagram of hair pencils in male moths (ventral view).


Stobbe's gland
segments 1&2
hair pencil
lever
segment 3
hair pencil in pocket
segment 4
pocket

emission of pheromones. The chemical composition of some of these has been identified by Meinwald et al. (1969), Edgar & Culvenor (1974), Aplin & Birch (1968) and Birch et al. (1976).

1.2.2 Eggs : The eggs are rarely mentioned in the literature and are not described at all in early writings. French (1893) merely states that they are small and can be seen with the naked eye. McKeown (1942) describes them as being light blue in colour, darkening towards hatching. Other descriptions refer to them as pale yellowish or greenish in colour, becoming greyish before hatching (Anon., 1952; Zeck, 1955). In fact the eggs, when first laid are pale green. They are approximately 1 mm. in diameter, round in shape and finely ridged with a flat smooth bottom which is securely attached to the surface on which they are laid.

Under the microscope the development of the embryo can easily be followed because the outer shell of the egg is transparent. Within 24 hours of being laid, if the egg is fertile, brown specks appear. This is the beginning of embryonic development. The specks continue to form and congregate until the whole egg becomes brown in colour. Eventually the central dark patch becomes the head capsule and the rest is resolved into the body of the developing larva. A few hours before hatching, the head, mouthparts and body setae become very well defined. Just prior to hatching the egg becomes dry in appearance. The young larva chews a hole round the top of the egg-shell and emerges (it will continue to chew as long as the top of the shell rests on its head). Young larvae are pale and transparent with disproportionately large heads and prominent black setae.

1.2.3 Larvae : Descriptions of the larvae are very brief and general, most authors giving little more than the general colour (Anon.,

1934-1966; Bengston, 1961; Fenner, 1961; French, 1916; McKeown, 1942; Smith, 1938; Zeck, 1955). McCoy (1885) however gives a remarkably detailed and accurate description of the larval stages.

The first two instars are pale in colour with prominent setae. By the third instar they begin to develop the characteristic vine moth appearance. They are basically black with white stripes and markings and white setae. There is a patch of red dorsally on the penultimate abdominal segment. There are also red patches laterally at intervals along the length of the body. The head and thoracic legs are brown - the head with black markings. There is some variation in colour and although the basic pattern is the same, some larvae look darker or lighter than others.

There are 6 larval instars. The distribution of head-capsule widths is given in Figure 1.4, together with the mean head-capsule width for each instar. Although there is relatively little variation in these widths there was a large variation in the body size of the larvae. In particular larvae bred in the laboratory tended to be smaller than those found in the field. This size difference was most apparent in the 5th and 6th instars.

First instar larvae move by looping. Later instars crawl in the normal 'caterpillar' manner.

If disturbed, early instars drop from the leaf and hang suspended by a silken thread. Later instars do not do this but have other mechanisms to defend them from would-be predators and parasites. One such mechanism is to eject a green liquid from the mouth at the source of the disturbance. Fifth and sixth instars have a characteristic "aggressive" pose when threatened. The head is flung back so the thoracic legs point up and forwards (Figure 1.5). When in this position a fleshy tubercle is protruded from an opening in the ventral neck region.

Figure 1.4 Distribution of the head capsule widths for the 6 larval instars. (Mean widths are given beside each instar).

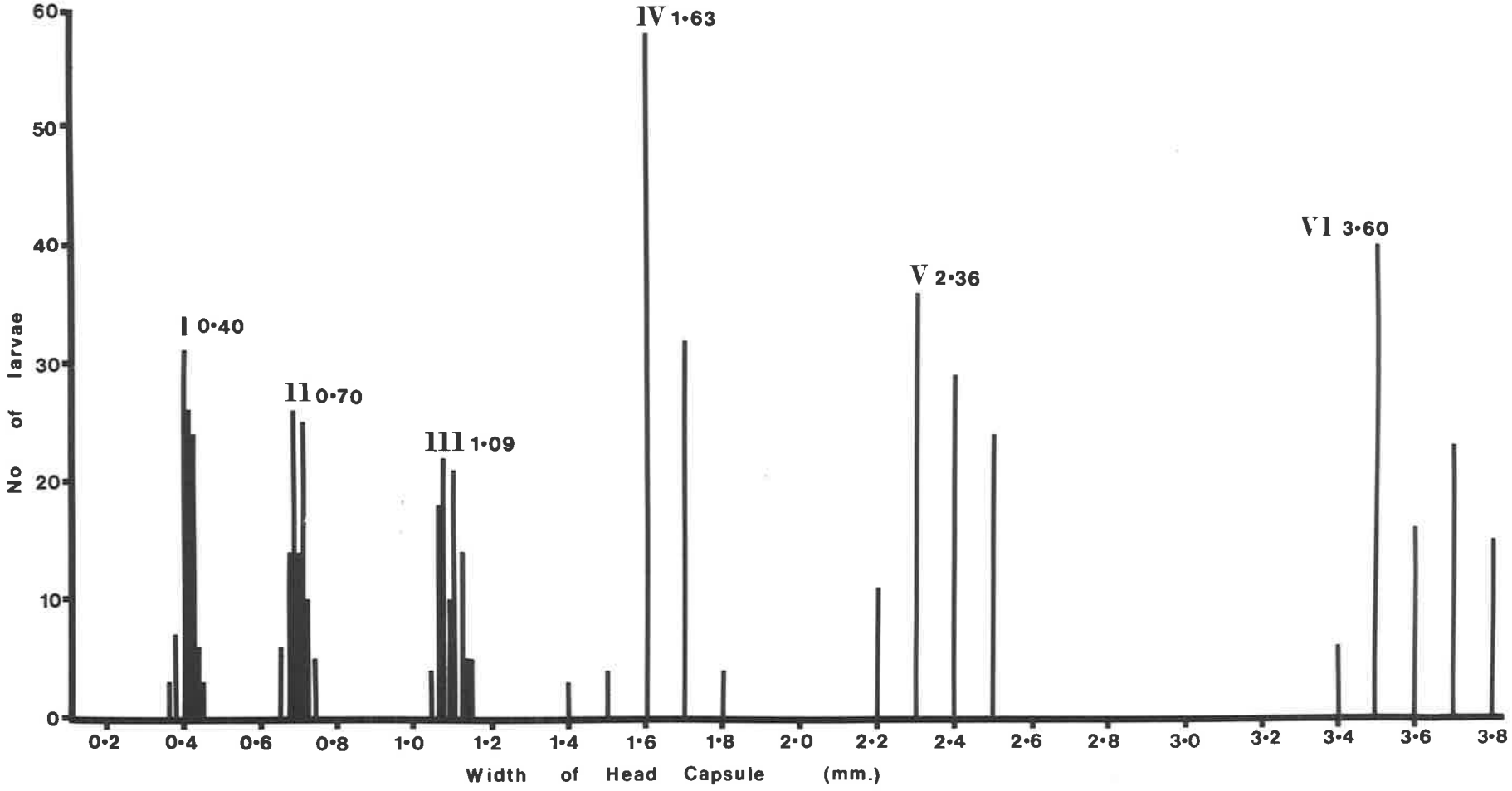
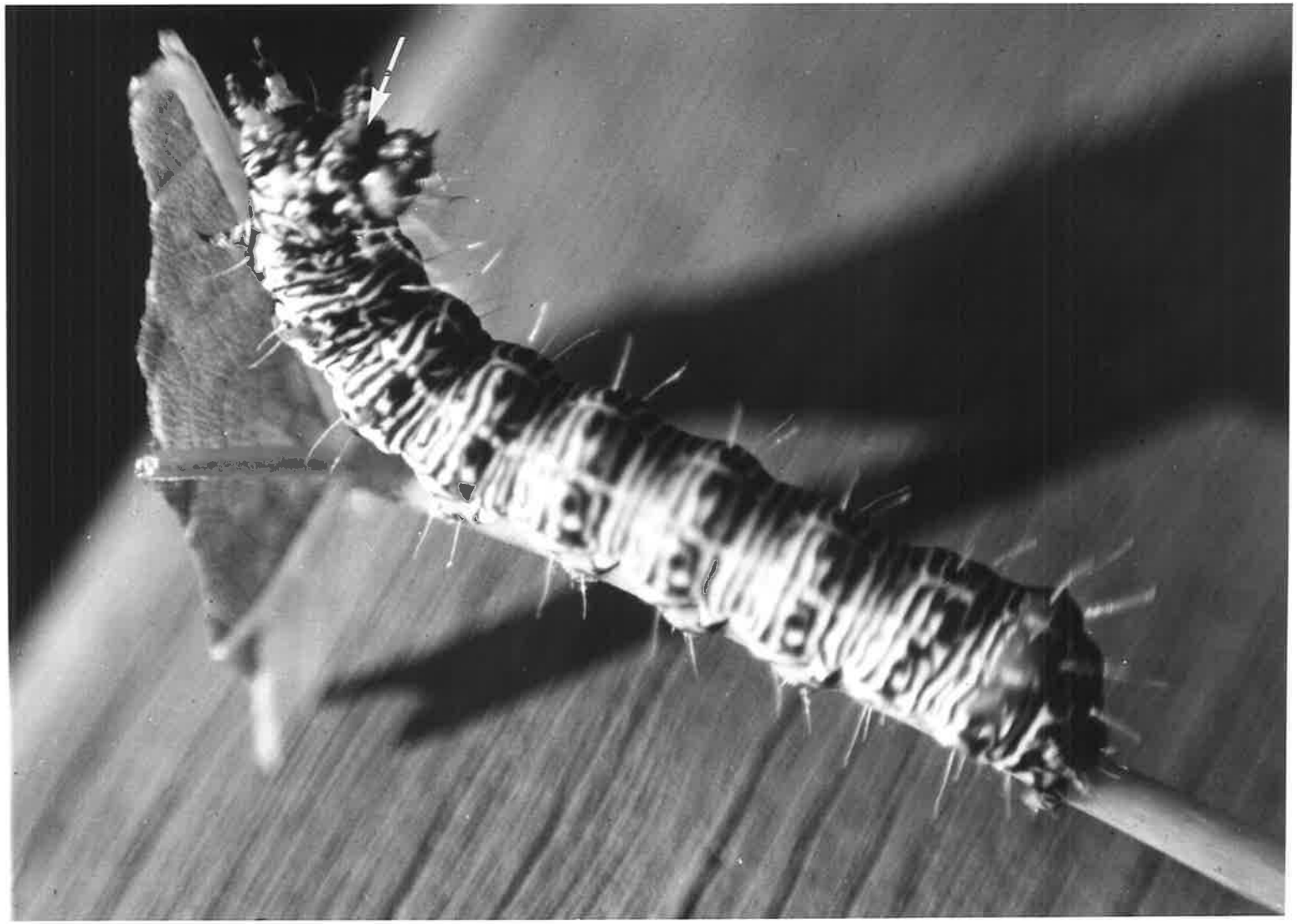

60
50
40
30
20
10
0
No of larvae
I 0·40
II 0·70
III 1·09
IV 1·63
V 2·36
VI 3·60
0·2
0·4
0·6
0·8
1·0
1·2
1·4
1·6
1·8
2·0
2·2
2·4
2·6
2·8
3·0
3·2
3·4
3·6
3·8
Width of Head Capsule (mm.)

Figure 1.5 Sixth instar larva in typical aggressive pose. Arrow points to the osmateria.



In other Lepidoptera, e.g. Papilio anactus, a similar structure, called an "osmateria", is present and this usually emits an unpleasant odour (McCubbin, 1971). Possibly the structure in Phalaenoides glycine is similar and serves to discourage enemies.

In the field and in the laboratory larvae displayed a 'head-flicking' behaviour. This did not seem to be a response to movement because it occurred even when the air and leaves were quite still. It usually occurred when larvae were kept in crowded conditions in small containers, but it was also observed in the field on vines with large numbers of larvae (but where there was no contact between larvae). Only 5th and 6th instars were involved. Head-flicking behaviour could also be induced by making a loud buzzing sound near the larva. Myers et al. (1976) mention that Green (1974) interpreted this as antagonistic behaviour important in larval spacing. Green cited evidence that showed the frequency of head-flicking was related to the density of larvae.

1.2.4 Prepupae : Nothing has been mentioned in the literature about prepupae. When 6th instar larvae stop feeding they leave the vines and wander for some time in search of a pupation site. The prepupa has a translucent appearance. After 1-2 days of wandering, the body shortens and thickens and the animal loses the ability to crawl. Eventually the larval skin splits to reveal the pupa beneath.

1.2.5 Pupae : Lewin (1822) described the pupating larva as spinning a slight web on the stem of the food-plant in which to pupate. McCoy (1885) disputed this, saying he could not understand Lewin describing it thus, as in fact it formed a cocoon structure in the soil. Monro (1957) comments on this discrepancy. Later descriptions consolidate McCoy's statement. In fact prepupae construct a 'cell', within which they pupate,

out of whatever materials are available at the pupation site. It is not a woven silk cocoon like those found in some Lepidoptera, although it is lined with a small amount of silk.

Larvae will pupate in the soil or in any cracks or crevices they can find. They will also pupate in leaves and debris on the ground (Anon., 1943, 1965; Zeck, 1955). McKeown (1942) states that pupae can be found naked in rubbish on the soil surface. In this study naked pupae were occasionally found on exposed areas of soil. Pupae were often found in cracks in fence posts and in the vine stems (Figure 1.6).

The pupae are reddish-brown in colour. Prior to emergence of the adult they turn dark brown and the pattern of the wings can be seen through the pupal skin. Pupae are approximately 24 mm in length but their size varies considerably according to their feeding habits in the larval stages. In general female pupae are heavier than males. The mean weight of 20 female pupae was 0.41 g (range 0.29-0.65 g) and that of 20 male pupae was 0.38 g (range 0.25-0.51 g).

Pupae of the second or third generation diapause over winter. Figure 1.7 shows the differences between male and female pupae.

1.3 Topics Discussed in This Thesis

1.3.1 Seasonal History

The first moths of the season appear about the time the vines come into leaf. This is usually in late September or early October depending on the locality, the weather and other factors. There are 2 or 3 generations per year over summer, again depending on the locality. The last generation begins in February or March and lasts until late April or early May. The seasonal history is discussed in Chapter 2.

Figure 1.6 Pupa in pupation cell in wood from a fence post.

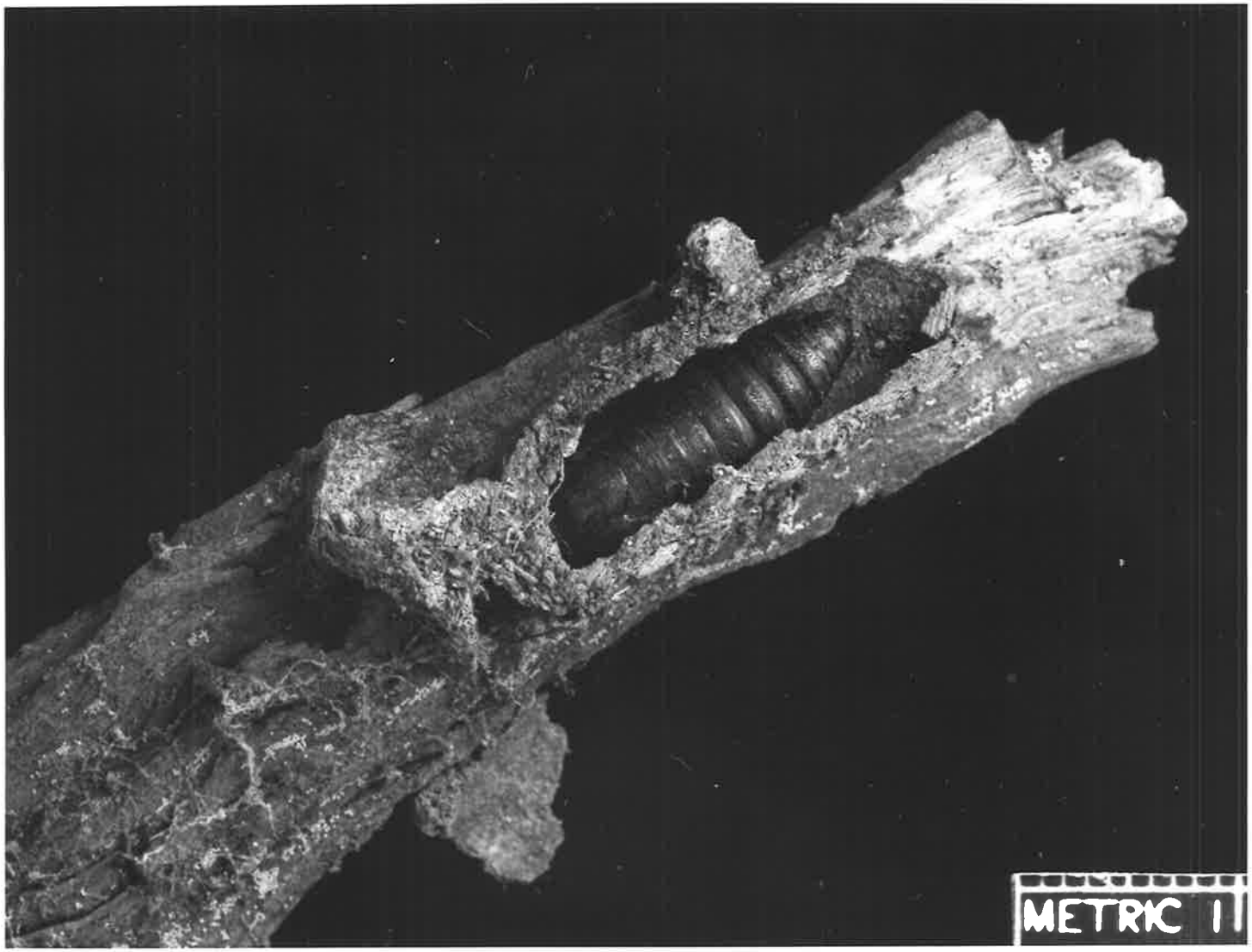
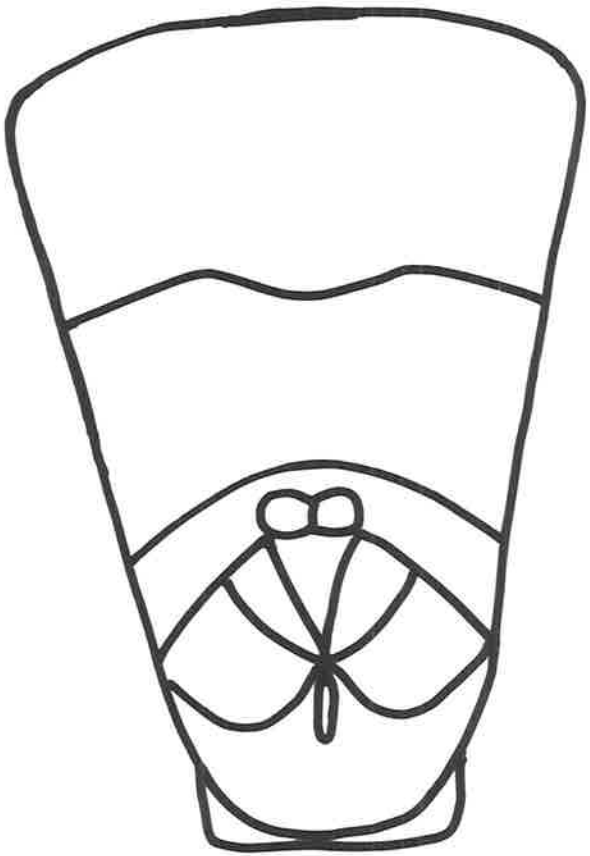
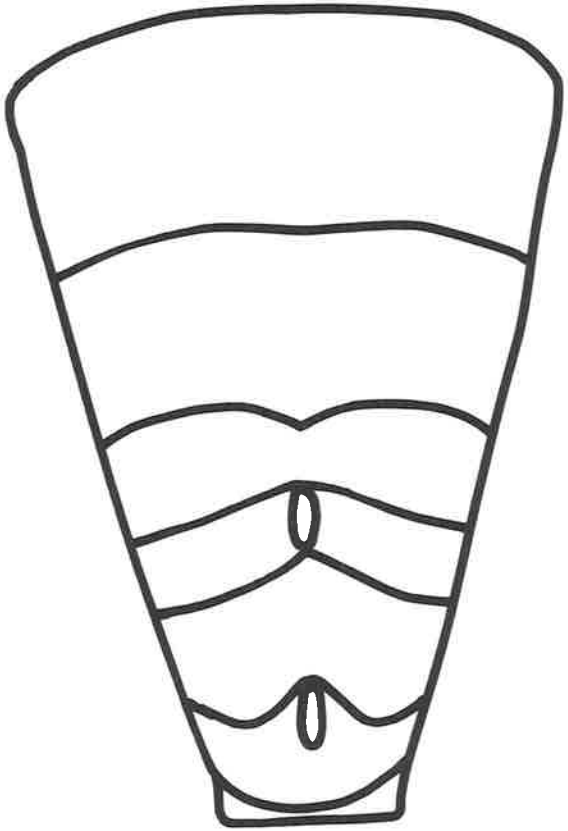

METRIC 1

Figure 1.7 Diagram of sex differences between male and female pupae.



♂



♀

1.3.2 Population Numbers

Changes in population numbers were followed through three seasons at Langhorne Creek. In each season in the first generation numbers were very small compared with those of the second generation. Numbers were never high enough to cause economic damage. They were very low in 1973-74, very high in 1974-75 and lower in 1975-76. The field area and sampling methods are described in Chapter 2 together with details of the population fluctuations.

1.3.3 Distribution in the Vineyard

When outbreaks of Phalaenoides glycine occur in vineyards and numbers are high enough to cause defoliation of the vines, defoliation occurs in patches and not uniformly over the whole vineyard. Usually nearly every vine had larvae on it but only some had enough to cause complete defoliation. Studies carried out to investigate the distribution of larvae in the vineyard, (Chapter 3), have confirmed that they occur in patches. This patchiness is most likely caused by the oviposition habits of the female moth. Although the female lays eggs singly, frequently several are laid close together on the same vine or the same part of the vine and this causes a 'clump' of larvae on that vine. If the numbers of larvae in the vineyard are high this behaviour is enough to cause patchy defoliation. Factors that affect oviposition behaviour and therefore affect the distribution of larvae are discussed in Chapter 5. The distribution of eggs was also studied but they were harder to find than larvae when numbers were low.

1.3.4 Oviposition

Moths mate within 1-2 days after emergence from the pupa. There is a pre-oviposition period during which they feed and the eggs begin to

mature in the ovaries. Each female contains approximately 1000 eggs. However rarely is thus number laid, particularly in the field where conditions are often unsuitable for oviposition. Even so, each female, given the right conditions, is capable of producing a large population of larvae. Mating behaviour, rate of oviposition, fecundity and the anatomy of the female reproductive tract are discussed in Chapter 4.

Early in the season, when the vines are just beginning to grow, eggs are found close to the main stem underneath the leaves and on suckers lower down on the vine. Later in the season eggs are mainly found on long trailing canes touching the ground. These are the most sheltered places in the vineyard. Eggs were never found high up on top of the vines. As the larvae grow, however, they move up to feed on the tops of the vines. Oviposition behaviour, oviposition sites and factors that influence their choice are discussed in Chapter 5.

1.3.5 Mortality

Large outbreaks of Phalaenoides glycine are not common. This is surprising considering the reproductive potential of the female moth and the fact that there is an abundant food supply. Thus there must be some factor or factors operating to keep numbers down. There is a considerable amount of information available on the natural enemies of Phalaenoides glycine. Among the predators are three species of bug, but only one of these, Oechalia schellenbergii is important. This is a Pentatomid bug which preys on the larval stages of the vine moth. Other predatory bugs are Cuspicona sp. (French, 1893) and Cermatulus nasalis (Anon., 1947), but neither of these were found in this study. Chisholm (1933) mentions the ladybird Halyzia galbula as a 'possible' predator of vine moth larvae. The ladybirds were not seen actually feeding on the larvae but the larvae all disappeared from leaves on which ladybirds were present.

Also predatory on vine moth larvae are several birds, namely the Bronze Cuckoo, Chrysococcyx basalis, the Pallid Cuckoo, Cuculus pallidus (French, 1893) and the Magpie Gymnorhina tibicen.

There are a number of parasites of the pupal and larval stages. Among these are flies and wasps of several species. The most important are the Tachinidae. There are two species, Exorista sp. cf. sorbillans and Winthemia sp. They are both internal parasites. There are four species of wasp, a Eulophid, Euplectrus agaristae, an external parasite of the larval stages and Ecthromorpha intricatoria, Lissopimpla semipunctata and Eurytoma sp. parasitic on the pupae.

Other mortality factors include a granulosis viral disease and occasional predators such as spiders and robber flies. Mortality is discussed in Chapter 6.

1.3.6 Native Foodplants

Phalaenoides glycine originally fed on several native species of plants. These included Hibbertia sp., Glycine sp. and Gnaphalium luteoalbum. Now it is found almost exclusively on grape vines, fuchsias and ornamental creepers such as Glory Vines, Vitis kaempferi, and Virginia Creepers, Vitis quinquefolia. The relationships between Phalaenoides glycine and its native foodplants were investigated in this study (Chapter 7). It was hoped that a population would be found in the wild and large areas were searched, but none was found. Wild populations may occur in other parts of Australia but not in South Australia.

1.3.7 Miscellaneous studies

Several interesting questions arose from this study and some of these were examined in detail. One concerned the wandering phase of the larvae just before pupation. During this phase larvae are attracted to

large upright objects yet they do not seem to be influenced by the canopy of vine foliage overhead. This behaviour was studied in the laboratory to determine factors that influence larvae in the wandering phase (Chapter 8).

The rate of development of larvae at different temperatures was also studied and is discussed in Chapter 8.

Phalaenoides glycine has a facultative pupal diapause that enables it to survive over winter when there are no leaves on the vines. It is very variable in intensity, some pupae taking 100 or more days to emerge as adults and others taking 40-50 days (non-diapausing pupae complete development in approximately 30 days).

The onset of diapause is caused by low temperatures and short daylengths such as occur in autumn. The quality of food eaten may also influence the onset. Some aspects of diapause are discussed in Chapter 8.

CHAPTER 2

POPULATION STUDIES

Fluctuations in the population numbers of *Phalaenoides glycine* were studied at Langhorne Creek over a three year period from 1973-1976 inclusive. Before discussing these it is necessary to describe the seasonal history of the insect and also the sampling site and methods.

2.1 Seasonal History

There has been some difference of opinion as to the number of generations per season. Monro (1957) stated that there were 3 generations per season in Adelaide. Fenner (1961) stated there were 2 in South Australia while McCoy (1885) stated there were 2 or 3. At Langhorne Creek there are two, from September to April, while in Adelaide there are three, the third being partial.

The adult moths emerge for the first generation after winter, about the time the vines first come into leaf. Bud-burst varies from place to place and moth emergence usually varies with it, however the first moths are usually seen about mid-September. Second generation moths first appear in mid-January. Males tend to emerge first at the beginning of each generation (Section 2.5). Table 2.1 gives the dates of the first recording of adults, eggs and larvae in weekly samples. It also gives the dates of the peaks in numbers and the date of disappearance of each stage.

Weather conditions on the sampling days affected moth flight but if moths were not flying they could usually be found amongst the vines or on weeds around the edges of the vineyard. Thus their presence or absence could be recorded despite adverse weather.

Laboratory studies showed that female moths begin oviposition

TABLE 2.1 Seasonal history of *Phalaenoides glycine* for the seasons 1973-76 at Langhorne Creek.

Generation	Date of first sighting	Date of peak in numbers	Date by which stage absent
MOTHS			
(1) 1973-74	*	2/10/73	20/11/73
(1) 1974-75	10/9/74	28/10/74	28/11/74
(1) 1975-76	12/9/75	16/10/75	11/12/75
(2) 1973-74	*	5/2/74	14/3/74
(2) 1974-75	16/1/75	13/2/75	27/3/75
(2) 1975-76	13/1/76	3/2/76	25/3/76
EGGS			
(2) 1973-74	5/2/74	1/3/74	21/3/74
(2) 1974-75	13/2/75	27/2/75	27/3/75
(2) 1975-76	28/1/76	12/2/76	11/3/76
LARVAE			
(1) 1973-74	11/10/73	30/10/73	6/12/73
(1) 1974-75	31/10/74	19/11/74	20/12/74
(1) 1975-76	27/10/75	4/11/75	4/12/75
(2) 1973-74	17/1/74	21/2/74	18/4/74
(2) 1974-75	20/2/75	6/3/75	1/5/75
(2) 1975-76	3/2/76	26/2/76	15/4/76

* = beginning of flight missed.

3-5 days after emergence. Thus eggs should be present soon after the first moths appear. However due to the sampling technique used (Section 2.3) eggs were not found in the field until their numbers were quite high. Similarly each stage in the life cycle was not recorded in the samples until numbers were high.

Extensive sampling for eggs was not carried out during the first generation each year, except in 1975-76, as the numbers were low. In the second generations numbers were considerably higher.

From laboratory studies (Section 8.2) the duration of the egg stage is from 4-14 days depending on temperature, so it can be assumed that larvae are present in the field 1-2 weeks after the appearance of the first eggs.

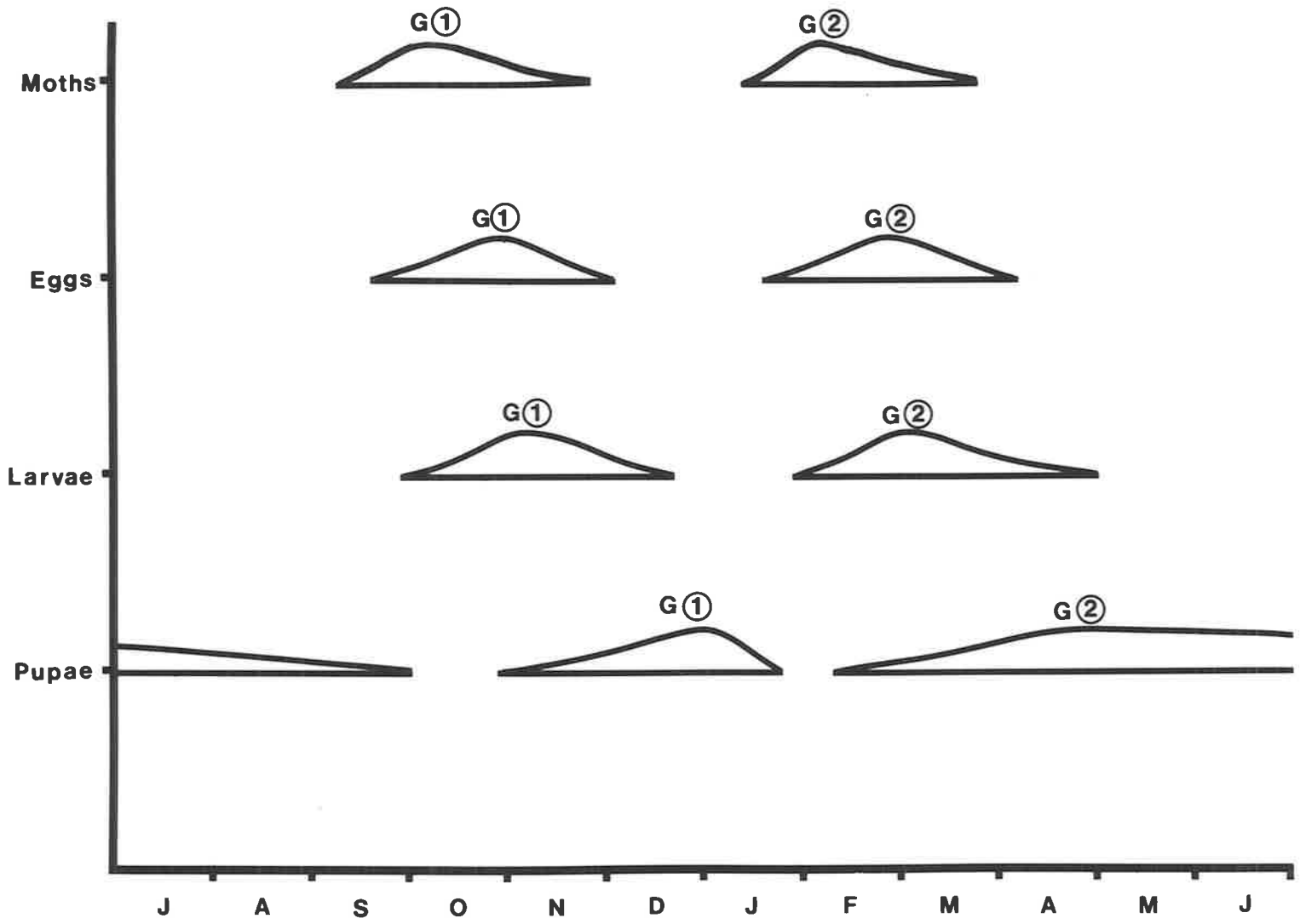
Pupae were not sampled regularly either throughout the season or over the winter period. From laboratory studies the first larvae would be expected to pupate 2-6 weeks after their appearance in the vineyard. The duration of the larval stage is very dependent on temperature and thus for larvae of the first generation, when temperatures in the field are low (average temperatures for October and November are 14.6 and 15.1^{o}C), the development time will be longest. For larvae in the second generation which occurs over summer, development will be much faster (average temperatures for February and March are 19.7 and 21.1^{o}C). Thus pupae of the first generation would be present in the field from about the beginning of November through to mid-January and those of the second generation from mid-February to the following September or October. The seasonal cycle is summarized in Figure 2.1. The two generations are discrete.

The previous description has been concerned with populations at Langhorne Creek. Observations were also made in Adelaide, both at the Waite Institute and in North Adelaide. There are three generations per

Figure 2.1 Seasonal cycle of Phalaenoides glycine.

G(1) = generation 1.

G(2) = generation 2.


Moths
Eggs
Larvae
Pupae
G①
G②
G①
G②
G①
G②
G①
G②
J
A
S
O
N
D
J
F
M
A
M
J

season in Adelaide, the third being only partial and overlapping with the second generation. The vines in Adelaide come into leaf about 2-3 weeks earlier than those at Langhorne Creek and coinciding with this the moths also emerge several weeks earlier. The first moths usually appear in late August - early September for the first generation and at the end of December for the second generation. The moths of the third or partial third generation appear in April. The larvae that result from eggs laid by these moths usually do not have time to complete their development before the vine leaves drop in late autumn. This generation is smaller than the second generation because most second generation pupae over-winter and emerge the following spring. The occurrence of a third generation is linked with diapause which varies greatly in intensity (Section 8.3.4). At Langhorne Creek a third flight of moths has not been observed.

2.2 Sampling Area

Field work was carried out at Langhorne Creek, approximately 70 km south-east of Adelaide (Figure 2.2). The Langhorne Creek area is a small wine-growing district isolated from other wine producing areas, the nearest being the Southern Vales district, 35 km away. Approximately 260 hectares of vines are grown here under a system of winter flood irrigation which is used to supplement the inadequate annual rainfall of 355 mm (S.A. Year Book, 1975).

The area of vines used in this study was small, on the edge of a much larger patch of vines (Figure 2.3). It consisted of 832 vines arranged in 13 rows (i.e. 64 vines per row). Within each row the vines were trellised along a single strand of wire approximately 1 metre above the ground. Small wooden posts were situated at intervals along the rows and between each of these posts were 4 vines. At the ends of the rows

Figure 2.2 Map of South Australia showing the major wine growing areas (dotted).

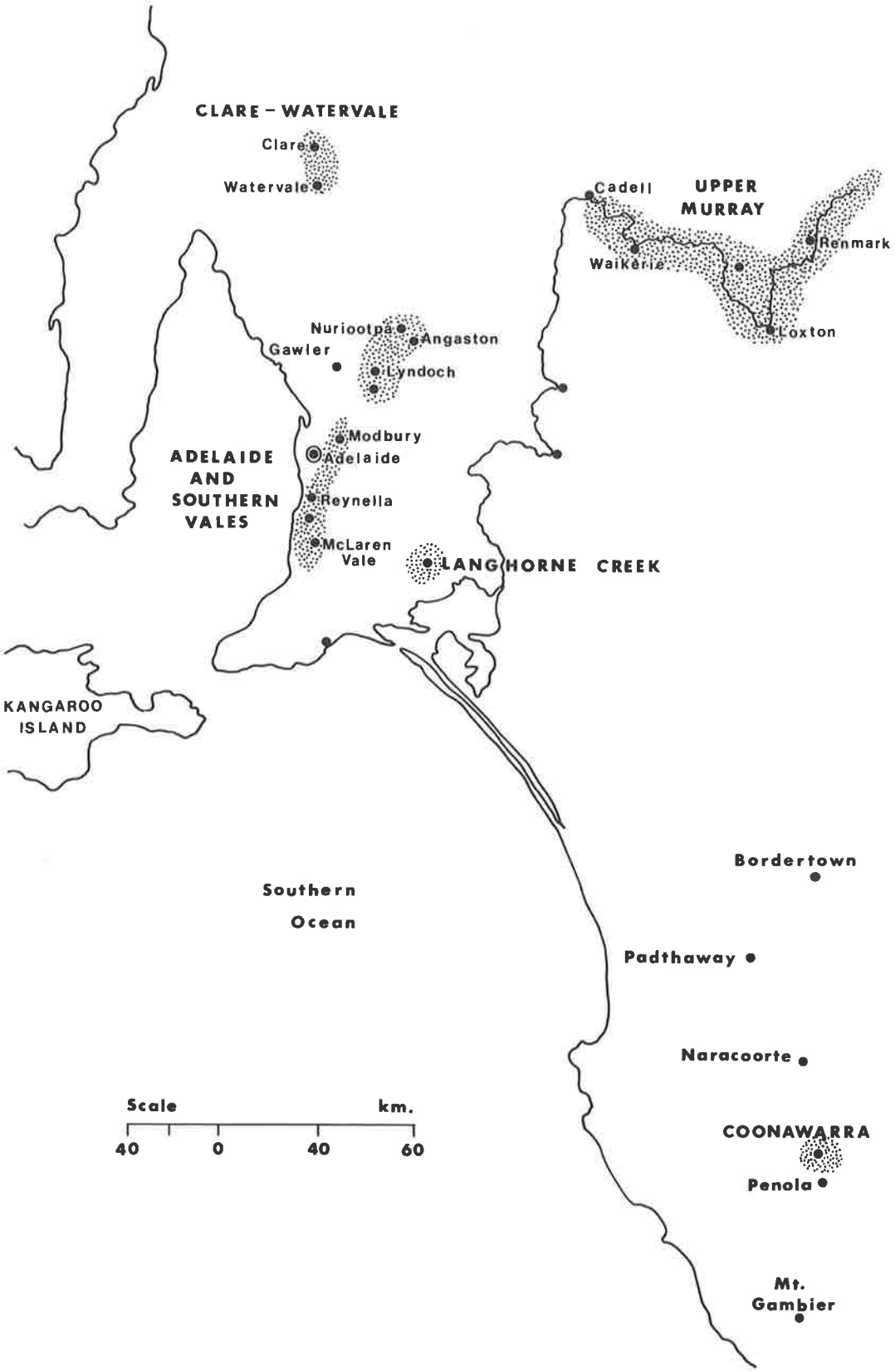
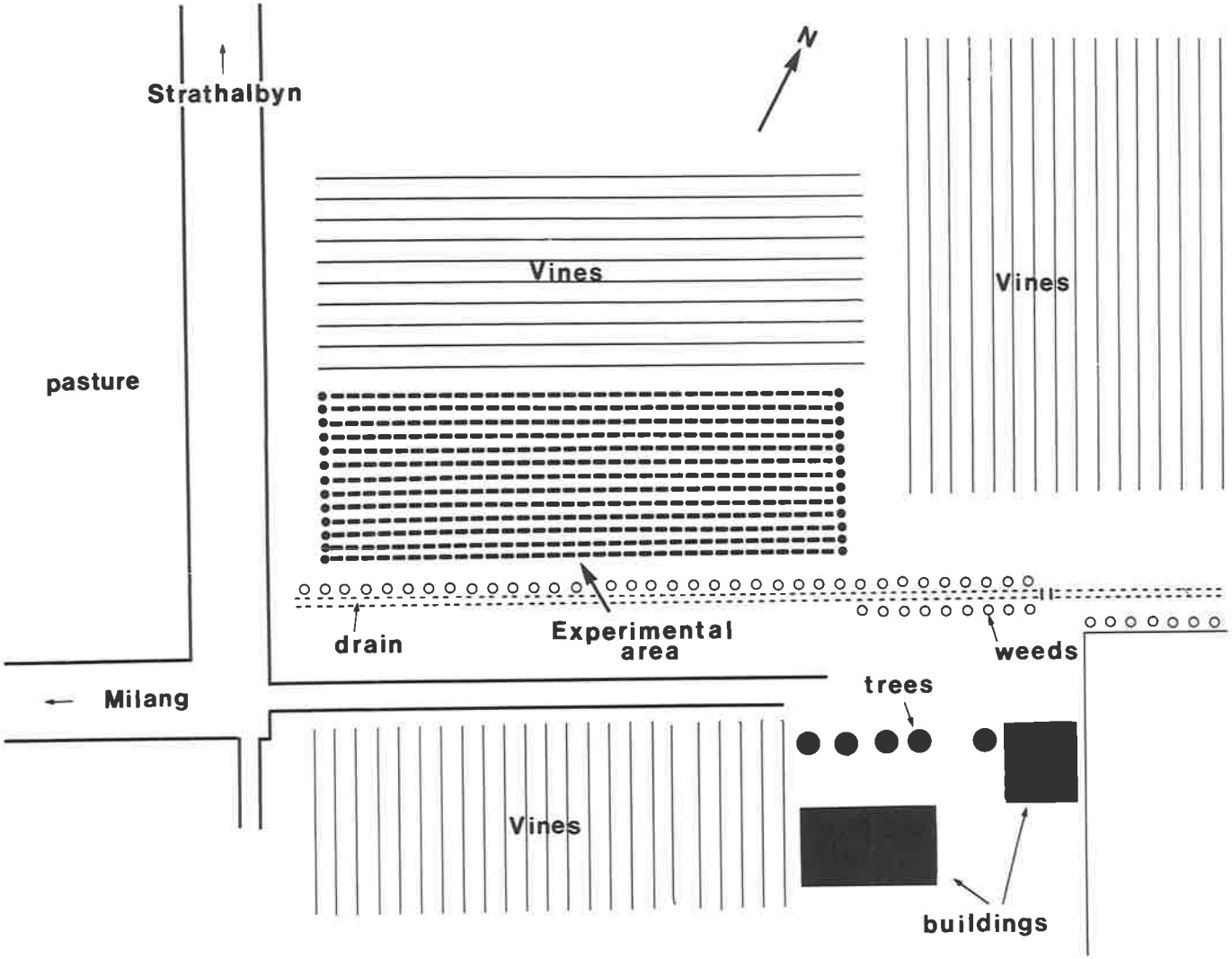

CLARE – WATERVALE
Clare
Watervale
Cadell
UPPER MURRAY
Renmark
Waikerie
Loxton
Nuriootpa
Angaston
Gawler
Lyndoch
Modbury
Adelaide
ADELAIDE AND SOUTHERN VALES
Reynella
McLaren Vale
LANGHORNE CREEK
KANGAROO ISLAND
Southern Ocean
Bordertown
Padthaway
Naracoorte
COONAWARRA
Penola
Mt. Gambier
Scale
km.
40
0
40
60

Figure 2.3(a) General view of the vineyard at Langhorne Creek in late summer.

Figure 2.3(b) Diagram of vineyard at Langhorne Creek showing the experimental area.


Strathalbyn
N
Vines
Vines
pasture
drain
Experimental area
weeds
Milang
trees
Vines
buildings

were large strainer posts approximately 30 cm. in diameter. The rows of vines ran in a southeast - northwest direction. On two sides of this area were more rows of vines of varying ages and along the other two sides were weeds (Fennel, Foeniculum vulgare and some Salvation Jane, Echium plantagineum), and grass (Figure 2.4). The vines in the area studied were about 4 years old when the study began.

Outside the vineyard were several large Eucalypt trees. These are mentioned because they were the resting and feeding site of many moths. Moths were also seen feeding on the weeds around the vineyard.

This particular patch of vines was chosen because when the study began at the end of the 1972-73 season the vines were very badly damaged by vine-moth larvae. At that time the damage here was much greater than in other parts of the vineyard (Section 3.1).

Some field work was done in other areas, namely the Barossa Valley, the Southern Vales and the Clare - Watervale district but this work did not involve continuous observations.

2.3 Sampling Methods

2.3.1 Adults

To obtain data on the relative numbers and changes in numbers of adults in the vineyard from week to week, the following method was devised. A section of the vineyard bordered on two sides by rows of vines and measuring 3 m x 10 m was marked out. On sampling days the moths flying in this area were counted for a five minute period every hour. This gave an estimate of the number of moths/area flying each week. These figures however were only for moths flying and gave no indication of how many moths were present on the vines themselves or visiting the foodplants. As this information was essential if a meaningful estimate

Figure 2.4 Weeds surrounding the experimental vineyard at Langhorne Creek.

of the number of moths in the vineyard was to be obtained, it was necessary to sample adults in these areas. So the moths resting on the vines were sampled, by an observer walking up one row of vines and down the next (this took approximately 5 minutes) and counting the number of moths seen on the vines or disturbed from them. The moths feeding on weeds on the edges of the vineyard were also sampled by walking along the edges for a 5-minute period and counting the number of moths. Thus moths were sampled flying over and resting on the vines and feeding on weeds for three consecutive 5-minute periods each hour.

Emergence traps (Figure 2.5) were placed over some of the large posts at the ends of the vine rows. These posts were known to accommodate a large number of pupae and therefore the emergence of adults at the beginning of each generation could be followed.

It was necessary to catch moths to obtain data on the sex ratio throughout the season as their sex could not be determined unless they were caught and examined. Female moths were kept and dissected to obtain information about the reproductive state at different times in the season. Moths flying over vines and resting among them as well as moths feeding on weeds around the vineyard were caught with a net. Females were kept and dissected.

2.3.2 Eggs and Larvae

Similar methods were employed to sample both eggs and larvae. The vines studied were arranged in 13 rows of 64 vines each and within each row, vines were divided into lots of 4 separated by posts, so a type of stratified-random sampling was adopted. Each row was numbered as was each vine in the row. During the first season (1973-74) 40 vines were sampled for eggs and larvae each week. These were chosen from 5 rows (8 vines from each row) and the 5 rows were randomly selected in such a

Figure 2.5 Emergence trap at Langhorne Creek.

way that 2 of the 5 sampled the previous week were chosen together with 3 rows that had not been selected the previous week. Once the 5 rows to be sampled were decided, the vines within these rows were chosen. Each row was divided into 8 groups, each group containing 8 vines. Then one vine was chosen at random from each of the 8 groups in the row. This procedure was used for each of the 5 rows.

In the 1974-75 season when other field work was in progress, sampling 40 vines each week became too time-consuming and the number of vines sampled was reduced to 20 per week.

Early in the season when the vines were just coming into leaf, the whole vine was searched and the number of larvae found recorded. Later, as the vines grew, half-vines were sampled and by the time the vines had completed their growing phase, ¼ vines were sampled (one quarter was randomly selected for sampling). The same methods were used for sampling eggs which were sampled only during the second generations (except in 1975-76).

2.3.3 Pupae

The prepupae leave the vines and 'wander' for some time before pupation (Section 8.1). It was not possible to follow them through to the completion of this wandering phase. It is known that they pupate in the ground, in cracks in vine stems and in fence posts, particularly the strainer posts at the ends of the rows (Figure 2.6). These areas were searched in order to estimate the size of the pupal population. Because the vines on which this work was done were relatively young, their stems were not yet thick or gnarled and so were not suitable as pupation sites. Thus they were not included in the sampling.

Soil samples were taken from the following sites as it was not known

Figure 2.6 Prepupae (arrowed) crawling into cracks and holes in a strainer post at the end of a row of vines.

exactly where in the soil pupae were to be found:

(1) Between the rows of vines

(2) Underneath the vines

(3) Around the base of the vine stems

(4) Around the base of the posts

(5) Outside the vineyard.

In each case, 20 x 20 cm square samples were dug at two depths in the soil, 0-7 cm and 7-18 cm. Later the deeper sampling was discontinued because pupae were not found at this depth. The soil was sieved with a 7 mm. mesh sieve and the numbers of pupae recorded.

Sampling pupae in the fence posts proved difficult as the cracks were deep and the pupae cemented in, one on top of the other, making them hard to remove. The main problem was in determining whether the pupae (alive or dead) were the product of the previous generation or earlier ones as there was a build-up of pupae over many years. This problem was not overcome. However samples were taken from the posts that provided information for parasite studies. Twenty live pupae were dug out of the posts each week and brought back to the laboratory to complete their development. Records were kept of parasites emerging.

2.4 Population Numbers

2.4.1 Adults

Adults were sampled in both first and second generations in the 1974-75 and 1975-76 seasons. Table 2.2 shows the mean numbers of moths in the different sampling sites in 1975-76. Table 2.3 shows the overall mean and peak numbers.

In the first generation in the 1975-76 season the mean and peak numbers were greater than in 1974-75. However it should be noted that the peak number in 1974-75 (and therefore the overall mean) is misleading

TABLE 2.2 Mean numbers of moths/5 minutes at each sampling site in the 2nd generation, 1975-76 season.

Date	Sampling Site		
	over vines	among vines	on weeds
20/1/76	3.3	7.3	2.3
28/1/76	10.5	10.0	7.0
3/2/76	32.8	39.0	20.5
12/2/76	23.0	23.0	11.0
19/2/76	38.0	25.8	27.3
26/2/76	10.5	8.0	1.0
4/3/76	2.0	6.5	2.0
11/3/76	0.0	0.5	0.0

TABLE 2.3 Mean and Peak Numbers of moths/minute/area at Langhorne Creek.

Season	Generation	No. moths/min./area	
		mean	peak
1974-75	(1)	0.75	1.67
1975-76	(1)	1.04	4.05
1974-75	(2)	31.46	98.50
1975-76	(2)	6.97	18.45

because in the middle of the sampling period weather conditions were unsuitable for flight and therefore low numbers were recorded. This effect of weather on flight and therefore on oviposition can be followed through to the larval population in the first generation (see later). Figure 2.7 shows the fluctuation in the numbers of moths throughout each first generation. In 1974-75 (see above) it was assumed that the peak in numbers occurred sometime late in October. In the following season the peak occurred earlier, about the middle of October. Figure 2.8 shows the fluctuations throughout the second generation each season. Population numbers in 1974-75 were far greater than in 1975-76. In 1975-76 two peaks occurred approximately 2 weeks apart in early and mid-February. The peak in 1974-75 occurred in mid-February. It is unfortunate that samples were not taken during the period 23/1/75 to 13/2/75 as the population may not have increased as steadily as shown but may have produced a smaller peak during this time which was expected from the larval population fluctuations in the previous generation (see later).

2.4.2 Eggs

Eggs were often difficult to find, especially if they had been laid less than twenty-four hours before sampling, in which case they were still green in colour and well camouflaged on the leaves. Consequently the mean number of eggs is an underestimate.

The mean and peak numbers of eggs/¼ vine for the years 1973-76 are given in Table 2.4. Figures are only given for the second generation each year. Eggs were not sampled in the first generations, (except in 1975-76), because population numbers were low and eggs were difficult to find. Even in 1975-76 no eggs were found on most sampling days (the mean over this first generation was 0.13 with a peak of 0.4 eggs/¼ vine). Over the three years the population numbers fluctuated from being fairly low, to rising

Figure 2.7 Mean number of moths/minute/area (and standard errors) in the first generation in 1974-75 and 1975-76.

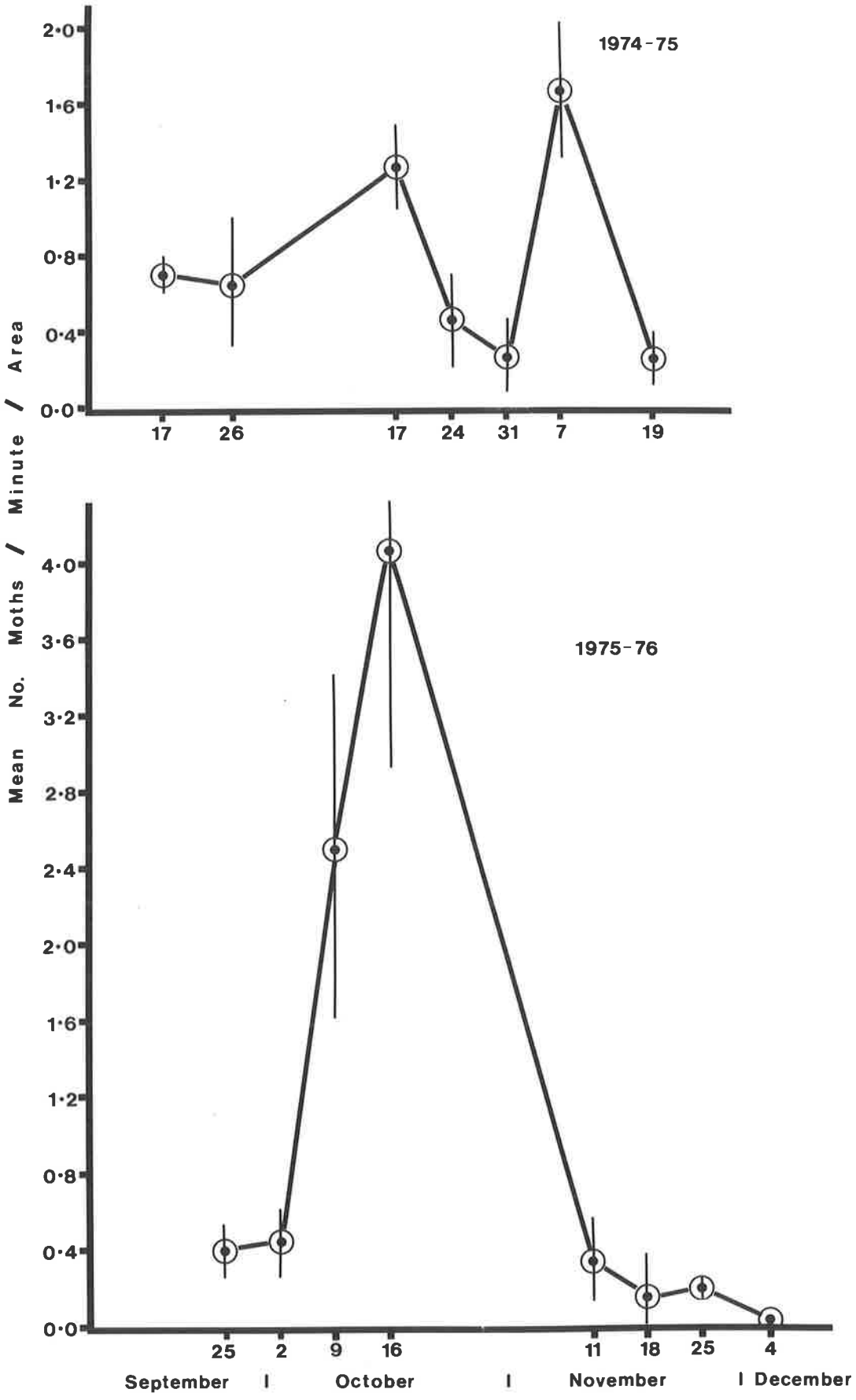

1974-75
2·0
1·6
1·2
0·8
0·4
0·0
17
26
17
24
31
7
19
Mean No. Moths / Minute / Area
1975-76
4·0
3·6
3·2
2·8
2·4
2·0
1·6
1·2
0·8
0·4
0·0
25
2
9
16
11
18
25
4
September
October
November
December

Figure 2.8 Mean number of moths/minute/area (and standard errors) in the second generation in 1974-75 and 1975-76.

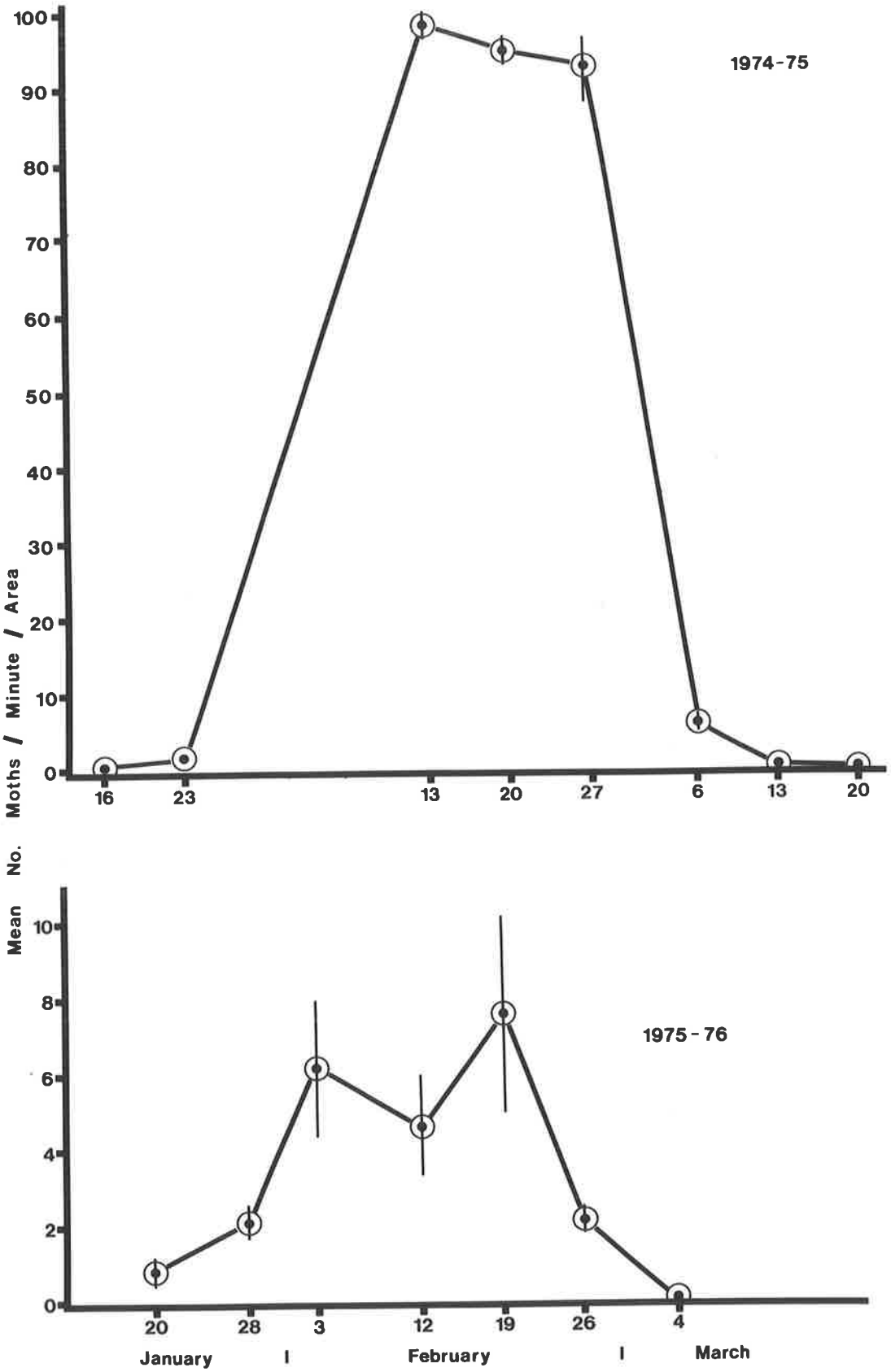

1974-75
Moths / Minute / Area
100
90
80
70
60
50
40
30
20
10
0
16
23
13
20
27
6
13
20
1975-76
Mean No.
10
8
6
4
2
0
20
28
3
12
19
26
4
January
February
March

TABLE 2.4 Mean and Peak numbers of eggs/¼ vine in the 2nd generations 1973-76.

Season	Generation	No. eggs/¼ vine Mean	Peak
1973-74	(2)	3.35	6.83
1974-75	(2)	4.65	10.50
1975-76	(2)	4.20	10.63

TABLE 2.5 Mean, peak and range numbers of larvae/¼ vine at Langhorne Creek.

Season	Generation	No. larvae/¼ vine Mean	Peak	Range
1973-74	(1)	0.33	0.90	0-4
1974-75	(1)	0.29	0.55	0-4
1975-76	(1)	0.59	0.95	0-6
1973-74	(2)	2.80	7.20	0-45
1974-75	(2)	14.65	21.81	0-86
1975-76	(2)	7.96	24.83	0-110

to a peak and then beginning to decline again.

Figure 2.9 shows the fluctuations in egg numbers in the second generation each season. The peak in population numbers occurred earlier in each successive season, the peak in 1973-74 about the beginning of March, that in 1974-75 at the end of February and that in 1975-76 earlier still, about the beginning of February. The general fluctuation in population numbers was similar in both 1974-75 and 1975-76 and occurs over a similar length of time. That of 1973-74 is slightly different. However the whole generation is spread over much the same length of time as in the other two seasons.

2.4.3 Larvae

The results of larval sampling are presented in Table 2.5. The distribution was patchy (Chapter 3) and some vines had no larvae or very few while others had numbers far greater than the mean. Thus the range of values is shown also.

The figures for the first generation each year show the population of larvae was low in 1973-74, slightly lower in 1974-75 and higher in 1975-76. However in each case the numbers were small in comparison with those in the second generation. A small first generation is typical of Phalaenoides glycine.

Figures 2.10 and 2.11 show the mean number of larvae/¼ vine plotted against time. The peak in the 1973-74 first generation occurred at the end of October, that in 1974-75 in mid-November and in 1975-76 in early November. In the second generations, in 1973-74 the peak was reached towards the end of February. In 1974-75 it was later, in early March and in 1975-76 earlier again at the end of February.

The fluctuations from year to year in the first generation reflect the population trends in the second generation of the previous season.

Figure 2.9 Mean number of eggs/¼ vine (and standard errors) in the second generation 1973-76.

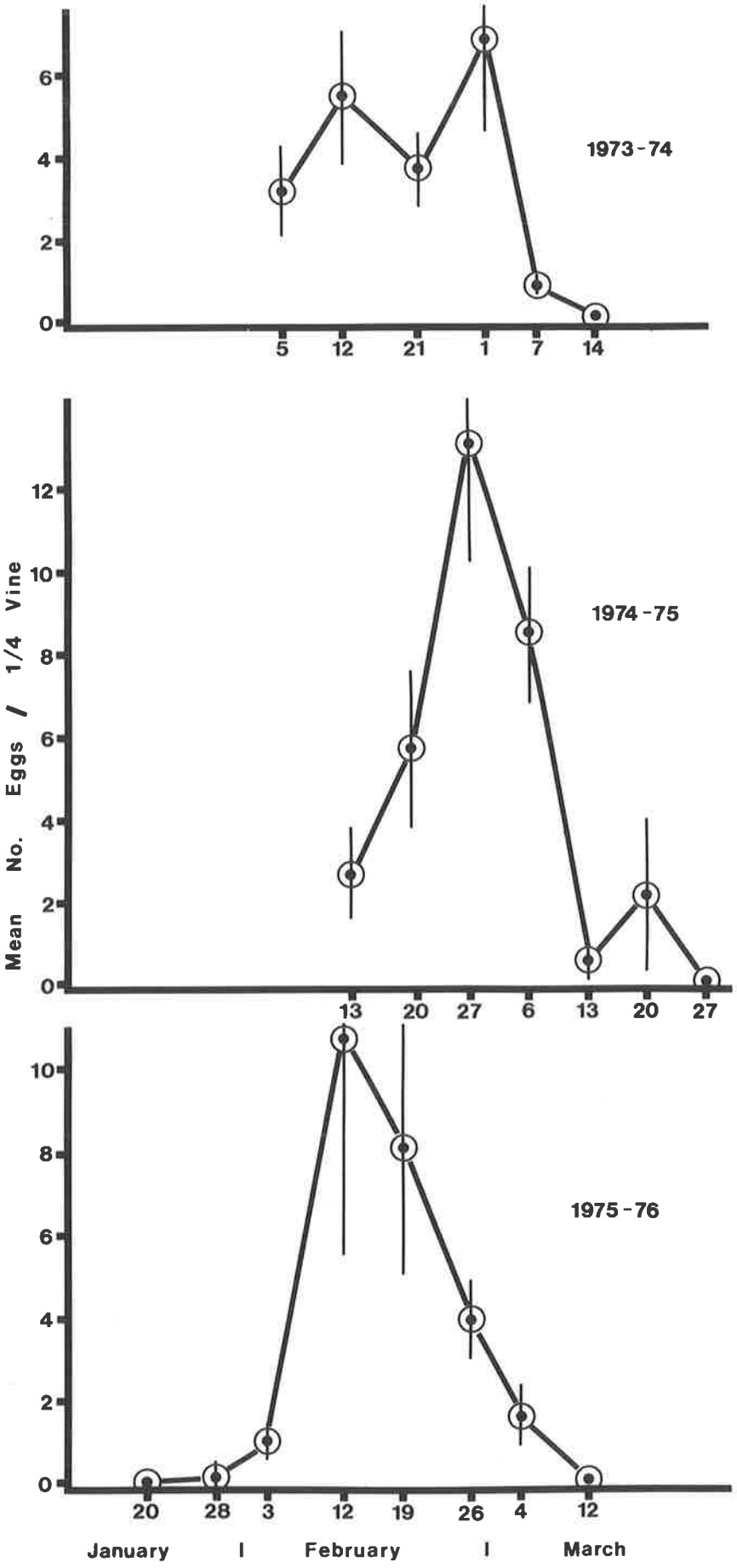

1973-74
1974-75
1975-76
Mean No. Eggs / 1/4 Vine
0
2
4
6
8
10
12
5
12
21
1
7
14
13
20
27
6
13
20
27
20
28
3
12
19
26
4
12
January
February
March

Figure 2.10 Mean number of larvae/¼ vine (and standard errors) in the first generation 1973-76.

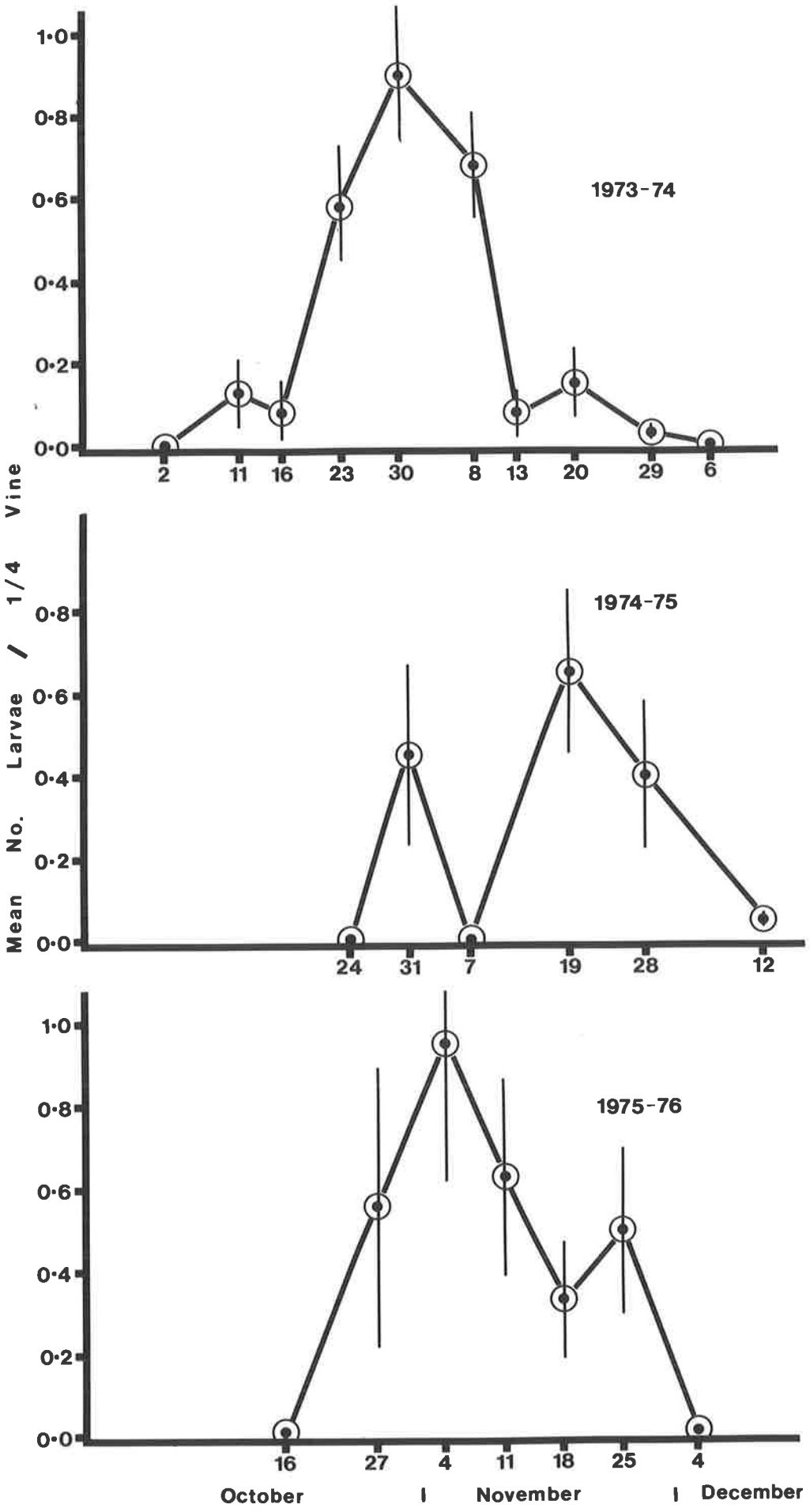
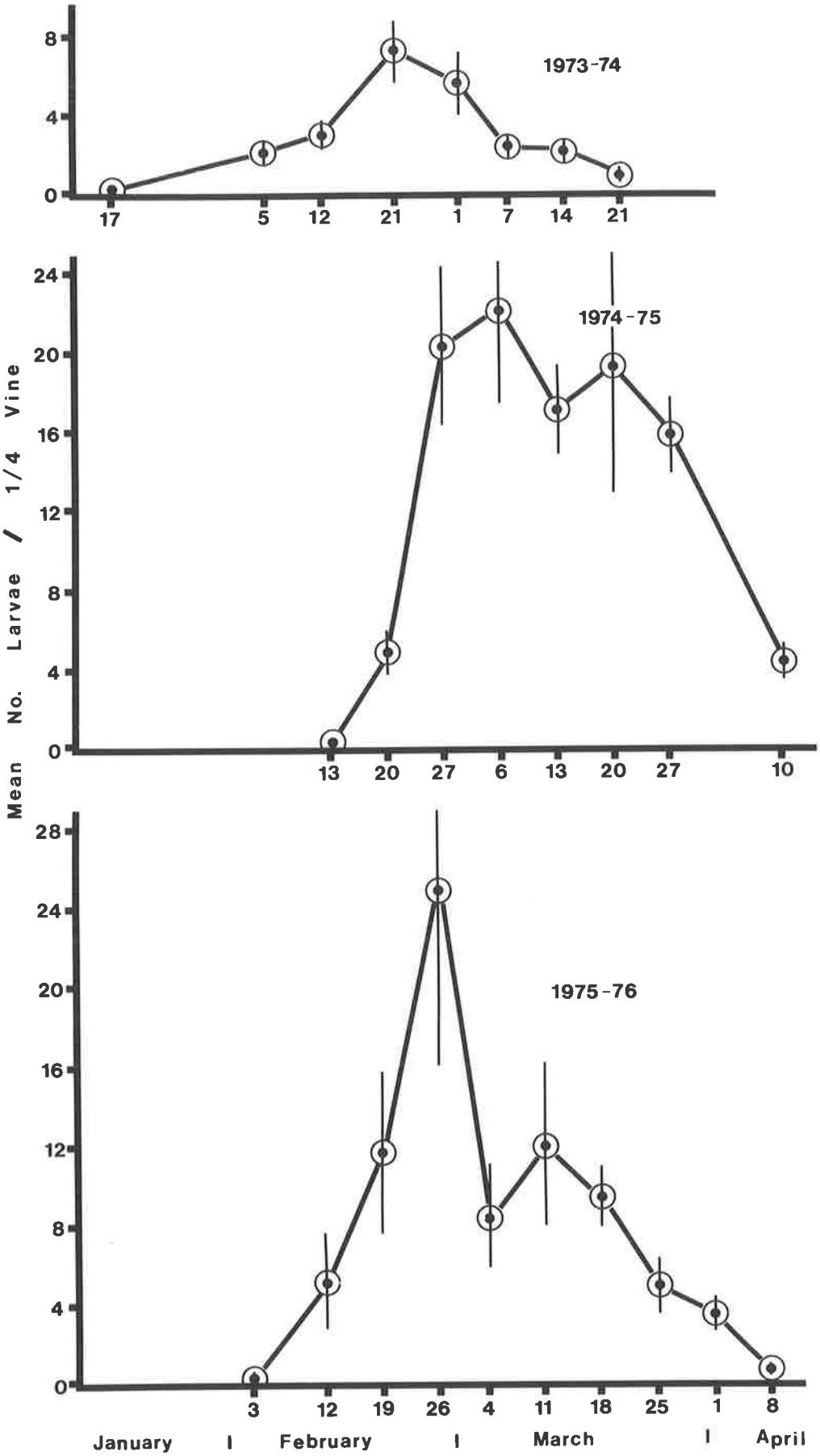

1·0
0·8
0·6
0·4
0·2
0·0
1973-74
2
11
16
23
30
8
13
20
29
6
Mean No. Larvae / 1/4 Vine
1974-75
24
31
7
19
28
12
1975-76
16
27
4
11
18
25
4
October
November
December

Figure 2.11 Mean number of larvae/¼ vine (and standard errors) in the second generation 1973-76.


1973-74
1974-75
1975-76
Mean No. Larvae / 1/4 Vine
0
4
8
12
16
20
24
28
17
5
12
21
1
7
14
21
13
20
27
6
13
20
27
10
3
12
19
26
4
11
18
25
1
8
January
February
March
April

The higher mean number of larvae/¼ vine in the first generation of 1975-76, for example, reflects the large population of larvae in the second generation in 1974-75.

2.4.4 Pupae

Soil sampling for pupae was carried out in the winter of 1974, but was not continued in the following years because few pupae were found. The main aim of this work was to establish where the pupae were and to estimate the pupal population numbers in the soil. Table 2.6 shows the results. The numbers found were very low. No pupae, alive, dead or emerged, and no parasitized pupae or dead larvae were found in samples taken between the rows of vines or outside the vineyard. No live pupae were found either underneath the vines or around the base of the vines and posts (however in later samples they were).

Table 2.6 also shows the proportion of samples taken from each sampling site that yielded results. The samples taken around the base of the vine stems yielded best results and so further samples were taken from this site. The results are given in Table 2.7. In the second series of samples live pupae were found but again the numbers were very low.

The above results showed that only a small proportion of larvae pupate in the soil. Population numbers in the second generation in 1973-74 were quite high and there were approximately 10,000 larvae in the vineyard (mean number of larvae/¼ vine = 2.80). The whole vineyard covers an area of approximately 2700 sq. m. The total area sampled was 256 sq. m. and in this area there should be approximately 1000 individuals. However only 32 individuals were found. It is known that larvae pupate in cracks in the vines and in fence posts. However these vines were not old enough to provide pupation sites in their stems. It was not

TABLE 2.6 Results of soil sampling at different sites at Langhorne Creek.

Sampling Site	Live pupae	Dead pupae	Emerged pupae	Parasitized larvae	Dead larvae	No. samples	No. Samples yielding results
Between row	0	0	0	0	0	10	0
Under vines	0	0	2	4	0	20	4
Around stems	0	2	3	7	5	20	10
Around posts	0	0	1	6	2	20	4
Outside vines	0	0	0	0	0	10	0

TABLE 2.7 Mean numbers of pupae, parasitized larvae and dead larvae in 20 samples taken from the base of the vines.

Sample of	Mean no./sample
live pupae	0.38
dead pupae	0.06
emerged pupae	0.50
parasitized larvae	0.75
dead larvae	0.31

possible to obtain acceptable results from sampling the posts. Because no pupae or remains of pupae (or larvae) were found outside the vineyard and so few were found in the soil it was assumed that most pupae must be in these fence posts.

2.4.5 Discussion

Over the three years of the study the population at Langhorne Creek was observed to fluctuate from low numbers in the 1973-74 season to a peak in the 1974-75 season and begin to decline again in the 1975-76 season. Population numbers in the 1972-73 season, which occurred just prior to the commencement of the study, were particularly high - much higher than in the following three years when, in general, only a limited amount of damage occurred to the vines.

On examination of the data for the population numbers of adults in the first generation 1974-75, two of the points (on 24/10/74 and 31/10/74) are lower than expected. These low numbers were due to weather conditions on the sampling days which were unsuitable for flight. When the weather data were examined for this period, most days were overcast, wet and windy - conditions which would prevent the moths flying. (Wind is an important factor affecting flight. Moths will not fly in winds stronger than 12.0 km/hr. (see Section 5.3.2)). Thus during this time there would be less oviposition in the vineyard than normal for that part of the season. The egg population in the first generation was not sampled so it was not possible to tell if this reduction in oviposition was apparent in that stage. There is some mortality in the egg stage (Section 6.4.2) but any cessation or reduction in oviposition in the middle of the oviposition period was expected to be apparent in the following larval period. This is seen in the larval population of the first generation in 1974-75 in which there is a drop in the number of larvae/¼ vine in the middle of

the larval period when numbers were expected to reach a peak.

A similar spell of bad weather in the adult stage in the 1973-74 season (when adults were not sampled) could explain the decrease in numbers of eggs/¼ vine in the middle of the second generation in 1973-74 (Figure 2.9).

In Figure 2.8, which shows the population changes in adults flying in 1975-76 (second generation), there was a drop in the number of moths/minute/area in the samples taken on 12/2/76. In this case the decrease in numbers cannot be attributed to weather conditions because they were ideal for flight on that day, as they had been on the sampling days either side of this date.

Inevitably the above explanation is a simplified one as many factors operate simultaneously to produce changes in population numbers.

2.5 Sex Ratio

During population studies it was noticed that males tended to emerge first at the beginning of each generation. Moths were caught at weekly intervals, their sexes determined and sex ratios calculated. The data are given in Table 2.8. Within each generation, the proportion of males in the field declines i.e. the sex ratio changes from a male dominated one at the beginning to a female dominated one at the end of the generation. Because the length of life for males and females is approximately the same, at the end of each generation some females may still be alive and ovipositing after the male population has declined. However all female moths caught at the end of the season had mated.

In the laboratory, larvae were reared through to the adult stage, sexed and the sex ratios examined. The results showed that out of 200 moths, 92 (46%) were males and 108 (54%) were females. This gave a ratio

TABLE 2.8 Numbers of male and female moths caught in the field in the 1975-76 season.

Date	Number of ♂	Number of ♀		
2/10/75	6	2		
9/10/75	4	2		
16/10/75	14	7		
			Generation (1)	
11/11/75	1	3		
25/11/75	0	1		
TOTAL	25	15		
28/1/76	7	2	early	
3/2/76	14	7		
12/2/76	3	1	middle	Generation (2)
19/2/76	15	13		
26/2/76	2	8	late	
4/3/76	1	6		
11/3/76	0	1		
TOTAL	42	38		

of males to females of 1:1.17. This was not significantly different from a 1:1 ratio at the 5% level.

In the field the sex ratio was determined for each generation as a whole because in weekly samples numbers were often low. In the first generation (1975-76) (Table 2.8) the ratio did not differ significantly from 1:1 (χ^2 = 2.5) at the 5% level. Sixty three percent of moths caught were male and thirty eight percent were female. However for 2 weeks in the middle of the sampling period, when the sex ratio changed from male dominated to female dominated, samples were not taken because the vineyard was flooded and most vines were under water. By the time sampling could be resumed the population was declining and so the overall ratio is biased towards the males. Thus the χ^2 value, even though not significant is quite high.

The second generation was divided into three sections, early, middle and late. The sex ratios were calculated in each section to show how they varied throughout the generation. In the early part 70% of moths were males, in the middle 56% and late in the generation only 17% were males. However the overall sex ratio was approximately 1:1 with 52.5% males and 47.5% females (χ^2 = 0.2, not significant at the 5% level). Thus the sex ratio varied within each generation but overall it was 1:1, the same as that in the laboratory.

Field results could well be influenced by the activity and behaviour of the different sexes. Consequently the sampling site, i.e. amongst the vines or around the weeds on the edge of the vineyard, could influence the ratio. The differences between the ratios, if any, at the different sites would indicate the relative amounts of time spent in each area by each sex. It was expected that female moths would spend more time amongst the vines ovipositing than around the weeds feeding. The data are given

in Table 2.9. As expected there were more females amongst the vines than males and the reverse in the weeds. So the ratio of males to females was low amongst the vines and higher amongst the weeds.

Thus even though the overall ratio of males to females in the population is 1:1, this ratio differs both with the time of sampling and with the sampling site.

TABLE 2.9 Numbers of moths at different sampling sites.

Date	No. moths in vines		No. moths in weeds	
	♂	♀	♂	♀
28/1/76	1	1	6	1
3/2/76	1	2	1	2
12/2/76	2	0	1	1
19/2/76	4	7	11	6
26/2/76	2	8	-	-
4/3/76	1	6	-	-
11/3/76	0	1	-	-
TOTAL	11	25	19	10
%	30.6	69.4	65.5	34.5

CHAPTER 3

DISTRIBUTION IN THE VINEYARD

3.1 Introduction

In the summer of 1972-73 the vineyard at Langhorne Creek was heavily infested with Phalaenoides glycine. Damage to the vines (Figure 3.1) appeared to occur in patches. These patches consisted sometimes of just a single vine, sometimes a group of vines, usually all in the same row but on a few occasions in adjacent rows. Figure 3.2 shows the distribution of damage at the end of the second generation in 1972-73 (which occurred before this study began). Vines were given a damage rating on a scale of 1-5 (1 = a few chewed leaves, 5 = complete defoliation) (Figure 3.2). The damage appeared to occur mainly in the north-east corner of the vineyard but there were a few badly damaged vines elsewhere. Morisita's Index (see Section 3.5) was calculated for each row to determine if the damage was patchy. Results are given in Table 3.1. The distribution of damage was fairly even over the vineyard except in the north-east corner where it was patchy.

During most seasons (in the second generations) there were larvae or evidence of larvae on nearly every vine examined but the amount of damage was not uniform over the whole vineyard. Vines were completely defoliated in some areas, showing that these patches of vines had supported a larger number of larvae than other vines. So the distribution of eggs and larvae in the vineyard was investigated with the aim of defining the distribution and explaining the likely causes of the 'patchiness', if the distribution proved to be patchy. Eggs and larvae were sampled at weekly intervals by the methods described in Section 2.3.

3.2 The Distributions

Much has been written about the distribution of organisms and many

Figure 3.1 (a) Patch of defoliated vines in the experimental vineyard at Langhorne Creek.

(b) Close up of a defoliated vine.

a

b

Figure 3.2 Map of the vineyard at Langhorne Creek showing damage ratings, on a scale of 1-5, at the end of the second generation 1972-73.

- 1 = almost no defoliation
- 2 = little defoliation
- 3 = moderate defoliation
- 4 = much defoliation
- 5 = complete defoliation.

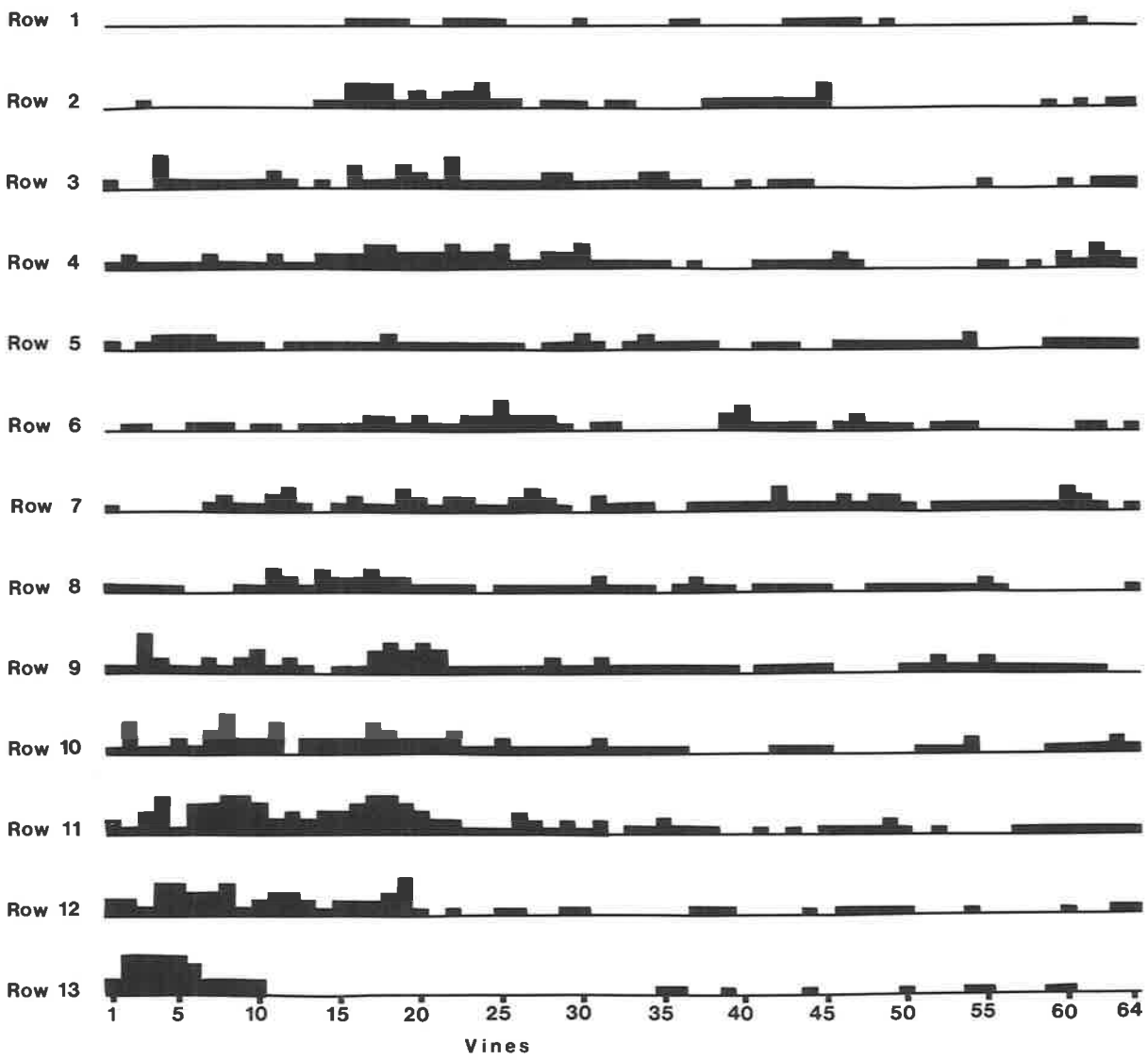

Row 1
Row 2
Row 3
Row 4
Row 5
Row 6
Row 7
Row 8
Row 9
Row 10
Row 11
Row 12
Row 13
1
5
10
15
20
25
30
35
40
45
50
55
60
64
Vines

TABLE 3.1 Morisita's Index (I_δ) and F values (calculated) for damage to vines by larvae.

Row	I_δ	F_o calc.
1	*	-
2	1.13	1.09
3	0.92	0.94
4	0.71	0.64
5	0.28	0.31
6	0.66	0.71
7	0.63	0.56
8	0.49	0.47
9	0.81	0.75
10	0.98	0.98
11	1.13	1.23
12	1.25	1.28
13	3.62	2.74

* too few categories to calculate I_δ.

distributions have been defined mathematically. In general populations can be distributed at random, uniformly or in aggregations. Southwood (1966) and Waters (1959) explain these distribution patterns and the difference between them.

3.2.1 The Poisson Distribution

This results from sampling a population whose individuals are randomly distributed in space. The variance equals the mean. It is described by many authors e.g. Andrewartha & Birch (1954), Bailey (1959), Bliss (1958), Johnson & Kotz (1969), Pielou (1969), Wadley (1950), Southwood (1966) & Snedecor (1962). To test the goodness of fit of data to this distribution the expected frequencies are calculated and compared with the observed frequencies using a χ^2 test. This distribution is rather rare in nature (Harcourt, 1960; 1961).

3.2.2 The Negative Binomial Distribution

This results from sampling a population whose individuals are aggregated in space. It is an extension of the Poisson distribution and is defined by the mean and an exponent 'k'. It is described in detail by Anscombe (1949, 1950). Bliss & Fisher (1953), Bliss (1958), Fisher (1941) and Quenouille (1949). It has been used on many occasions in describing the distribution of insects, e.g. Harcourt (1960, 1961), Miller *et al.* (1972), Mukerji (1970), Waters (1959) & Waters & Henson (1959). In this distribution the variance is greater than the mean. As the variance approaches the mean, the value of k increases and the distribution approaches a Poisson. As the variance departs from the mean, $k \longrightarrow o$ and the distribution approaches the logarithmic series described by Fisher *et al.* (1943) & Williams (1947, 1944).

The value of k gives a measure of the degree of aggregation, and can

be calculated by three different methods. These methods and their efficiencies are outlined by Anscombe (1949, 1950) and Bliss & Fisher (1953). Methods 1 and 2 are approximate while Method 3 is exact. However Methods 2 and 3 involve balancing both sides of an equation and thus are tedious to execute. Method 1 is simple to calculate, $k = m^2/(s^2-m)$ where (m = mean, and s^2 = variance), and in many cases it is used to give an approximate value of k which is then used in the more accurate methods. It was the method used by Harcourt (1960, 1961), Miller et al. (1972) & Mukerji et al. (1970). In this study Method 1 was used to calculate values of k for each weekly sample. For data on egg and larval populations in the second generation of each season, where the means varied considerably but k values were usually low, the efficiency of estimating k by Method 1 varied from approximately 40% to over 90%. For data on the larval population in the first generations where both means and k values were small, the efficiency varied from 70 to 90%.

To test the goodness of fit of data to the Negative Binomial distribution, k is first computed. Then expected frequencies are calculated and compared with the observed frequencies using a χ^2 test.

3.3 Fitting Data to the Poisson Distribution

Before fitting the observed data to the theoretical distributions, the mean and variance was calculated for each weekly sample (Table 3.2). A characteristic of the Poisson distribution is that the variance is equal to the mean. However in most cases the variance was much greater than the mean (see Tables 3.2-3.4). This was particularly so in the second generations (in both egg and larval populations). Consequently data for the second generations were not fitted to the theoretical Poisson distribution. In the first generations (when only larvae were

TABLE 3.2 Mean and variance for each weekly sample of larvae in the first generation each season.

Season	Date	$\bar{x}$	S^2
1973-74	11/10/73	0.13	0.18
	16/10/73	0.08	0.23
	23/10/73	0.58	0.87
	30/10/73	0.90	1.27
	8/11/73	0.68	0.74
	13/11/73	0.08	0.12
	20/11/73	0.15	0.18
1974-75	31/10/74	0.45	0.10
	19/11/74	0.65	0.77
	28/11/74	0.40	0.67
1975-76	27/10/75	0.56	1.03
	4/11/75	0.95	2.16
	11/11/75	0.63	0.91
	18/11/75	0.33	0.24
	25/11/75	0.50	0.80

$\bar{x}$ = mean

S^2 = variance

sampled) the variance often exceeded the mean but differences were usually small and this data was fitted to the Poisson distribution. The results are shown graphically in Figure 3.3 (the data used in fitting are given in Appendix 1). The expected frequencies i.e. the expected number of larvae/¼ vine if the distribution followed a Poisson series, were calculated using the method outlined by Snedecor (1962) pp. 482-486.

In the first generations in 1974-75 and 1975-76 the observed distributions did not differ significantly from the theoretical Poisson distribution. In the first generation in 1973-74, the data followed a Poisson distribution on all but two occasions. On these occasions the data fitted well except for one sample in each case which contained a larger number of larvae than expected. On 16/10/73 one sample contained 3 larvae (expected frequency of 3 larvae = 0.003) and on 13/11/73 one sample contained 2 larvae (expected frequency of 2 larvae = 0.10). Because the mean number of larvae/¼ vine was very low, (0.08 on both dates), the occurrence of 2 and 3 larvae caused high χ^2 values for these weeks when the goodness of fit test was applied and therefore caused the differences between the observed distribution and the theoretical Poisson distribution to be significant.

On those occasions when the data did not fit the Poisson distribution, they were fitted to a Negative Binomial distribution.

3.4 Fitting Data to the Negative Binomial Distribution

Data on egg and larval populations in the second generation each season were fitted to theoretical Negative Binomial distributions. The method of fitting was that described by Bliss & Fisher (1953). The means, variances and k values for the data are given in Tables 3.3 and 3.4 together with the maximum number of eggs or larvae/¼ vine found in each

Figure 3.3 Results of fitting data for larvae of the first generation (1973-76 seasons) to theoretical Poisson distributions.

N = Number of samples.

⊛ = Significant at the 2% level.

* = Significant at the 5% level.

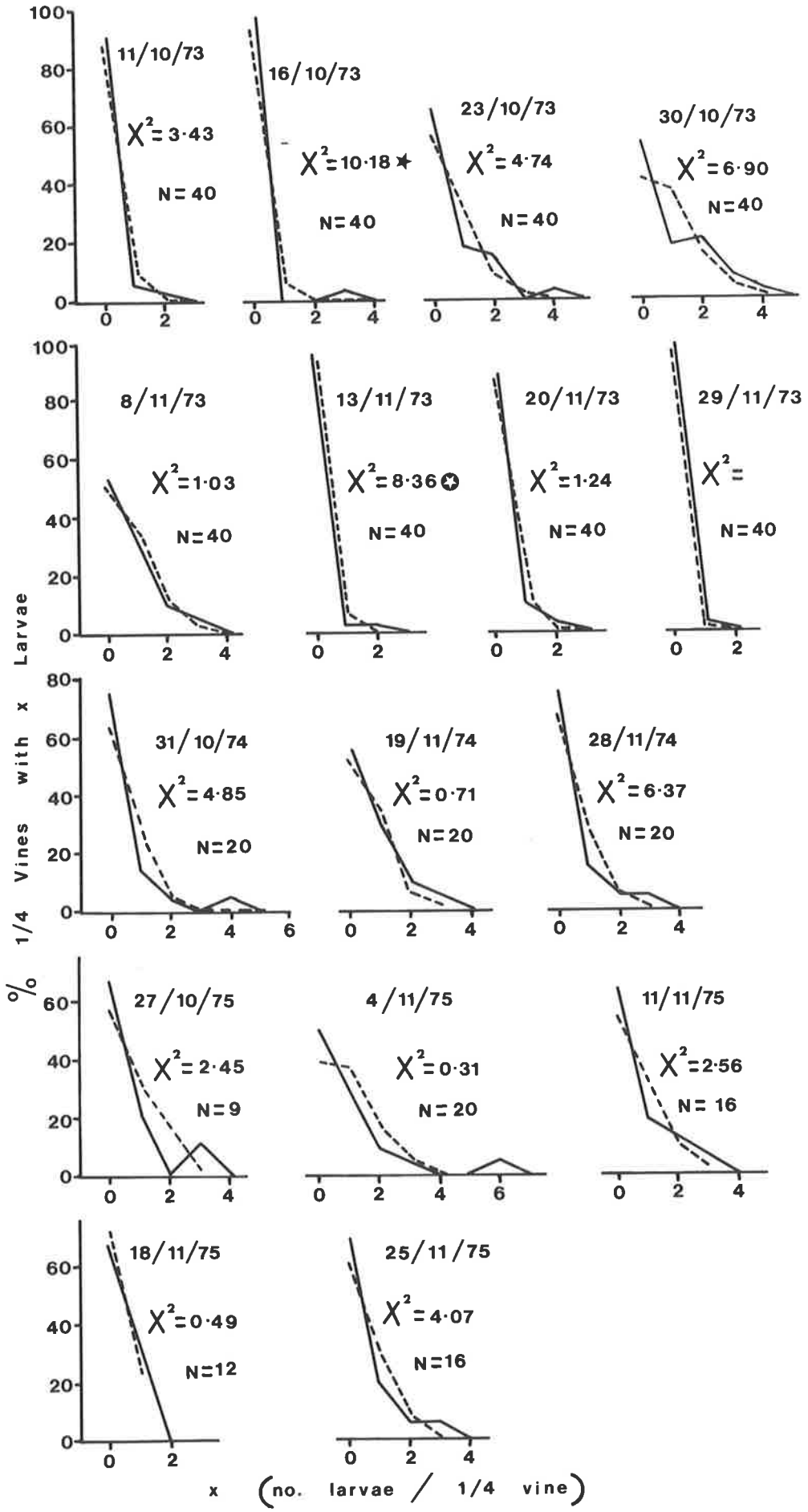

11/10/73
X^2 = 3·43
N = 40
16/10/73
X^2 = 10·18 ★
N = 40
23/10/73
X^2 = 4·74
N = 40
30/10/73
X^2 = 6·90
N = 40
8/11/73
X^2 = 1·03
N = 40
13/11/73
X^2 = 8·36 ✪
N = 40
20/11/73
X^2 = 1·24
N = 40
29/11/73
X^2 =
N = 40
31/10/74
X^2 = 4·85
N = 20
19/11/74
X^2 = 0·71
N = 20
28/11/74
X^2 = 6·37
N = 20
27/10/75
X^2 = 2·45
N = 9
4/11/75
X^2 = 0·31
N = 20
11/11/75
X^2 = 2·56
N = 16
18/11/75
X^2 = 0·49
N = 12
25/11/75
X^2 = 4·07
N = 16
% 1/4 Vines with x Larvae
x (no. larvae / 1/4 vine)

TABLE 3.3 Mean ($\bar{x}$), variance (S^2), k value and maximum number of eggs/¼ vine (max. x) in the second generation each season.

	Date	$\bar{x}$	S^2	k	Max. x
1973-74	5/2/74	3.15	64.69	0.16	41
	12/2/74	5.48	124.20	0.25	48
	21/2/74	3.68	43.66	0.34	26
	1/3/74	6.83	141.23	0.35	52
	7/3/74	0.83	3.79	0.23	8
1974-75	20/2/75	5.70	78.01	0.05	37
	27/2/75	13.13	131.85	1.45	40
	6/3/75	8.50	43.60	2.06	20
	13/3/75	0.56	2.00	0.22	5
	20/3/75	2.19	7.52	0.09	30
1975-76	3/2/76	1.00	4.00	0.33	7
	12/2/76	10.63	205.13	0.58	40
	19/2/76	8.08	118.74	0.59	40
	26/2/76	3.92	12.27	1.84	12
	4/3/76	1.58	9.17	0.33	10

TABLE 3.4 Mean ($\bar{x}$), variance (S^2), k value and maximum number of larvae/¼ vine (Max. x) in the second generation each season.

	Date	$\bar{x}$	S^2	k	Max. x
1973-74	5/2/74	1.90	14.14	0.30	22
	12/2/74	2.78	17.97	0.51	17
	21/2/74	7.20	86.42	0.65	42
	1/3/74	5.43	82.82	0.38	45
	7/3/74	2.23	17.26	0.33	20
	14/3/74	2.00	10.41	0.48	12
	21/3/74	0.80	3.65	0.23	10
	28/3/74	0.05	0.05	-	-
	3/4/74	0.03	0.03	-	-
1974-75	20/2/75	4.75	17.04	1.84	14
	27/2/75	20.13	252.25	1.75	50
	6/3/75	21.81	224.70	2.34	47
	13/3/75	16.88	89.85	3.90	42
	20/3/75	19.13	706.38	0.53	86
	27/3/75	15.69	60.50	5.49	35
	10/4/75	4.19	9.90	3.08	9
1975-76	3/2/76	0.13	0.12	1.70	1
	12/2/76	5.00	44.00	0.64	19
	19/2/76	11.46	224.46	0.62	53
	26/2/76	24.83	986.61	0.64	110
	4/3/76	8.33	81.55	0.95	26
	11/3/76	11.92	235.13	0.64	55
	18/3/76	9.25	38.20	3.00	20
	25/3/76	4.83	20.17	1.52	15
	1/4/76	3.38	13.72	1.10	15
	8/4/76	0.50	0.80	0.83	3

sample. This was needed to calculate the expected numbers of eggs or larvae/¼ vine. It also shows the spread of the observed data. The data used in fitting the Negative Binomial distributions are given in Appendix 2.

In testing the goodness of fit of data to the Negative Binomial distribution, frequencies with small expectations are usually pooled, preferably so that no expectation is less than 5 (Bliss & Fisher, 1953). In a recent paper, Pahl (1969) discussed this commonly accepted rule and assessed the feasibility of grouping data into classes with expected frequencies considerably less than 5 (as low as 0.05). He concluded that the grouping of data into such classes was allowable. In most cases in the present study it was not possible to group data into classes so that expected frequencies were greater than or equal to 5 because either none of the expected frequencies were greater than 5 or, if frequencies less than 5 were pooled, there would be only 2 classes to fit to the distribution. Therefore data was grouped so that the expected frequencies were either greater than 1.5 or greater than 0.5.

The results of fitting the data on eggs to the Negative Binomial distribution are shown in Figure 3.4. In the second generation 1973-74, the differences between the observed number of eggs/¼ vine and the expected number were not significant at the 5% level on all occasions except on 1/3/74 when the level of significance was between 1% and 2%. In the second generation in the 1974-75 season, again all differences were non-significant except on 20/2/75 when the χ^2 value was 67.18 ($P_{.05} = 5.99$). In the second generation in the 1975-76 season all data fitted the Negative Binomial distribution.

The results of fitting the data on larvae (for the second generation each season) to the Negative Binomial distribution are shown in Figure 3.5. In all cases the data fitted reasonably well. Differences

Figure 3.4(a) Results of fitting the data for eggs of the second generation, 1973-74 to theoretical negative binomial distributions. N = number of samples.

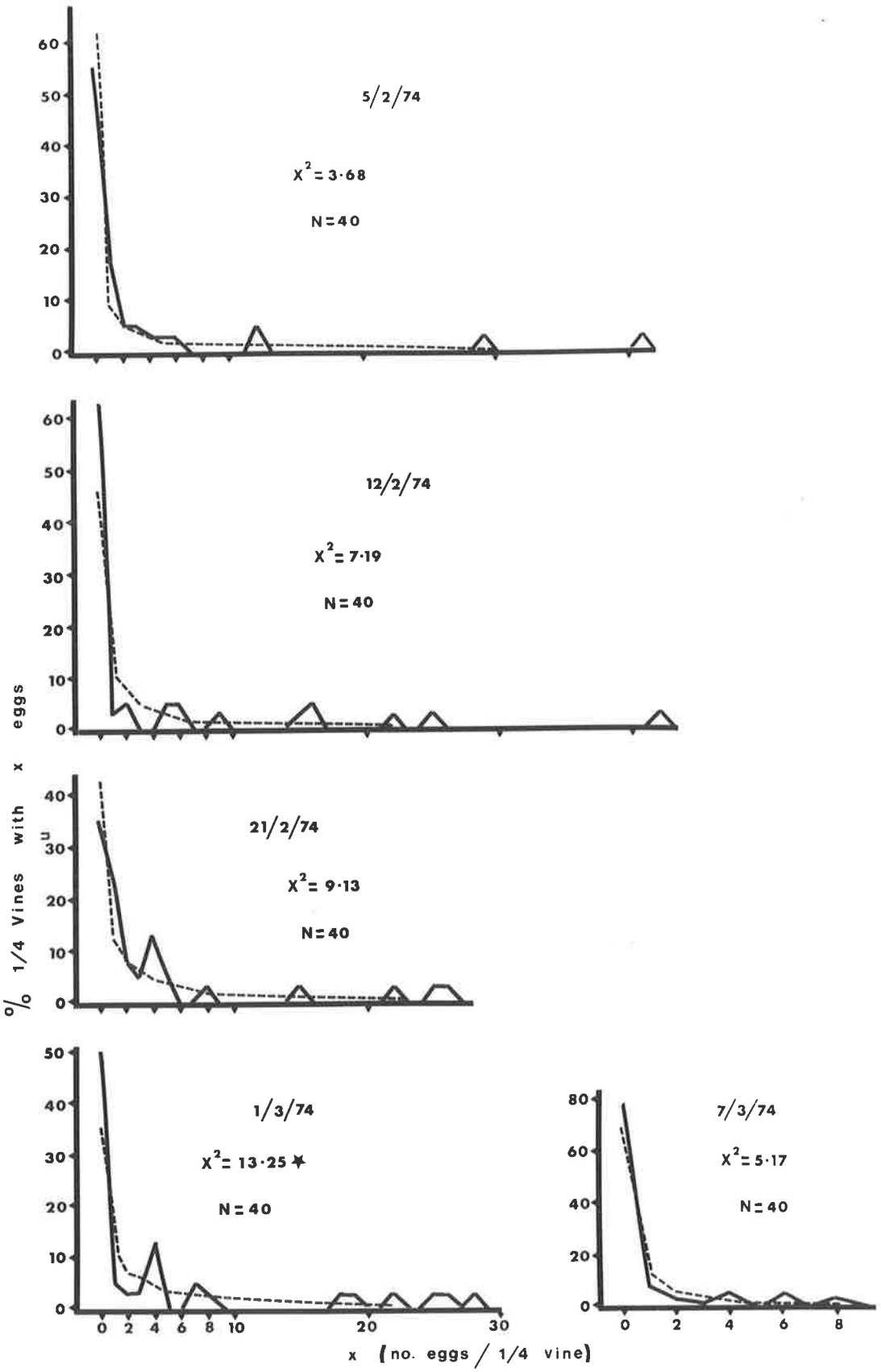

5/2/74
X^2 = 3·68
N = 40
12/2/74
X^2 = 7·19
N = 40
21/2/74
X^2 = 9·13
N = 40
1/3/74
X^2 = 13·25 *
N = 40
7/3/74
X^2 = 5·17
N = 40
% 1/4 Vines with x eggs
x (no. eggs / 1/4 vine)

Figure 3.4(b) Results of fitting the data for eggs of the second generation, 1974-75 to theoretical negative binomial distributions.

N = number of samples

* = significant at the 5% level.

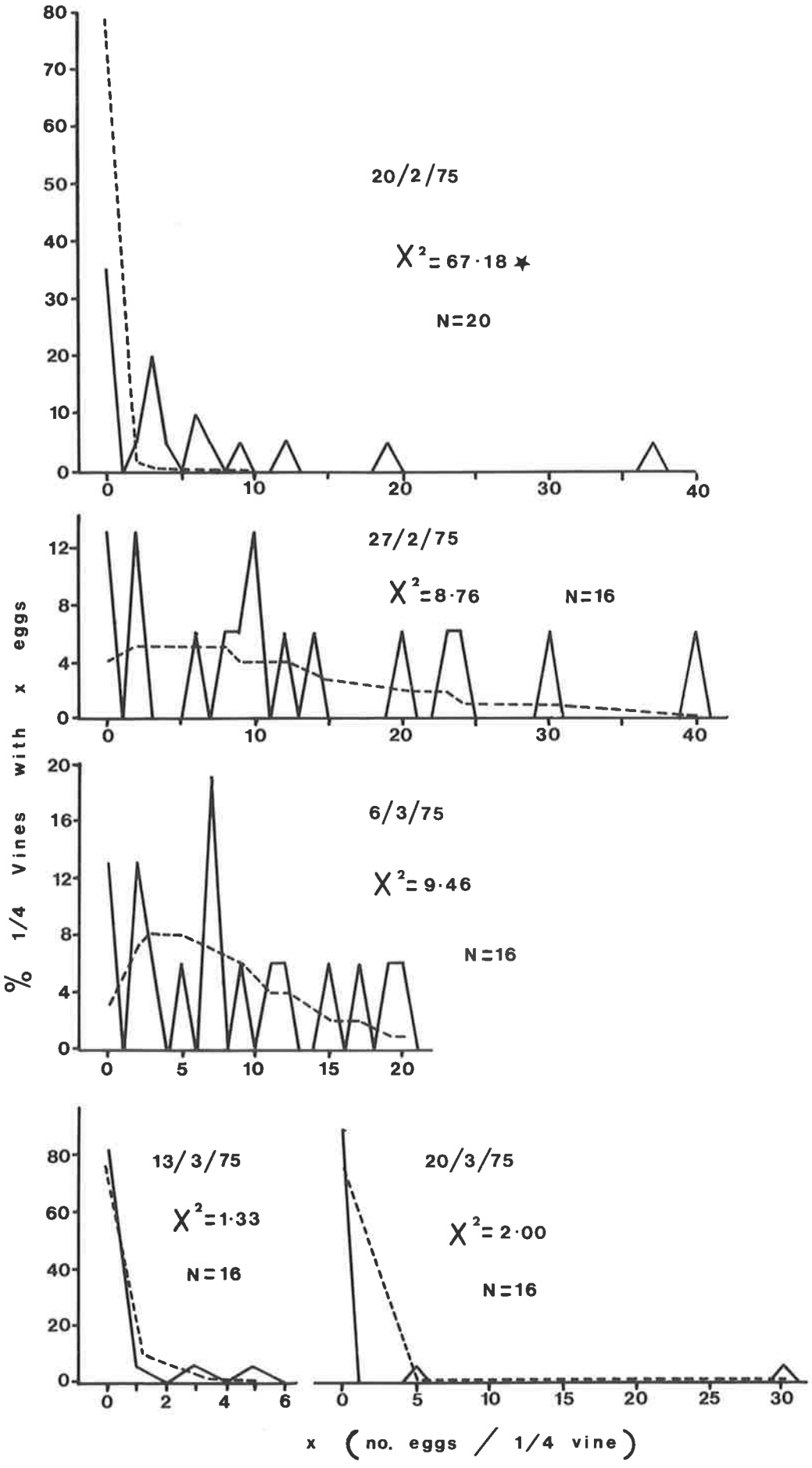

20/2/75
X^2 = 67·18 *
N=20
27/2/75
X^2 = 8·76
N=16
6/3/75
X^2 = 9·46
N=16
13/3/75
X^2 = 1·33
N=16
20/3/75
X^2 = 2·00
N=16
% 1/4 Vines with x eggs
x (no. eggs / 1/4 vine)

Figure 3.4(c) Results of fitting the data for eggs of the second generation, 1975-76 to theoretical negative binomial distributions. N = number of samples.

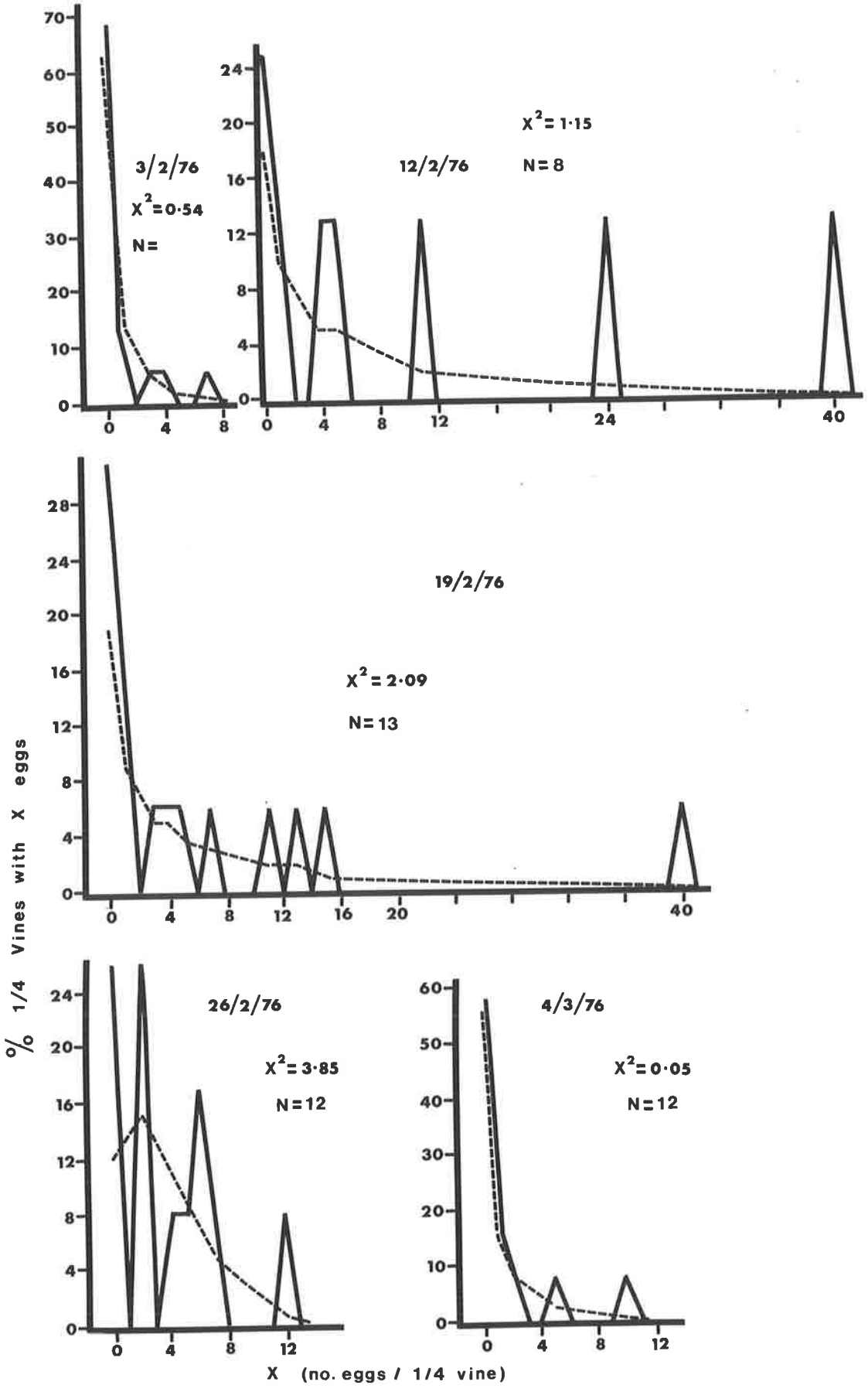

3/2/76
X^2=0·54
N=
12/2/76
X^2= 1·15
N= 8
19/2/76
X^2= 2·09
N= 13
26/2/76
X^2= 3·85
N=12
4/3/76
X^2= 0·05
N=12
% 1/4 Vines with X eggs
X (no. eggs / 1/4 vine)

Figure 3.5(a) Results of fitting the data for larvae of the second generation, 1973-74, to theoretical negative binomial distributions. N = number of samples.

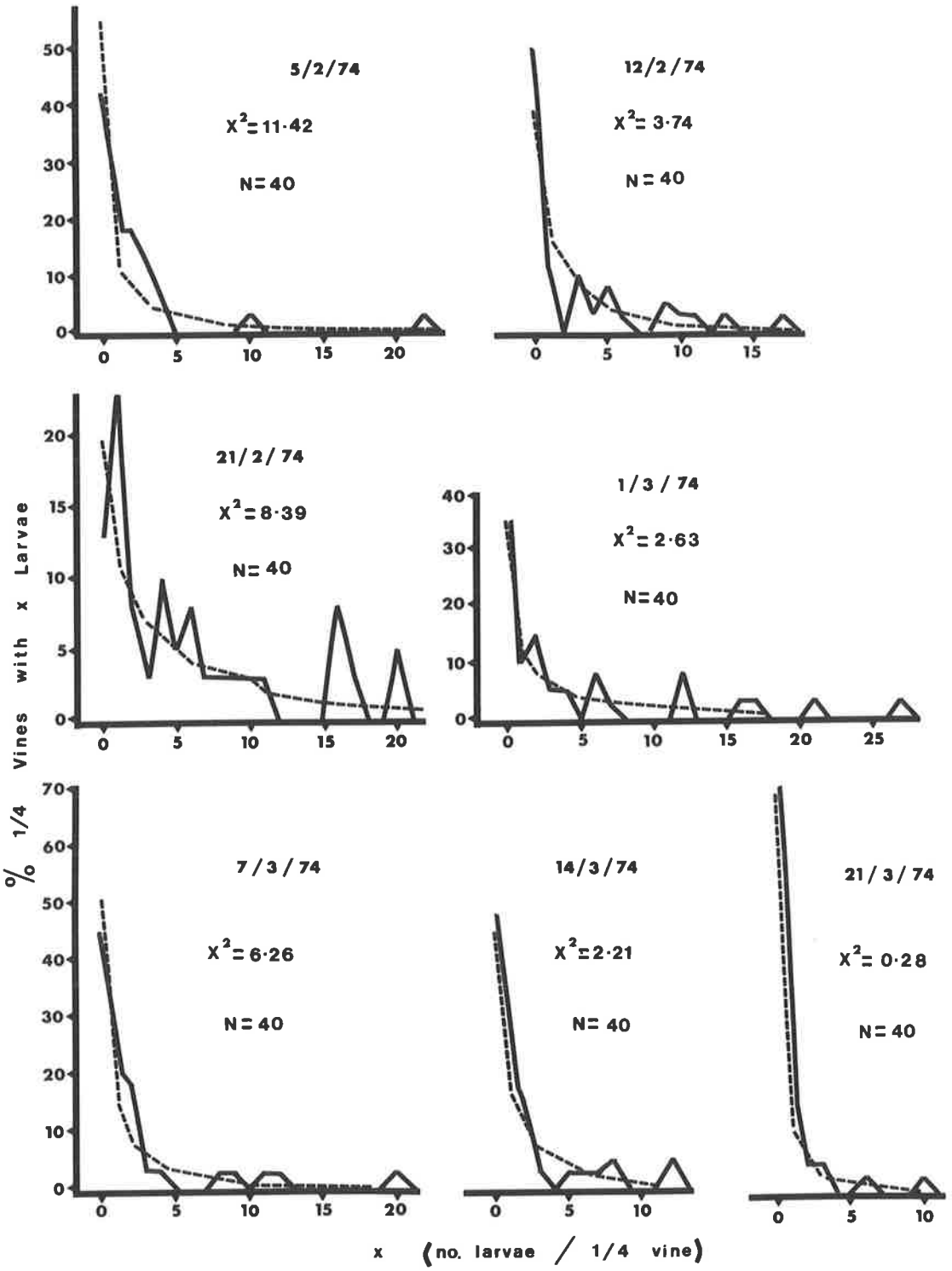

5/2/74
X^2= 11·42
N= 40
12/2/74
X^2= 3·74
N= 40
21/2/74
X^2= 8·39
N= 40
1/3/74
X^2= 2·63
N= 40
7/3/74
X^2= 6·26
N= 40
14/3/74
X^2= 2·21
N= 40
21/3/74
X^2= 0·28
N= 40
% 1/4 Vines with x Larvae
x (no. larvae / 1/4 vine)

Figure 3.5(b) Results of fitting the data for larvae of the second generation, 1974-75, to theoretical negative binomial distributions. N = number of samples.

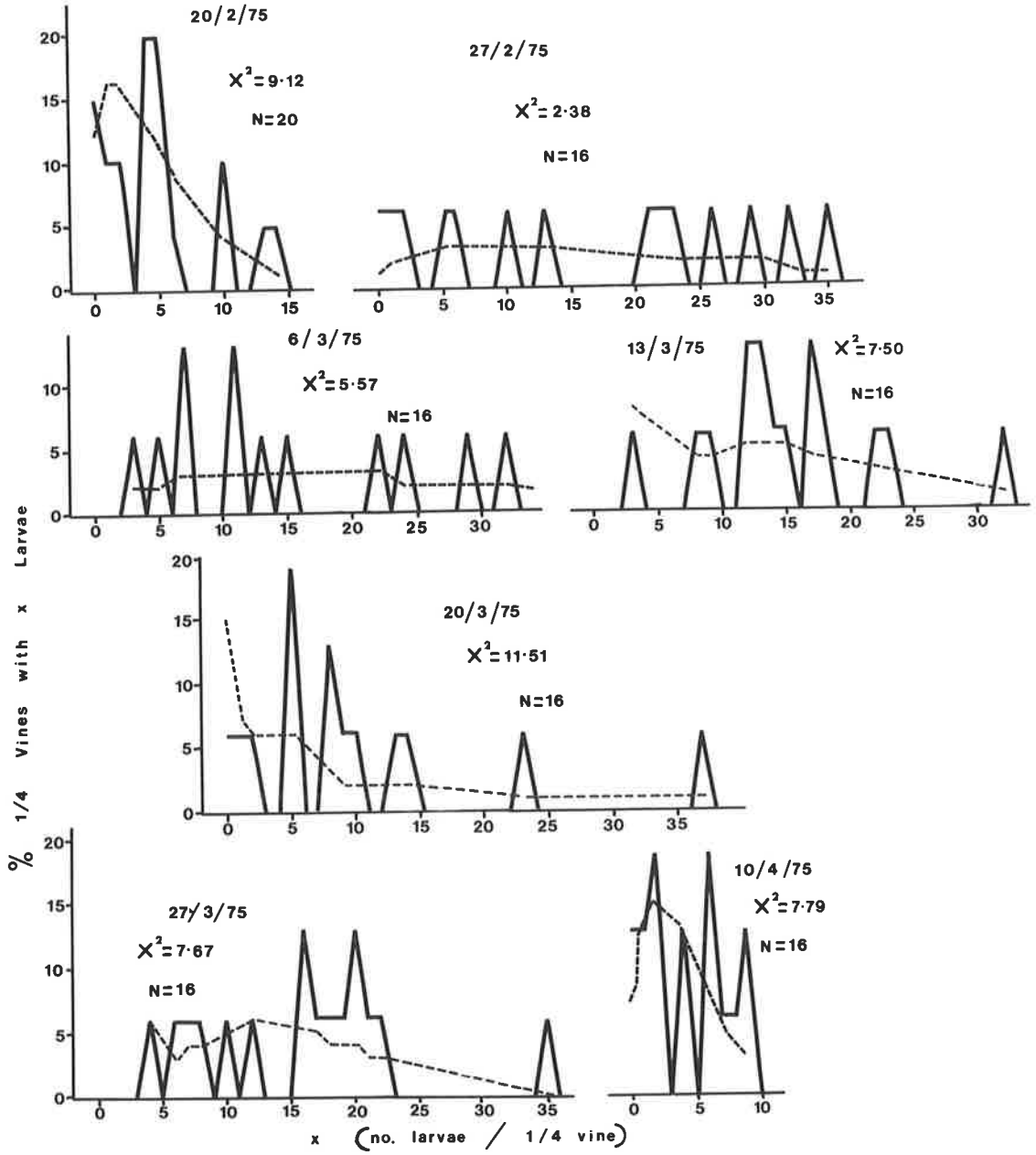
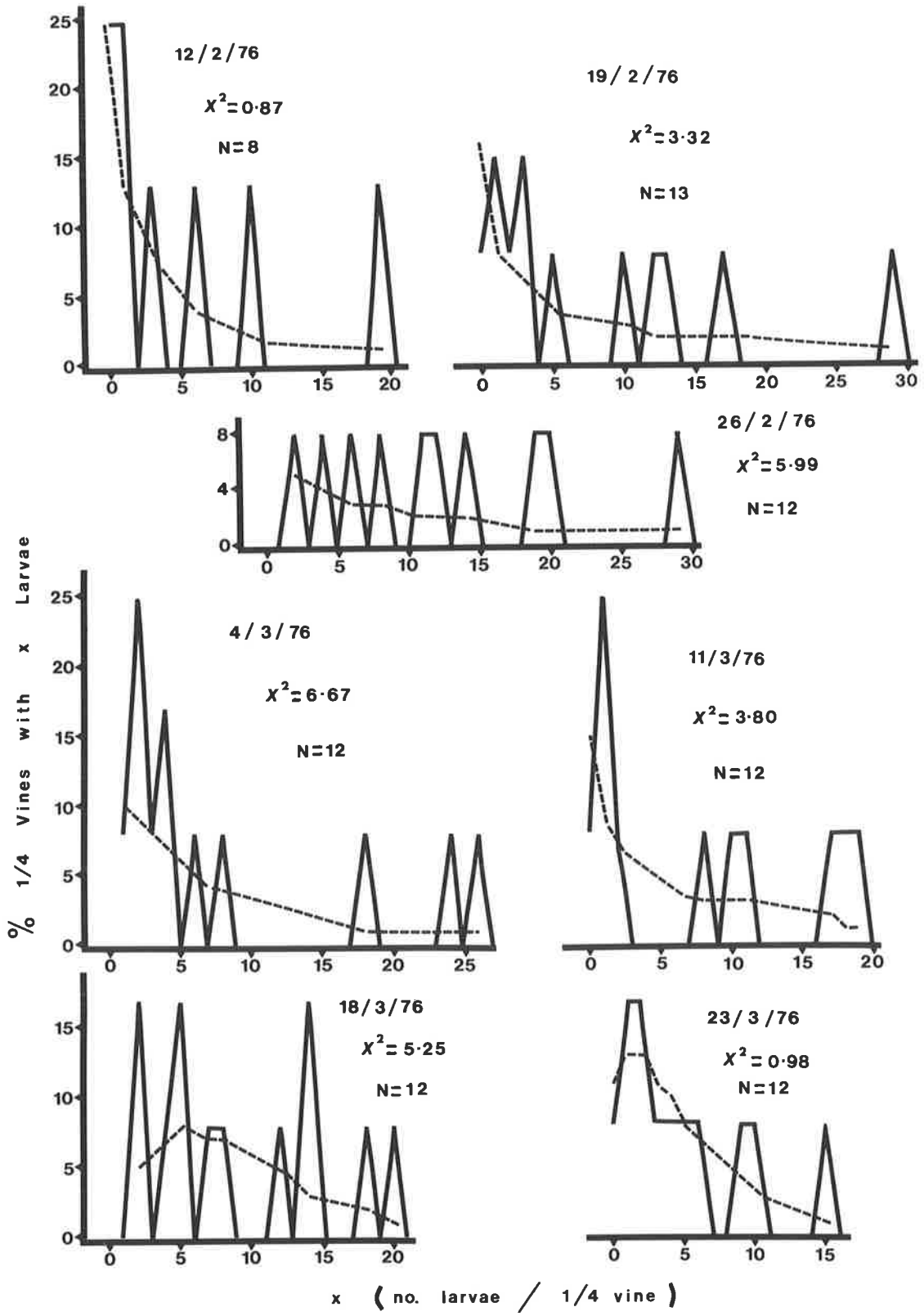

20/2/75
X^2=9·12
N=20
27/2/75
X^2=2·38
N=16
6/3/75
X^2=5·57
N=16
13/3/75
X^2=7·50
N=16
20/3/75
X^2=11·51
N=16
27/3/75
X^2=7·67
N=16
10/4/75
X^2=7·79
N=16
% 1/4 Vines with x Larvae
x (no. larvae / 1/4 vine)

Figure 3.5(c) Results of fitting the data for larvae of the second generation, 1975-76, to theoretical negative binomial distributions. N = number of samples.


12/2/76
X^2=0·87
N=8
19/2/76
X^2=3·32
N=13
26/2/76
X^2=5·99
N=12
4/3/76
X^2=6·67
N=12
11/3/76
X^2=3·80
N=12
18/3/76
X^2=5·25
N=12
23/3/76
X^2=0·98
N=12
% 1/4 Vines with x Larvae
x (no. larvae / 1/4 vine)

were not significant at the 5% level in all but 2 cases in which differences were not significant at the 0.1% level.

Data on larvae in the first generations that did not fit the Poisson distribution were also fitted to the Negative Binomial distribution. Differences were not significant at the 5% level.

3.5 Measuring the Dispersion

Mathematical models can be used to determine the type of distribution but most give no indication of the degree to which the population departs from random. If the data can be fitted to a Negative Binomial distribution, the value of k gives a measure of the dispersion or degree of aggregation of the data. The smaller the value of k, the greater the aggregation. Southwood (1966) states that k values greater than about 8 indicate a Poisson or random distribution. The value of k may be influenced by the size of the sampling unit and thus it often does not give a true indication of the degree of aggregation (Harcourt, 1961; Southwood, 1966; Waters & Henson, 1959). Similarly the "index of dispersion" (described by Southwood (1966) and used by Milne (1964), Salt & Hollick, (1946) and others) is influenced by the size of the sampling unit.

In 1959, Morisita proposed a new index of dispersion, I_δ (see also Morisita, 1962; 1964). This index has the advantage of being independent of the type of distribution, the size of the sampling unit and the number of samples. When the distribution is random (i.e. follows a Poisson series), $I_\delta = 1$. When the distribution is aggregated (i.e. Negative Binomial), $I_\delta > 1$ and when the distribution is regular, $I_\delta < 1$. I_δ values for larvae in the first and second generations and eggs in the second generations, are shown in Tables 3.5-3.7. In all cases I_δ values were >1. To test whether I_δ values differed significantly from 1, i.e. whether the

TABLE 3.5 Morisita's Index (I_δ) and F values (calculated) for eggs in the second generation each season.

	Date	I_δ	F_o calc.
1973-74	5/2/74	7.10	20.55
	12/2/74	4.88	22.69
	21/2/74	3.91	11.89
	1/3/74	3.82	20.67
	7/3/74	5.38	4.59
1974-75	20/2/75	3.13	13.67
	27/2/75	1.65	10.06
	6/3/75	1.46	5.14
	13/3/75	5.78	3.55
	20/3/75	11.97	25.87
1975-76	3/2/76	4.00	4.00
	12/2/76	2.53	19.36
	17/2/76	2.58	14.69
	26/2/76	1.51	3.13
	4/3/76	3.93	5.79

TABLE 3.6 Morisita's Index (I_δ) and F values (calculated) for larvae in the first generation each season.

	Date	I_δ	F_o calc.
1973-74	11/10/73	5.33	1.42
	16/10/73	40.00	3.00
	23/10/73	1.90	1.51
	30/10/73	1.46	1.41
	8/11/73	1.14	1.09
	13/11/73	13.33	1.63
	20/11/73	2.67	1.21
1974-75	31/10/74	3.89	2.22
	19/11/74	1.28	1.18
	28/11/74	2.86	1.69
1975-76	27/10/75	2.70	1.85
	4/11/75	2.34	2.27
	11/11/75	1.78	1.47
	25/11/75	2.29	1.60

TABLE 3.7 Morisita's Index (I_δ) and F values (calculated) for larvae in the second generation each season.

	Date	I_δ	F_o calc.
1973-74	5/2/74	4.35	7.44
	12/2/74	2.94	6.47
	21/2/74	2.50	12.04
	1/3/74	3.58	15.29
	7/3/74	3.99	7.75
	14/3/74	3.08	5.21
	21/3/74	5.48	4.56
1974-75	20/2/75	1.52	3.57
	27/2/75	1.54	12.56
	6/3/75	1.40	10.28
	13/3/75	1.24	5.30
	20/3/75	2.77	36.99
	27/3/75	1.17	3.83
	10/4/75	1.31	2.36
1975-76	12/2/76	2.40	8.80
	19/2/76	2.51	19.62
	26/2/76	2.43	39.61
	4/3/76	1.98	9.82
	11/3/76	2.45	19.72
	18/3/76	1.31	4.10
	25/3/76	1.61	4.16

distributions differed significantly from random, F values were calculated (Tables 3.5-3.7) using the formula given by Morisita (1959). These were then compared with variance ratio tables (5% probability). If the calculated F value was greater than the variance ratio value in the tables, differences were significant. All I_δ values for second generation eggs and larvae were significantly greater than 1 and thus these populations can be considered to be aggregated. I_δ values for first generation larvae did not differ significantly from 1 (except on 16/10/73 and 13/11/73 (when differences were large), on 31/10/74 and 28/11/74 (only just significant) and on 4/11/76). In each case the value of I_δ gives the degree of aggregation of individuals in the population. Those with values of I_δ close to 1 can be considered to be less aggregated than those with higher I_δ values.

Thus the I_δ values confirmed the results of fitting the data to a Negative Binomial distribution, that the distribution of Phalaenoides glycine in the field was aggregated.

3.6 Discussion

The results of fitting data on egg and larval populations at Langhorne Creek to the Poisson and Negative Binomial distributions indicate that in the first generations there was no evidence to suggest that the distribution of individuals was aggregated. Female moths do not oviposit at random (Chapter 5) and there is evidence to suggest that larvae do not move very far, (Larval movement was followed in the field for 3 weeks. No larvae moved further than approximately 40 cm. in this time), but population numbers are so low in the first generations that aggregations were not apparent and therefore the distribution could not be distinguished from a random distribution.

Second generation eggs and larvae had an aggregated or 'patchy' distribution. In 1973-74, when second generation larval numbers were lower than in the following two years, the distribution fitted the Negative Binomial very well. In 1974-75 and 1975-76, when numbers were high and larvae were present on almost every vine, the data still fitted a Negative Binomial distribution but not as well as in 1973-74. Thus, when population numbers are low, the distribution cannot be distinguished from random but as the numbers increase the distribution is seen to be patchy. This apparent change in distribution has often been observed in insect populations e.g. in Pieris rapae (Harcourt, 1961) and in wireworms (Finney, 1941).

In the 1974-75 second generation when egg and larval numbers were higher than in the other years, the k values were also higher (Tables 3.3, 3.4) i.e. k values followed the same trends as population density. This indicates that as population numbers increase further the distribution tends to become random again. A similar pattern was observed in Rhyacionia frustrana (Waters, 1959).

Morisita's Index, (which is independent of the mean), showed that second generation egg populations were highly aggregated as were second generation larval populations. First generation larval population numbers were very low. Thus aggregations were not apparent and Morisita's Index indicated that the populations were essentially randomly distributed.

CHAPTER 4

MATING, REPRODUCTION AND OVIPOSITION

In this chapter various aspects of mating and oviposition are discussed. Oviposition behaviour, oviposition sites and factors that influence their choice are discussed in Chapter 5.

4.1 Mating Behaviour

The mating behaviour of *Phalaenoides glycine* has been observed both in the field and in the laboratory. Mating usually takes place in the afternoon. Most moths mate within two days of their emergence from the pupal stage (Table 4.1) and on rare occasions females have been seen mating before their wings were properly dry.

In the field mating occurs either in the vineyard or on the weeds surrounding the vineyard. Moths do not mate in flight but are capable of flying *in copula* if disturbed. In the laboratory mating usually occurs on the mesh walls of the cage.

The mating process in the field begins with the male chasing the female in an erratic flight in and out of the vines and over the weeds. Often the male will break away to chase other moths flying nearby, either male or female. In the laboratory these flights were restricted because the mating cages were small and the moths could fly only short distances. [This lack of space was one reason why it was difficult to get moths to mate in the laboratory (light and temperature were also important). No moths mated in cages smaller than 47 x 47 x 62 cm. and even in these cages not all moths mated (approximately 70% mated)]. During these flights the male opens and shuts the claspers and continually extends the reproductive organs. The female may also extend her ovipositor. She then lands on a vine or fence post. The male follows and

after much fluttering and probing with the abdomen, backs towards the female and mating occurs. After pairing the male folds his wings over those of the female. Mating usually lasts for a considerable time, the average (for 10 moths) being 62.5 minutes with a range of 40 to 93 minutes. After mating the male immediately flies off while the female remains.

4.2 Pre-oviposition Period

When the moth first emerges none of the eggs are mature. Those nearest the common oviduct mature first and there is a gradation along the length of each ovariole from mature at one end to a completely undifferentiated mass of tissue at the other end. Thus eggs are continually maturing throughout the life of the moth.

In the laboratory, oviposition did not usually begin until approximately 3 days after emergence (Table 4.2). The moths could mate at any time during this period but oviposition did not normally begin immediately after mating. This pre-oviposition period is assumed to occur in the field where it may be considerably longer than 3 days, depending on weather conditions. In rare instances (in the laboratory), some moths began ovipositing within a few hours of mating. The resulting eggs were all fertile. Thus while a pre-oviposition period is usual, it is not necessary for the production of fertile eggs.

4.3 Rate of Oviposition

The oviposition rate varies depending on the mated state, activity and age of the moths. Mated moths begin oviposition earlier than unmated moths and lay more eggs (Table 4.3). The activity of moths in the laboratory depends on the size of the cage, the light/dark regime and the temperature. Moths would mate only in large cages (see above) yet

TABLE 4.1 Number of days from emergence to mating in the laboratory.

Days from emergence to mating	No. of moths
1	2
2	10
3	7
4	1

TABLE 4.2 Length of pre-oviposition period in days in the laboratory.

Length of pre-oviposition period	No. of moths
1	2
2	8
3	11
4	2
5	2

TABLE 4.3 Mean fecundity and length of pre-oviposition period for mated and unmated moths.

Moths	Mean no. eggs laid/♀	Mean length of pre-oviposition period (days)
Mated	460.2	3
Unmated	65.5	9

TABLE 4.4 Rate of oviposition for 10 female moths at 25°C.

Days	No. eggs/♀ for moth no.										
	1	2	3	4	5	6	7	8	9	10	Mean
1	220	*	79	1	86	117	*	97	104	180	110.5
2	358	241	361	418	144	291	105	247	197	226	258.8
3	200	16	133	127	79	162	9	136	95	113	107.0
4	242	205	183	164	127	93	41	189	146	88	147.8
5	135	53	94	82	114	106	113	62	104	77	94.0
6	14	55	50	17	50	42	29	56	31	53	39.7
7	90	56	45	74	95	62	1	87	72	55	63.7
8	129	86	9	69	12	80	27	89	101	145	74.7
9	103	9	53	123	2	92	53	21	44	50	55.0
10	10	20	37	46	0	35	17	33	10	15	22.3
11	154	0	0	10	0	0	0	0	0	0	16.4

* = numbers not counted

would oviposit readily in small canisters approximately 14 x 14 cm. (but would not oviposit in containers smaller than this).

In an experiment to investigate the rate of oviposition, female moths were kept at 25°C in a light regime of 14 hours light : 10 hours dark. They were placed in these conditions after 2 days in the mating cages i.e. 2 days after emergence. Only moths that had mated were used to determine the rate of oviposition. The numbers of eggs laid were counted and removed each day. Results for the 10 most fecund moths are given in Table 4.4. There was a peak in the rate on the second day after oviposition began, after which it decreased (with minor fluctuations), until the moths died.

4.4 The Female Reproductive Tract

The anatomy of the female reproductive tract was examined in detail and is described below. The terminology used has been adapted from Callahan & Chapin (1960), Holt & North (1970) & Stern & Smith (1960). This section should be read in conjunction with Figure 4.1.

In Phalaenoides glycine there are two genital apertures, the ostium bursae or copulatory aperture and the ovipore or oviposition aperture. The ostium bursae is ventral to the ovipore and is chitinized.

The bursa copulatrix is divided into the ductus bursae and the corpus bursae - there is no appendix bursae. The ductus bursae leads from the ostium bursae to the corpus bursae. The point at which it enters the corpus bursae is the cervix bursae. The corpus bursae is a large sac-like structure, its shape and appearance depending on the mated state of the moth (Section 4.5). Often a green object can be seen in the corpus bursae. This is the remains of the spermatophore that formed during mating. Davey (1965) states that in the few instances where the

Figure 4.1 Diagram of the female reproductive tract.

ag = accessory gland

agr = accessory gland reservoir

bs = bulla seminalis

ceb = cervix bursae

co = common oviduct

cob = corpus bursae

db = ductus bursae

ds = ductus seminalis

e = egg

lr = Lagena

o = ovariole containing eggs

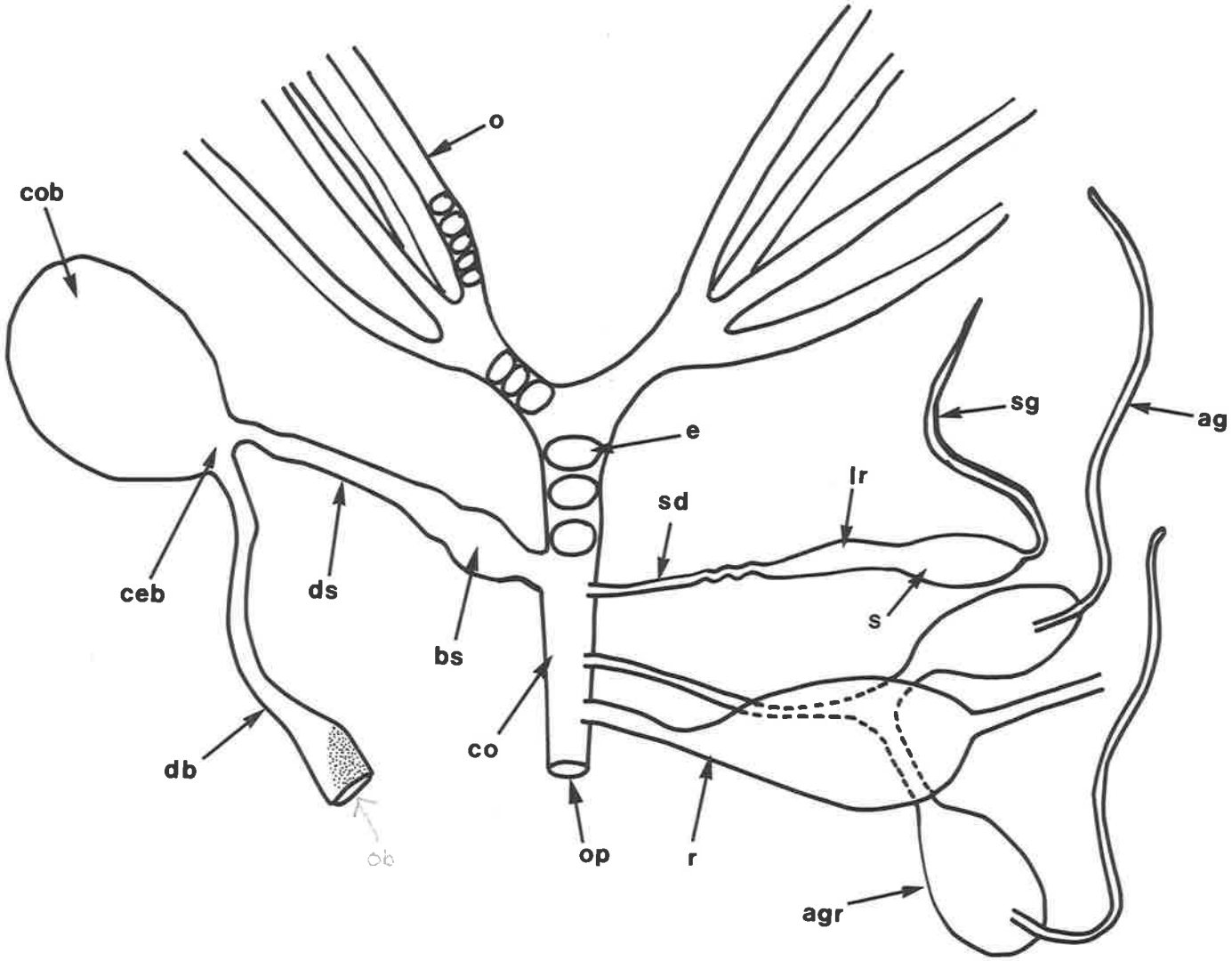
op = ovipore

r = rectum

s = spermatheca

sd = spermathecal duct

sg = spermathecal gland.


o
cob
e
sg
ag
lr
sd
ceb
ds
bs
s
db
co
op
r
agr
ob

spermatophores of Lepidoptera have been examined, the spermatophore has been found to consist of one or more sperm sacs embedded in a gelatinous matrix. This is so in Phalaenoides glycine.

In Colias philodice (Stern & Smith, 1960) a lamina dentata is present in the corpus bursae. No such structure was found in Phalaenoides glycine. The lamina dentata is thought to be responsible for tearing open the spermatophore and thus releasing the sperm (Petersen, 1904). However in some Lepidoptera spines on the lining of the bursae or proteolytic enzymes are thought to cause the breakdown of the spermatophore (Davey, 1965). It is not known how sperm are released in Phalaenoides glycine.

The ductus seminalis is a narrow duct leading from the corpus bursae to the common oviduct. Sperm pass down this on their way to the spermatheca for storage. As the ductus seminalis nears the opening into the common oviduct it enlarges into two bulb-like structures. These are the bulla seminalis.

The spermatheca, consisting of a small lobe or lagena and a large lobe or utriculus, is connected to the common oviduct by the spermathecal duct (ductus receptaculi). This enters the common oviduct close to the junction of the common oviduct and the ductus seminalis. Sperm are transferred from the corpus bursae to the spermatheca along these two ducts. The spermathecal duct is twisted along its length. It opens into the lagena which in turn opens into the utriculus. From here a long, thin, single spermathecal gland extends.

Also joining the common oviduct, but low down near the rectal opening, is the duct leading to the accessory glands. This duct branches into two, each branch leading to a large, bulbous, white, accessory gland reservoir. A single accessory gland empties into each reservoir. Secretions from these glands are thought to play a part in cementing the

eggs to the substrate on which they are laid (Norris, 1932). The ducts leading from each reservoir unite in a mass of tissue (thought to be muscular) surrounding the hindgut and rectum.

The common oviduct extends from the ovipore to a point beyond the openings of the ductus seminalis and ductus receptaculi, where it divides into two lateral oviducts. These each branch into 4 ovarioles. Eggs at all stages of development are found in the ovarioles. Those near the oviduct are usually mature and are enclosed in a shell. They become less mature along the length of the ovariole. In mature females that are ovipositing, eggs are found in the common oviduct. Occasionally mature eggs were found in the ductus seminalis but only rarely. This phenomenon was also observed in Colias philodice (Stern & Smith, 1960).

4.5 Age and Reproductive State

Female moths of known age and mated state were dissected and their reproductive systems examined. These were used as references so that the reproductive states of moths caught in the field could be determined at various times in the season. The moths were classified into the following reproductive states:

(1) Young virgin females (newly emerged)

(2) Young mated females

(3) Middle-aged virgin females

(4) Middle-aged mated females

(5) Old virgin females

(6) Old mated females

(i) Young virgin females

These were newly emerged moths. Each abdomen examined was very empty,

the whole reproductive system being small and undeveloped. (As the moths become older the eggs begin to mature and the ovaries expand until eventually they fill the whole abdominal cavity. This occurs regardless of whether or not the moth has mated).

At emergence there was no food in the gut but the moths usually fed as soon as possible after their wings dried and they could fly. In general there was a large amount of fat body in the abdomen.

The corpus bursae and spermatheca were small and in some moths contained a whitish substance. No eggs were found in the common oviduct.

The mean number of mature eggs in virgin females 1-4 days old was 114.6 with a range of 7 eggs/female in a 1-day-old moth to 311 in a 4-day-old moth.

(ii) Young mated females

Moths in this category were 1-5 days old and had mated but not begun to oviposit. Most were 2-3 days old and by this stage many eggs were mature and the ovaries had expanded to fill the whole abdomen.

Food was usually present in the gut but the amount varied. There was a medium to large amount of fat body. The corpus bursae was very inflated and contained a large amount of the whitish substance mentioned earlier. In this were small amounts of a green gelatinous substance, the spermatophore. This was very obvious in newly mated females. The spermatheca was also inflated and filled with a whitish substance.

These moths had not yet begun oviposition so no eggs were present in the common oviduct. The mean number of mature eggs was 121.6/female with a range of 64-203 eggs/female.

(iii) Middle-aged virgin females

Moths in this category were never found in the field but were

present in laboratory cultures. However it is likely that they do occasionally occur in the field.

The abdomen of these moths was usually fat-looking and remained so much longer than in similarly aged, mated moths. This was because unmated moths tended not to begin oviposition until much later than normal and they frequently died without laying any eggs.

There was usually a little food in the gut and a small to medium amount of fat body. The corpus bursae and spermatheca were both small and undeveloped. Eggs were present in the common oviduct of moths that had begun oviposition.

(iv) Middle-aged mated females

Moths were placed in this category if they were more than 3-4 days old, had mated and were ovipositing.

At the start of oviposition, the abdomen of these moths was fat and filled with eggs, both mature and immature. As oviposition continued the abdomen gradually decreased in size. By this stage there was usually only a small amount of food in the gut. The amount of fat body depended on the age of the moth, young moths having a large amount and older moths having comparatively little.

The corpus bursae and spermatheca were inflated and filled with a whitish substance. The green, gelatinous spermatophore was not always visible. It is thought that it gradually breaks down. However the moth could still be identified as having mated because the corpus bursae was always inflated, often to a huge size.

These moths were ovipositing, so eggs were present in the common oviduct. The mean number of mature eggs was 203.2/female, the range, 86 to 337/female.

(v) Old virgin females

This category of moths was also never found in the field but was sometimes present in the laboratory.

The abdomen was thin and very empty with no mature eggs. The whole reproductive system was shrunken and small. Little or no food was present in the gut and there was little fat body. Few unmated moths lived long enough to be put into this category. Most died in middle-age without laying any eggs.

(vi) Old mated females

Moths in this category were thin looking and their abdomens fairly empty of eggs. There was usually no food in the gut and no fat body present. The corpus bursae and spermatheca were large but deflated (like deflated balloons). There were usually eggs present in the common oviduct. The mean number of mature eggs was 45.6/female with a range of 0-120/female.

4.6 Reproductive States in the Field

4.6.1 Live Females

Female moths caught in the first generation in the 1974-75 and 1975-76 seasons and in the second generation in 1975-76, were dissected and their reproductive states examined. The numbers of moths in each weekly sample were small (sometimes only one moth). This was particularly so in the first generations when population numbers were very low. In each case the size of the abdomen, the presence or absence of food in the gut, the amount of fat body, the state of the corpus bursae and spermatheca, the presence or absence of eggs in the common oviduct, the number of mature eggs in the ovaries and the amount of the abdominal cavity occupied by the reproductive system was examined. Their mated state was determined by comparing them with the moths of known age and mated state described in

Section 4.5. The number of mated moths, the number ovipositing and the mean number of mature eggs are given in Table 4.5.

Some moths were seen on dates other than those shown in the table but none were caught. Newly emerged moths were seen throughout each season, even late in the season when the population had declined in numbers. Thus it was not possible to tell how far advanced the season was by capturing female moths and determining their reproductive state.

4.6.2 Dead females

Towards the end of the second generation flight periods each season, dead moths were found in the field. They were not found in the first generations because population numbers were always low and the chances of finding dead moths slight (once they are dead the moths rapidly disintegrate and are usually carried away by ants. Thus all moths collected had died recently).

Nine moths were dissected in all and their reproductive systems examined. The moths were all found dead on the ground near Eucalyptus trees at Langhorne Creek. No dead moths were found in the vineyard itself, apart from those caught in spiders webs.

All the moths had tattered, torn wings, which suggests that they were old. They all had little or no fat body and no food in the gut. The reproductive systems had shrunk and the corpus bursae and spermathecae all contained a whitish substance. These moths exhibited all the characteristics of old mated moths (Section 4.5). An important fact was that by the time they died, the moths had few eggs in their ovaries, (mean number of eggs/female was 45.1, range 0-120 eggs/female), and since the reproductive systems were all shrivelled it was assumed they had realized most of their reproductive potential.

TABLE 4.5 Reproductive states of females caught live in the field in the first generation 1974-75 and 1975-76 and the second generation 1975-76.

Date	No. moths mated	No. ovipositing	Mean no. mature eggs	Total moths
G(1) 1974-75				
2/10/74	2	1	320	2
11/10/74	0	0	(240)	1
17/10/74	5	5	264	5
31/10/74	2	2	20 (0)	3
G(1) 1975-76				
16/10/75	1	0	200 (71.7)	4
11/11/75	2	1	198	2
25/11/75	1	1	105	1
9/12/75	1	1	136	1
G(2) 1975-76				
20/1/76	2	1	152.5	2
28/1/76	1	1	238 (245)	2
3/2/76	4	2	108.5 (39)	7
19/2/76	6	4	184.7 (276)	8

( ) = mean no. mature eggs in unmated females.

4.7 Fecundity

In the preceeding sections only mature eggs (eggs with a chorion) were counted. However these figures cannot be used to estimate the total number of eggs a female lays or is capable of laying. The number of eggs actually laid often bears no resemblance to the reproductive potential of the moths. To estimate this, 3-day-old moths, from a laboratory culture (kept at 25°C), who had not yet begun to oviposit, were killed and the total number of eggs they contained counted. When the moth first emerges there are no mature eggs present but they rapidly develop and mature with time. At the terminal end of the ovarioles the eggs are present as a mass of undifferentiated tissue. This means that the estimates of the reproductive potential given below are underestimates. The eggs were counted as far up the length of the ovariole as individual eggs could be distinguished. The mean total number of eggs/female was 1099 (range 1021-1235). The mean number of immature and mature eggs was 800.3 and 298.7/female respectively.

4.7.1 Fecundity and Temperature

The influence of temperature on fecundity has been studied by many workers e.g. Isely (1938). The fecundity of moths was studied at different temperatures in the laboratory. On emergence, moths were placed in the mating cages for 2 days and then placed in canisters in the various temperatures. The number of eggs laid each day was recorded. The temperatures used were 15°, 20°, 25° and 30°C. Results are given in Table 4.6. No eggs were laid at 15°C. Most eggs were laid at 25°C. Moths lived longer at 15°C than at higher temperatures.

The potential fecundity is approximately 1100 eggs. Fecundity was highest at 25°C but in the field the temperature is constantly changing and thus the rate of oviposition changes also. There was a

marked drop in fecundity from 25 to 20°C and from 25-30°C. Thus if the weather is cold, the rate of oviposition is lower and even though moths live longer the fecundity is low.

4.7.2 Fecundity and Food

Food may influence fecundity because it influences longevity i.e. if adults feed then they will survive longer and thus have a longer period for oviposition. Work has been done in this field by Drooz (1975), Given (1944), Shorey (1963), Macaulay (1973), Cheng (1972), Beckwith (1970) and Latheef & Harcourt (1972).

The effect of adult food on longevity and fecundity was investigated in the laboratory. On emergence, female moths were placed in mating cages in one of the following treatments:

(1) with no food.

(2) with water.

(3) with 10% honey solution.

After 2 days in the mating cages they were placed in oviposition cages at 25°C (still in the treatments). The same moths were used in the 10% honey solution treatment as were used in the 25°C treatment in Section 4.7.1. The eggs laid were counted each day until death. Results are given in Table 4.7. There was no significant difference in longevity between moths fed on water and moths with no food at all. Differences in fecundity were significant. Moths fed on the honey solution lived longer and laid more eggs than those in the other two treatments.

4.7.3 Fecundity and Size

The relationship between moth size and fecundity has been studied by Martyn (1965), Cheng (1972) and Miller (1957). Size largely depends on the amount of food ingested in the larval stages. In the laboratory,

TABLE 4.6 Fecundity and longevity of ♀ moths at different temperatures.

Temperature	No. of moths	Mean longevity (days)	Range (longevity)	Mean fecundity	Range (fecundity)
15	11	19.1	6-27	0	-
20	10	15.3	11-18	69.2	3-167
25	11	10.5	5-15	445.7	105-944
30	13	8.0	4-13	58.2	0-227

TABLE 4.7 Fecundity and longevity of ♀ moths supplied with either no food, water only or 10% honey solution.

Treatment	No. of moths	Mean longevity (days)	Range (longevity)	Mean fecundity	Range (fecundity)
no food	17	6.0	5-7	121.7	0-219
water	17	5.8	3-7	81.0	0-214
honey	11	10.5	5-15	445.7	105-944

larvae were often much smaller than those in the field and the adults also differed in size. Female pupae were weighed soon after they had formed and the fecundity of the resulting moths noted. All moths were fed on 10% honey solution and kept at 25°C. Results are given in Table 4.8. They show that the mean number of eggs laid by heavier moths (i.e. weighing more than 0.3 g.) was almost twice the mean number laid by the lighter moths (weighing less than 0.3 g.).

Thus fecundity is affected by temperature, adult food and the size of the moth.

4.8 Fertility

Often the fertility of moths decreases with age and even mated moths are likely to lay an increasing number of infertile eggs towards the end of their lives. Eggs were sampled each week at Langhorne Creek and their fertility examined. If eggs are fertile, brown specks appear within 24 hours of being laid. If green eggs were found, they were marked and examined at a later date. In all cases they had either developed, hatched or disappeared, in which case it was assumed that they had hatched and the empty egg-shell was lost because once the larva has hatched, the shells dry out and are easily dislodged (field moths brought into the laboratory never laid infertile eggs, (unless they were collected just as they emerged)).

Moths were caught regularly in the field and dissected to determine whether or not they had mated. In all cases, moths that were classified as having begun oviposition, (having mature eggs in the common oviduct), had mated.

The sex ratio (Section 2.5) was shown to change throughout the season from a male dominated ratio early in the season to a female

TABLE 4.8 Influence of size of moth on fecundity.

Moth No.	Weight (g)	Fecundity	
13	0.251	359	
5	0.262	105	
27	0.264	341	mean =
21	0.273	606	334.2
28	0.278	390	
17	0.293	204	
23	0.329	203	
7	0.403	1034	mean =
54	0.417	610	623.0
34	0.478	645	

dominated ratio later. Thus, particularly early in the season when there is an abundance of males, it is unlikely that a female would not mate and lay fertile eggs. Later in the season when the male population has declined, the chances of mating would be less but as mentioned in Section 2.5, all female moths caught late in the season had mated.

In the laboratory infertile eggs were frequently laid because the conditions under which moths will mate are very rigorous. The situation in the laboratory however, has little relevance to the field.

From field data it was concluded that infertility is not an important factor in the biology of Phalaenoides glycine and therefore has little or no effect on the population dynamics of the species.

CHAPTER 5

OVIPOSITION SITES AND FACTORS THAT INFLUENCE THEIR CHOICE

"In our admiration for the unerring skill with which certain moths and butterflies select for oviposition just that plant upon which the larvae will feed, we are inclined to overlook the fact that many species either do not practice this skill or, if possessed of it, frequently err".

This quotation in a paper by Dethier (1959a) on the egg-laying habits of Lepidoptera in relation to foodplants, together with questions which arose from the distribution of vine moth eggs in the field, led to an examination of the oviposition sites of Phalaenoides glycine in the field and the factors that influence their choice.

Distribution studies indicated that the population at Langhorne Creek was not randomly distributed but was patchy (Chapter 3) and it was thought that this patchiness was due initially to the behaviour of the female moth.

5.1 Oviposition Behaviour

Female moths lay eggs singly and not in batches as do many moths. The eggs are usually laid on the undersides of the vine leaves, rarely on top. They are laid close to the edge of the leaf or close to the midrib or veins.

Prior to the deposition of an egg, the moth flutters about amongst the leaves, usually low down, close to the ground. The moth then lands and walks around the edge of the leaf exploring the underside with the tip of the abdomen. There is much extension and contraction of the ovipositor before the egg is actually laid as if many contractions are necessary to move the egg down through the common oviduct and ovipositor.

Once one egg is laid the female may continue probing with the ovipositor and lay another egg close by or she may fly to another site to lay more eggs. From observations in the field it appears that females often lay several eggs on the same leaf or on nearby leaves before flying off to another place where the sequence is repeated. There is evidence that the oviposition site is selected by the female and not chosen at random (see later).

5.2 Oviposition Sites

5.2.1 In the Field

During routine sampling of eggs and larvae to obtain data on population numbers at Langhorne Creek, it became obvious that eggs were being found mainly on the lower branches of the vines i.e. on the canes that were hanging down and trailing on or close to the ground. The position of the eggs, i.e. if they were on trailing or non-trailing canes and whether they were on the top, middle or bottom of the vines, was noted. It was also noted whether those vines with eggs on non-trailing canes, possessed trailing canes. Of the 104 eggs examined, 2 were on the top of the vines, 40 were on the middle and 62 were on the bottom. Differences between these positions were significant ($\chi^2 = 53.1$). Thus the bottom of the vine is the most common oviposition site.

Table 5.1 shows the number of vines with eggs on trailing and non-trailing canes. The χ^2 value for this data is 21.1 which is highly significant. It was concluded that eggs tend to be laid on vines with trailing canes rather than on vines with non-trailing canes and that they tend to be low, close to the ground. When eggs were found on non-trailing canes they were usually on vines that did not possess trailing

TABLE 5.1 2 x 2 contingency table showing the number of vines with trailing and non-trailing canes, with and without eggs.

	No. of vines with eggs	No. of vines without eggs	Total
Vines with trailing canes	52	54	106
Vines with non-trailing canes	38	136	174
Total	90	190	280

canes.

The above applies only to eggs laid in the second generation when the vines have reached their maximum extent of growth. In the first generation, which begins about the time the vines first come into leaf, the eggs are always found close to the main vine stem and on leaves near the main branches. If the vines have suckers sprouting from lower down the stem, these almost invariably have eggs on them.

The most common oviposition site, after the leaves, was the canes.

Dethier (1959a) stated "It is generally assumed that the continued existence of a species is evidence that the eggs are always properly placed", but this is not so. During observations at Langhorne Creek, moths were seen ovipositing in several 'unlikely' sites. One moth laid several eggs on clods of earth close to, but not touching, trailing vine canes. (Overall, though, very few eggs were found on the ground). Eggs were also found on the posts of the vine trellis but again these were always surrounded by vine shoots and leaves. The weeds on the edge of the vineyard on which the moths fed, and also weeds which often grew up through the vines, were searched but no eggs were found.

All the eggs found in the above places were laid within a few centimeters of vine leaves or tendrils and when they hatched, the young larvae would not be far from food.

In home gardens vines are often grown so that they climb over or on various structures. In such situations eggs have been found on rough surfaces adjacent to the vines, such as window sills and wooden balcony railings. The eggs were usually within 10 cm. of the nearest vine leaves. Often vines in home gardens grow amongst nearby plants but eggs were never found on these plants even though they were on the intertwining vine leaves.

5.2.2 In the Laboratory

In fecundity experiments in the laboratory female moths frequently laid eggs in places other than on the vine leaves provided. Each day moths in cages were examined, the eggs counted and their positions noted. These positions were on the

(1) lid

(2) leaf

(3) water container holding the leaf

(4) food or its container

(5) filter paper on the bottom of the cage

(6) clear perspex walls of the cage.

Results are given in Table 5.2. The filter paper was likely to give a biased estimate because old females tended to flap around on the bottom of the cage laying eggs. Thus the figures only include egg counts up to two days before death. If any moth seemed unable to fly properly she was discarded. The results show that the moths tended to lay their eggs on the leaves. The next most usual position was the filter paper. (Differences between the number on the leaves and filter paper are significant, $\chi^2 = 15.6$). In view of the fact that in the field moths have been observed laying eggs on structures close to the vines, it is surprising that more eggs were not laid on the water container holding the leaf, or on the walls. However these were made of clear, smooth perspex. The least "preferred" site was the food container which was clear, smooth glass (of those eggs laid on the food and water containers, the majority were laid on the rough plastic tops). All eggs laid on the lid were on or around the gauze covering the ventilation holes. Thus the moths tend to lay on rough sites.

TABLE 5.2 Oviposition sites in the laboratory.

Site	Average no. eggs/♀	Total no. eggs	% total eggs laid
lid	21.46	279	12.6
leaf	64.38	837	37.8
water container	11.54	150	6.8
food	3.85	50	2.3
filter paper	52.54	683	30.8
walls	16.69	217	9.8
Total	170.46	2216	100

5.3 Factors Influencing Oviposition

5.3.1 Shelter

During the study of oviposition sites in the vineyard most eggs were found on trailing canes and suckers and not on the top or outer parts of the vines. It was thought these were "preferred" sites because they offered the most shelter and protection from prevailing weather conditions. Experiments were conducted in the field at Langhorne Creek to test this hypothesis.

Because the prevailing winds and weather came from a south to south-westerly direction, an experiment was conducted to see if more eggs were laid on the north-eastern side of the vines. Data on the position of eggs on the vines were obtained from routine sampling for population studies. The results are given in Table 5.3. Of the vines with eggs, the mean number of eggs on the south side of the vines was 10.16 while that on the north side was 7.31 (65% and 35% respectively of the total number of eggs found). The results were analysed by a t-test as shown by Snedecor (6th edition pp 114-116, 1962). This method was chosen in preference to a similar method (pp 100, 104) because it does not assume the population variances are the same. The t-test showed that differences between the means were not significant ($t' = 1.19$) and thus it was concluded that there was no difference in the number of eggs laid on the north and south sides of the vines. It was realized later that these results were not unexpected for the observations were made during the second generation by which time the vines offered considerable shelter for the moths.

A new experiment was designed and carried out as follows. Wind-breaks, consisting of a framework of poles and wire netting covered with a dense material (Figure 5.1) were set up around several vines so that

TABLE 5.3 Number of eggs on different sides of the vine (1973-74 second generation).

Date	SOUTH SIDE			NORTH SIDE		
	No. of eggs	No. vines with eggs	Mean no. eggs	No. of eggs	No. vines with eggs	Mean no. eggs
5/2/74	115	12	9.58	11	6	1.83
12/2/74	125	10	12.50	94	5	18.80
21/2/74	26	10	2.60	121	16	7.56
1/3/74	232	13	17.85	41	7	5.86
7/3/74	15	4	3.75	18	5	3.60
14/3/74	5	2	2.50	0	0	-
Total	518	51	-	285	39	-

Figure 5.1 Windbreak around vine at Langhorne Creek.

they were sheltered from the prevailing south and south-westerly winds (they were open to northerly winds but these were not common). Frameworks were set up around other vines but were not covered with the windbreak material.

The windbreaks were set up at the beginning of the 1974-75 first generation just prior to the vines bursting into leaf and before the moths started flying. They remained in place throughout the following two seasons but the experiment was conducted only in the first generation because of the vine growth as explained above. The vines were examined at weekly intervals and the number of first instar larvae noted. The whole vine was carefully searched in each case. Larvae were counted rather than eggs because they were easier to find. Results are given in Table 5.4.

Throughout the generation more larvae were found on the windbreak vines than on the non-windbreak vines. However when the results were analysed it was realized that because larvae had not been removed from the vines each week it was not possible to tell if larvae were counted more than once. So the experiment was repeated in the first generation of the 1975-76 season. This time eggs were counted and were removed each week. Again the whole vine was searched. Results are in Table 5.5.

The results show that differences were large between the number of eggs laid on vines with windbreaks and those without ($t' = 3.13$). It was concluded that more eggs are laid on sheltered vines and thus moths "prefer" sheltered sites for oviposition.

The windbreaks provided not only shelter from the wind but also from rain. However wind is more important than rain in influencing the choice of oviposition site because moths will fly and oviposit in the wind (provided it is not too strong) but in rain they usually do not.

TABLE 5.4 Results of windbreak experiment, Generation (1), 1974-75 season.

Date	No. Larvae on Windbreak vines	No. Larvae on Non-Windbreak vines
31/10/74	1	0
7/11/74	1	0
19/11/74	16	0
28/11/74	21	3
5/12/74	7	0
12/12/74	0	0
Total	46	3

TABLE 5.5 Results of windbreak experiment, Generation (1), 1975-76 season.

Date	No. eggs on Windbreak vines	No. eggs on Non-windbreak vines
2/10/75	0	0
9/10/75	12	0
16/10/75	28	0
27/10/75	38	4
4/11/75	16	2
11/11/75	2	5
18/11/75	0	1
Total	96	12

5.3.2 Wind

Wind influences not only the choice of oviposition site but also moth flight and therefore oviposition.

The effect of wind velocity on flight was studied in the laboratory. Moths were placed in a cage in a wind tunnel and their flight activity noted at several different wind velocities i.e. at 3.3, 5.5, 8.2, 11.0, 13.7 and 22 km/hr. The temperature was approximately 27°C. Moths flew at wind velocities of 3.3, 5.5, 8.2 and 11.0 km/hr. They did not fly at 13.7 or 22 km/hr. At these velocities they flattened their wings and clung tightly to the sides of the cage.

Wind speed records were kept at Langhorne Creek throughout the 1974-75 and 1975-76 first and second generation flight periods. It was difficult to correlate windspeeds with the numbers of moths flying throughout these seasons because moth population numbers changed from week to week. However this data was used to explain the change in numbers in the first generation in 1974-75 (see Chapter 2). Figure 2.6 shows that moth numbers were lower than expected on 24/10/74 and 31/10/74. On these dates the mean windspeed was 24.3 and 16.9 km/hr respectively, thus making these days unsuitable for oviposition (these are mean figures and there were times on both these days, when the windspeed was low enough for flight to take place. Hence the numbers flying in Figure 2.6 on these days are not zero). In the field, in very windy conditions, moths cling to the vines and weeds around the edges of the vineyard. If disturbed they do fly but seem to be carried along by the wind rather than actively flying themselves. Thus in very windy conditions the oviposition rate is reduced in the field.

5.3.3 Food

The presence of adult food often influences the choice of oviposition

site i.e. often more eggs are laid close to a food source than far away.

At Langhorne Creek moths fed on weeds on two sides of the vineyard and on Eucalyptus sp. and fruit trees nearby when these were in flower. Vines close to these food sources were examined to determine if there was a "border" effect i.e. if more eggs were laid on the edge of the vineyard near the food sources than elsewhere in the vineyard. The results showed that the mean number of eggs/¼ vine was 5.63 on vines close to food and 6.44 on vines far away from food. Thus there was no border effect and there is no evidence that the presence of food influences the choice of oviposition site.

CHAPTER 6

MORTALITY

6.1 Predation

There are several predators of the vine moth, mainly of the larval stages, and although only one of these is important in reducing numbers, the others should be mentioned.

6.1.1 Types of Predators

Often insects that are brightly coloured are distasteful to birds and other predators, (or mimic ones that are), e.g. Papilio troilus (Frost, 1942). However vine moth larvae, which are brightly coloured and very conspicuous on both vine and Hibbertia leaves, are eaten by several bird species. These are the Bronze cuckoo Chrysococcyx basalis, the Pallid cuckoo, Cuculus pallidus, (French, 1893) and the Magpie, Gymnorhina tibicen. The Indian Myna, Acridotheres tristis, although introduced into Australia in the hope that it would feed on larvae, was not successful as a predator (McCoy, 1885). In this study no Bronze or Pallid cuckoos were seen feeding on larvae. Magpies were observed eating large larvae but this was not common and occurred in home gardens rather than in vineyards.

There are several bugs mentioned in the literature as being predatory on vine moth larvae. These are Cuspicona sp. (French, 1893), Cermatulus nasalis (Anon., 1947) and Oechalia schellenbergii, (also known as O. consocialis (Gross, 1975)), (Anon., 1938, 1943, 1947; Fenner, 1961; McKeown, 1942; Monro, 1957). The first two species have not been observed either in the vineyard or in home gardens. Thus though they might eat larvae if presented with them, they have not been found naturally feeding on them in this study. The third bug, Oechalia

schellenbergii is important as a predator not only of vine moth larvae but of other economically important pests also (Cullen, 1969).

The above are the only predators found of the larval stages. No predators (or parasites) have been found of the egg stage and no predators have been found of the pupal stage. In the adult stage predation has been observed but it seems mostly to have been accidental. Several moths were found caught in spiders webs but although the vineyard contains many spiders, the number of moths caught by them (approximately 7 over three years) was negligible. On rare occasions robber flies have been observed carrying off adult moths but robberflies were rarely seen in the vineyard.

6.1.2 Oechalia schellenbergii - Life History

O. schellenbergii is widely mentioned in literature on the vine moth. The adult bugs are large, approximately 12 mm long. They are easily recognized (Figure 6.1) by the large spines on either side of the thorax. The eggs are black and are laid in batches (Figure 6.2) on the vine leaves and on weeds growing in the vineyard. The mean number of eggs/batch for 15 batches is 18.5 (range 8-50). The young nymphs are black and red and they retain this colour (although in changing patterns) throughout the nymphal stages, becoming brown on moulting to adults. The young nymphs remain huddled about the egg batch from which they hatched, for several days after hatching and gradually move away as they become older.

All stages of the bug feed on vine moth larvae. Large bugs usually feed on large larvae (4th, 5th and 6th instars) while small bugs (nymphs) tend to feed on smaller larvae. However nymphs have also been seen feeding on large larvae. Adult bugs are frequently observed in the vineyard with larvae impaled on their very stout proboscis (Figure 6.3).

Figure 6.1 *Oechalia schellenbergii* - adults mating.

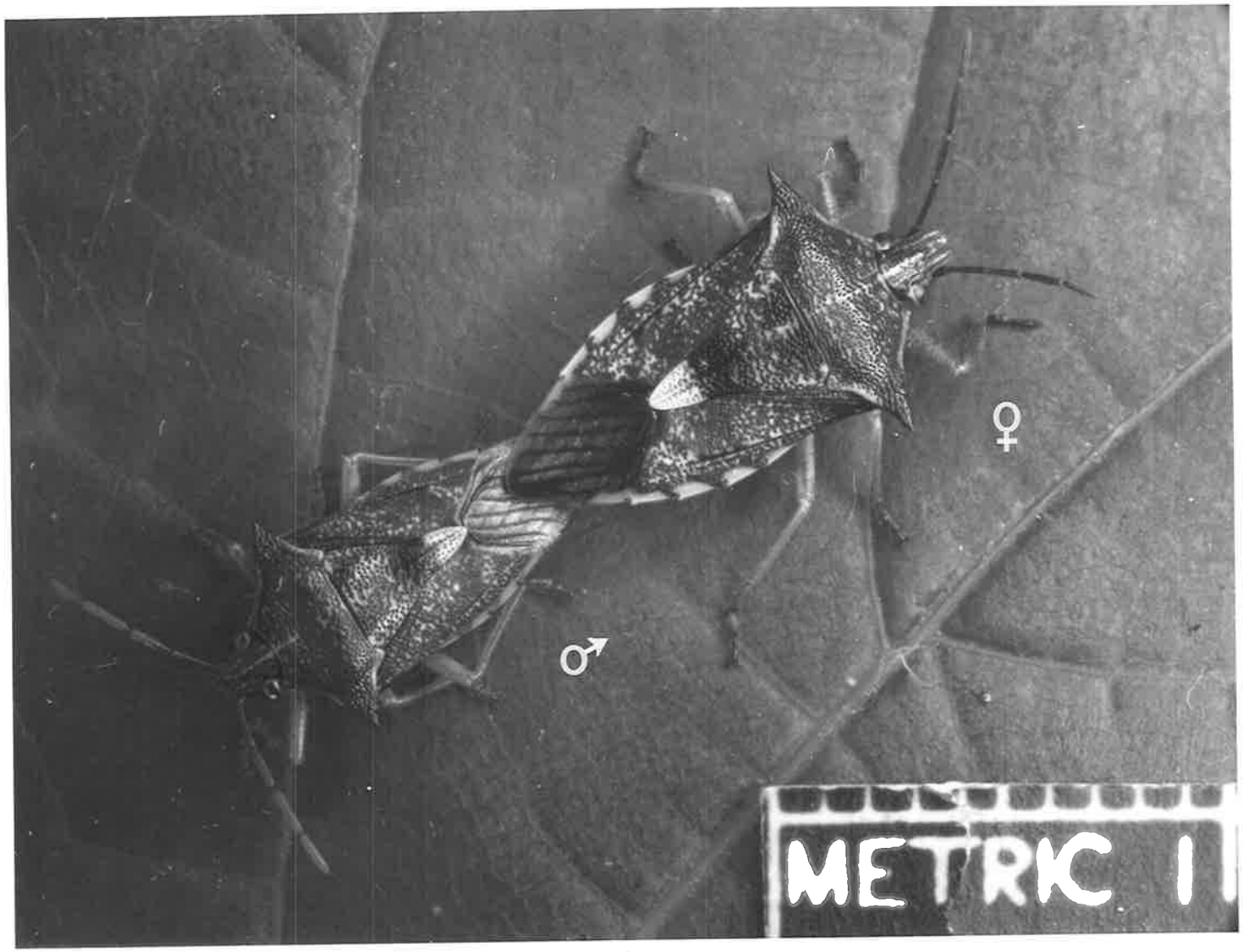

♀
♂
METRIC 1

Figure 6.2 *Oechalia schellenbergii* - eggs.

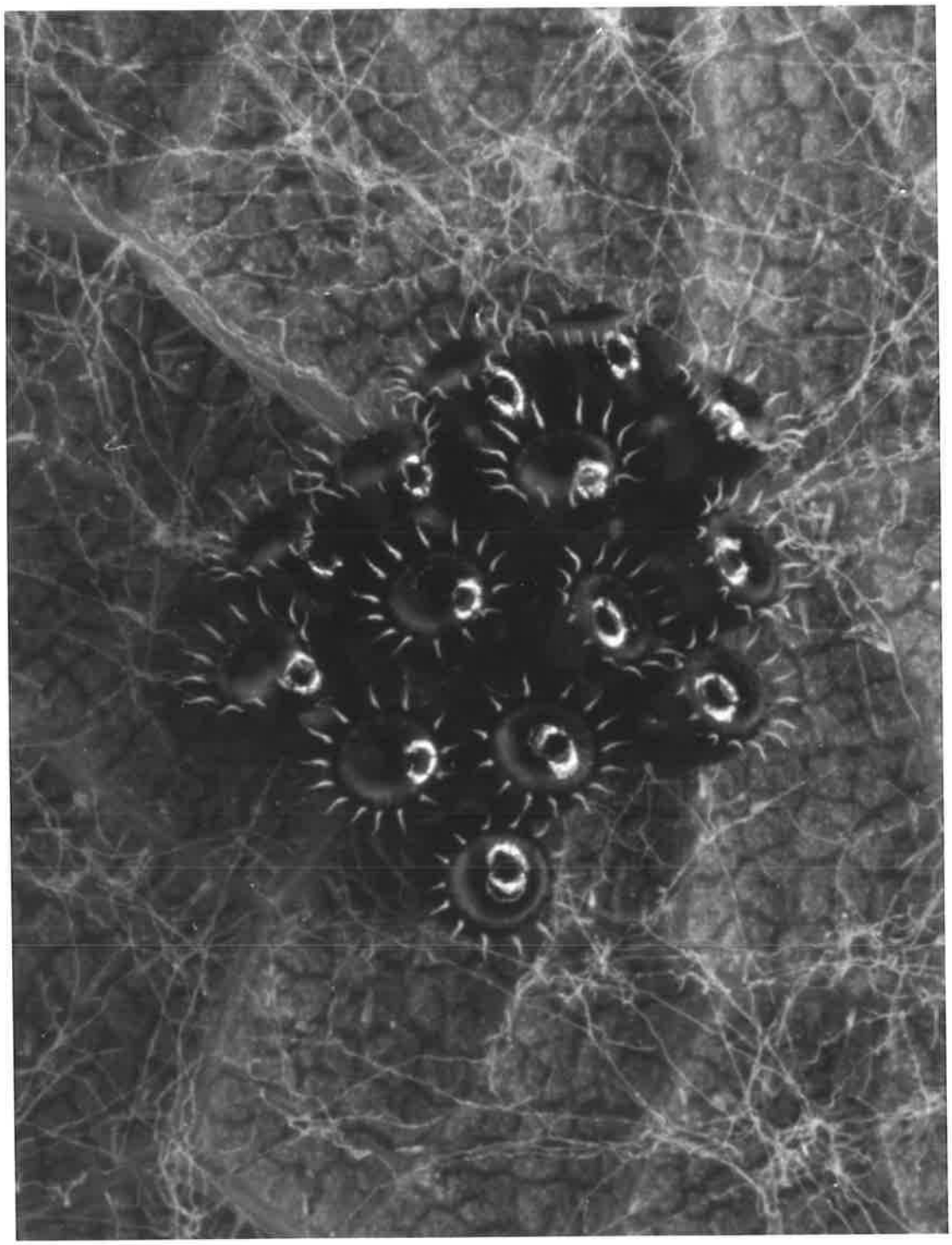


Figure 6.3 *Oechalia schellenbergii* - adult preying on a sixth instar larva of *Phalaenoides glycine*.

They kill the larva by sucking out the body contents and even if the bug only has one meal from a larva, that larva will die. Frequently the larvae are sucked completely dry.

In the laboratory, bugs, both adults and nymphs, were observed with the proboscisinserted into the vine leaf - presumably feeding or drinking. If they were not subsequently given larvae to eat they died. Bugs kept with a plentiful supply of larvae were never observed feeding on leaves and it is thought that they normally feed on leaves only when food is scarce. However if they are to survive and reproduce, a constant supply of larvae is necessary, although they can survive for several days without food.

An experiment was conducted in the laboratory to determine the number of larvae (on average) a bug would eat in its lifetime, from hatching to death as an adult. The bugs were kept at 23^{o}C with a constant supply of larvae. They fed, grew and reproduced readily as long as the food supply was adequate. It was found that in the nymphal stages each bug will consume approximately 8 larvae, and in the adult stage approximately 12 larvae. Thus the average number of larvae eaten per bug per lifetime was 20.

The behaviour of larvae and predators was observed in the laboratory. The bug, once it perceives the larva, usually proceeds straight towards it, stopping occasionally with antennae waving. Once it reaches the larva, the proboscis is extended and pushed into the larva. On first contact the larva usually thrashes the forepart of its body from side to side - a common defence reaction. However this has never been observed to deter the bug. Once the proboscis has penetrated the cuticle, the larva remains quiet. Occasionally even on penetration no resistance is offered and the larva seems to be unaware of the presence of the bug.

Usually bugs attack the posterior end of the larvae but they have also been seen feeding from the thoracic region.

A parasite of O. schellenbergii eggs was found in this study. Details are given in Appendix 4.

6.1.3 Oechalia schellenbergii - Seasonal History

In the field bugs first appeared in the vineyards in spring during the first generation of vine moth larvae. They were first observed in late October or early November when the larval population was building up to a peak. Bugs reached a peak in numbers approximately three weeks after the larval peak (Figures 6.4 —> 6.6) and then declined. By mid-January no bugs were present. It is not known where they go when they leave the vineyard.

Adults reappeared in February as the second generation of larvae was building up to a peak. Again the bug peak was approximately three weeks after the larval peak. By the end of April - early May they had gone again to reappear next spring.

6.1.4 Oechalia schellenbergii - Population Numbers

Bugs were sampled at Langhorne Creek to estimate the numbers present in the vineyard. Sampling adult bugs was difficult because they were very shy and flew off at the slightest disturbance. When they were seen, as soon as they became aware of any movement, they ran and hid either behind stems or under leaves. Thus the number of adults seen in the vineyard is a gross under-estimate because for every one observed many were missed. However all sightings of adults were noted. The bug population was estimated from the numbers of eggs and nymphs that were found. The nymphal stages were included because these cannot fly. Nymphs are brightly coloured (black and red) and unlike the greeny/brown adults are very conspicuous on the leaves. They were sampled each week

Figure 6.4 Mean number of bugs and larvae/¼ vine in the first generation 1973-74.

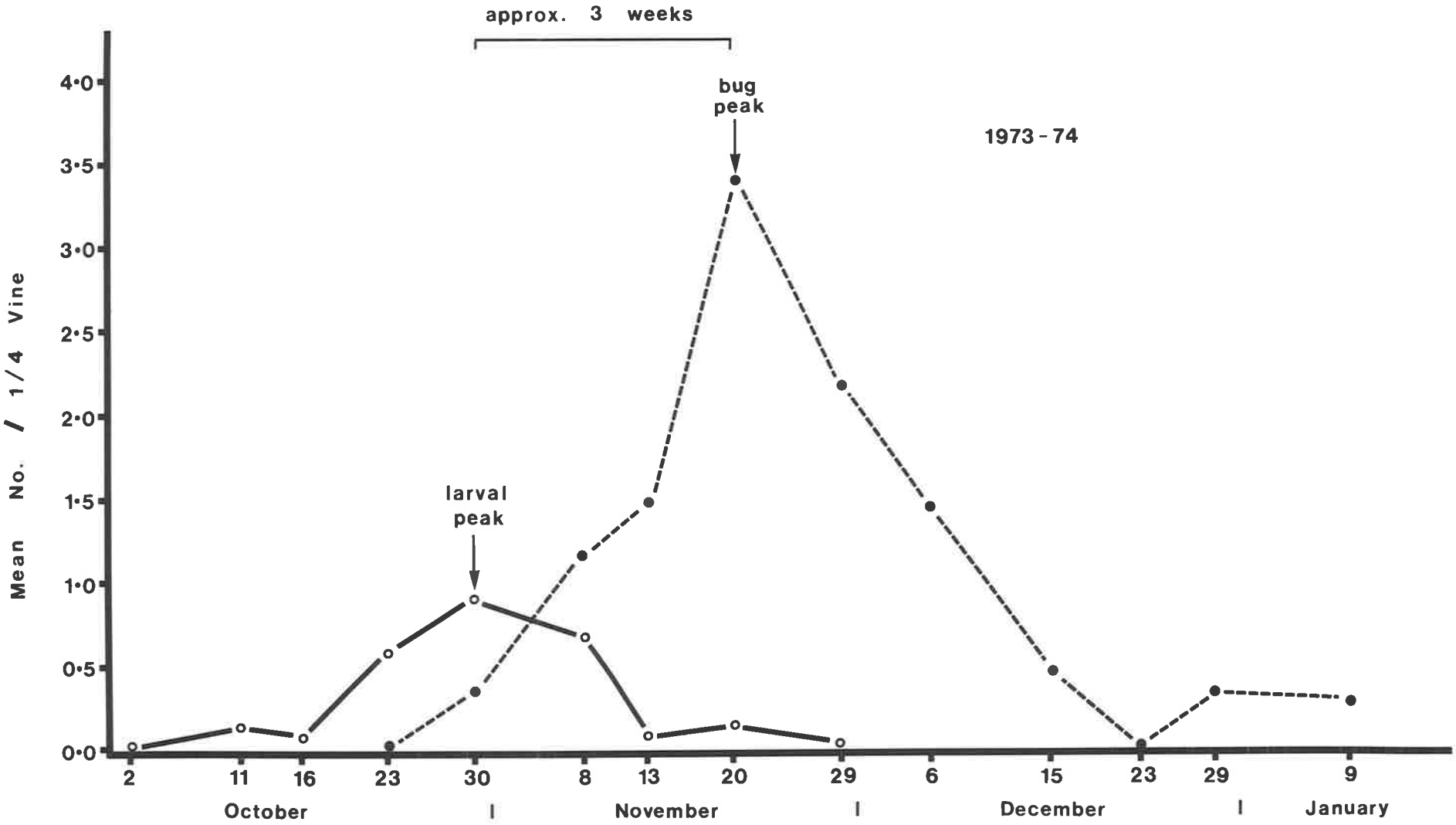

approx. 3 weeks
bug peak
1973 - 74
larval peak
Mean No. / 1/4 Vine
4·0
3·5
3·0
2·5
2·0
1·5
1·0
0·5
0·0
2
11
16
23
30
8
13
20
29
6
15
23
29
9
October
November
December
January

Figure 6.5 Mean number of bugs and larvae/¼ vine in the second generation 1973-74.

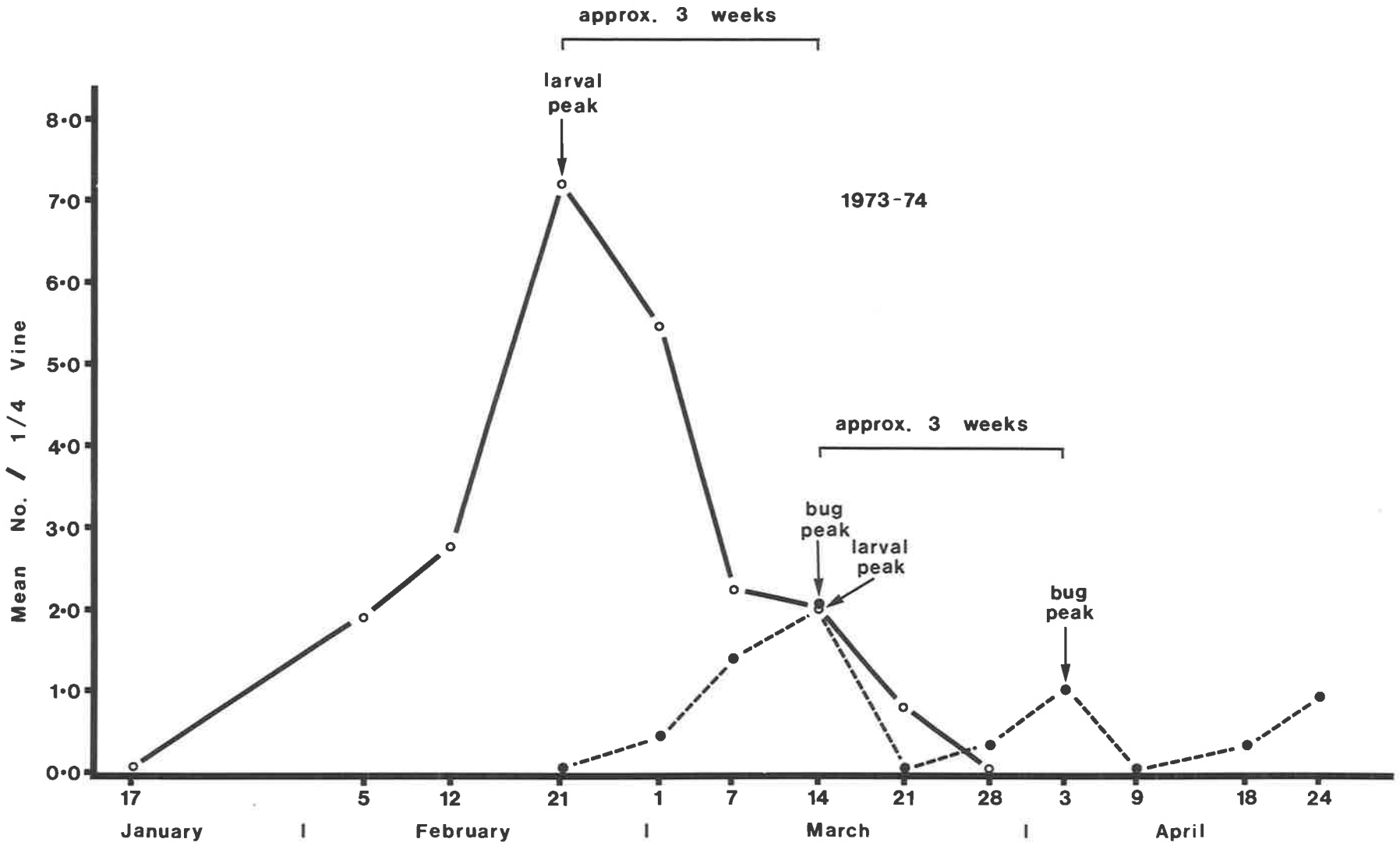
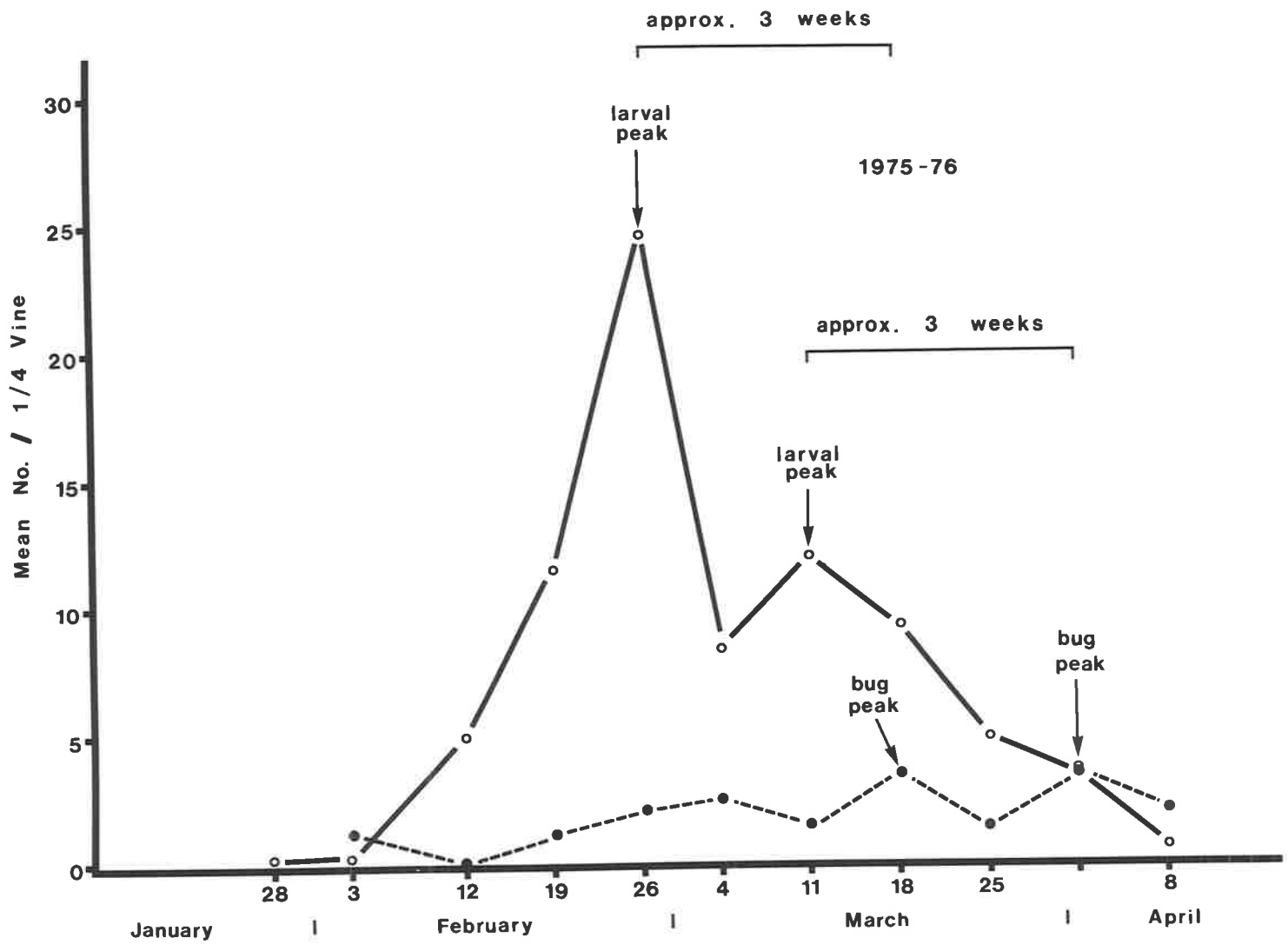

approx. 3 weeks
larval peak
1973-74
approx. 3 weeks
bug peak
larval peak
bug peak
Mean No. / 1/4 Vine
8·0
7·0
6·0
5·0
4·0
3·0
2·0
1·0
0·0
17
5
12
21
1
7
14
21
28
3
9
18
24
January
February
March
April

Figure 6.6 Mean number of bugs and larvae/¼ vine in the second generation 1975-76.


approx. 3 weeks
larval peak
1975-76
approx. 3 weeks
larval peak
bug peak
bug peak
Mean No. / 1/4 Vine
30
25
20
15
10
5
0
28
3
12
19
26
4
11
18
25
8
January
February
March
April

by the same methods used for larval sampling. Results are shown in Table 6.1.

In the first generation, 1973-74 season, the population numbers of bugs were large compared with those in the first generations in the 1974-75 and 1975-76 seasons. In 1973-74 the mean number of bugs/¼ vine was 1.18 (with a peak of 3.40). In 1974-75 no eggs or nymphs were found in the first generation and only 4 adults were seen. Thus the mean number/¼ vine could not be estimated. In 1975-76 only 28 eggs and nymphs were found altogether. The mean number/¼ vine was 0.64.

In the second generation, 1973-74, the number of bugs decreased slightly from that of the first generation, the mean number/¼ vine being 0.74 with a peak of 2.05. In the second generation 1974-75, a meaningful estimate of the number/¼ vine could not be obtained from the one sample, but population numbers were very low.

In the 1975-76 second generation, the bug population reached its highest peak in the study. The mean number of bugs/¼ vine was 1.92 with several peaks. Throughout this season evidence of bugs, either larvae killed by bugs (these were easily identified as their bodies had been sucked dry), fecal matter or eggs, nymphs or adult bugs themselves, was present on every vine examined after the end of February.

During this generation several vines were observed with 200 or more larvae and up to 40 or more bugs in all stages from egg to adult. Consequently many of the larvae were eaten, but not before the vines were defoliated.

6.1.5 Importance of Predators

In general birds, spiders and robberflies were not considered to be important predators of the vine moth, particularly in large vineyards where they were not often seen.

TABLE 6.1 Results of weekly sampling for bugs over 3 seasons at Langhorne Creek (1973-76) and the mean number of larvae/¼ vine.

Season	Generation	Total no. adults seen	Total no. eggs + nymphs	Mean no. eggs + nymphs/ ¼ vine	Mean no. larvae/ ¼ vine
1973-74	(1)	23	470	1.18	0.33
	(2)	3	267	0.74	2.80
1974-75	(1)	4	0	0	0.29
	(2)	1	45	2.81	14.65
1975-76	(1)	1	28	0.64	0.59
	(2)	19	246	1.92	7.96

The predator that does affect larval population number and therefore is important is Oechalia schellenbergii. Figures 6.4-6.6 show the population numbers for bugs (eggs + nymphs) and larvae throughout the first and second generations in 1973-74 and the second generation 1975-76. Examination of the mean numbers of larvae/¼ vine together with the mean numbers of bugs/¼ vine from 1973-76 (Table 6.1) shows that the bug and larval population fluctuations followed the same trends.

Once the mean number of bugs/¼ vine was obtained each week the total number of bugs in the vineyard each week could be estimated. Similar estimates were made for larvae. Only data from the first and second generations in 1973-74 and the second generation in 1975-76 were used. Table 6.2 shows the mean number of bugs and larvae/¼ vine and the estimated number of bugs and larvae present in the vineyard each week.

In the first generation in the 1973-74 season bugs were first observed on 30/10/73. At this time the larval population was at a peak. In the second generation 1973-74, bugs were first noted on 28/2/74, just after the peak in larval numbers. In both cases, as the larval population numbers declined, bug population numbers increased and for several weeks there were far more bugs in the vineyard than larvae. This immediately raised the question of how the bugs survive if there are not enough larvae for them to feed on. Some bugs may die from lack of food but they are capable of moving to other areas where there is food. Also, bugs are not dependent on vine moth larvae for food but will eat many other Lepidopterous larvae (e.g. Epiphyas postvittana - the Light Brown Apple Moth, which is also found in vineyards). In the laboratory, if short of food, they became cannibalistic.

The time lag between the peaks in larval and bug numbers ensures the survival of the vine moth. When the bug population is at its peak

TABLE 6.2 Estimated numbers of larvae and bugs in the vineyard.

Date	Mean no. larvae/ ¼ vine	Mean no. bugs/¼ vine	Estimated total no. larvae	Estimated total no. bugs
G (1) 1973-74				
30/10/73	0.90	0.35	2995	1156
8/11/73	0.68	1.15	2263	3827
13/11/73	0.08	1.48	266	4925
20/11/73	0.15	3.40	499	11315
29/11/73	0.03	2.18	100	7255
6/12/73	0	1.45	0	4826
29/12/73	0	0.35	0	1165
9/1/74	0	0.28	0	932
G (2) 1973-74				
1/3/74	5.43	0.43	18071	1431
7/3/74	2.23	1.40	7421	4659
14/3/74	2.00	2.05	6656	6822
28/3/74	0	0.33	0	998
3/4/74	0	1.05	0	3494
18/4/74	0	0.35	0	1165
24/4/74	0	0.95	0	3162
G (2) 1975-76				
3/2/76	0.13	1.07	433	3561
19/2/76	11.46	1.08	38139	3594
26/2/76	24.83	2.08	82634	6922
4/3/76	8.17	2.50	27190	8320
11/3/76	11.75	1.50	39104	4992
18/3/76	9.25	3.50	30784	11648
25/3/76	4.92	1.25	16374	4160
1/4/76	3.60	3.53	11981	11748
8/4/76	0.50	2.00	1664	6656

the larval population has already declined due to pupation and therefore is not available as food. This difference in timing is characteristic of predator-prey relationships and ensures the survival of both predator and prey species (Andrewartha & Birch, 1954 pp 414).

In the second generation 1975-76, larval population numbers were high. Bugs were present throughout the larval period but except at the very beginning and end of the generation, there was always a large excess of larvae.

From the above discussion it is evident that even though vine moth larvae have only one main predator, this predator is an important one, one that is capable of being very destructive to a population of larvae and is therefore very important as an agent in the biological control of Phalaenoides glycine. There is much scope for further work on the relationships between the vine moth and this bug.

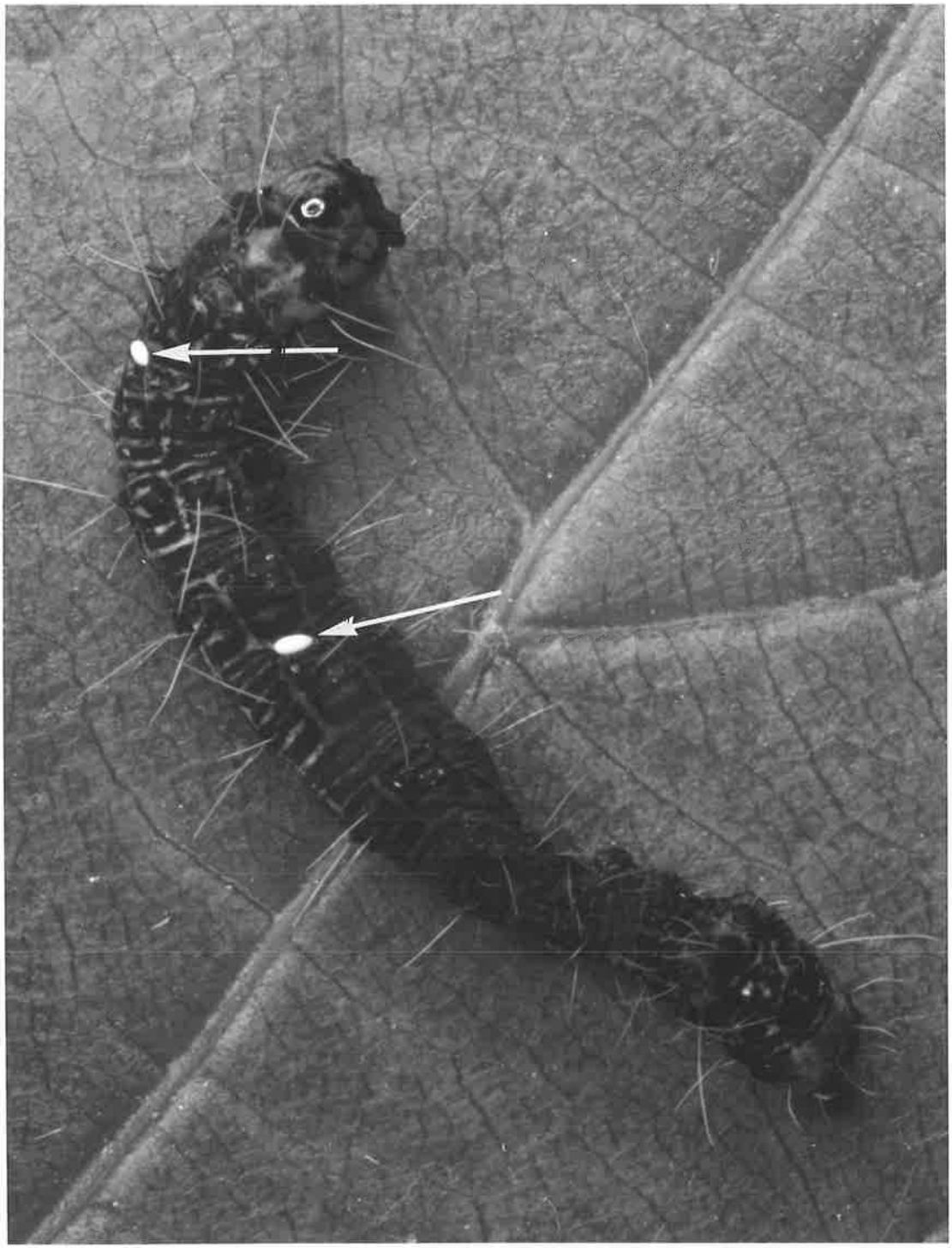
6.2 Parasitism

There are several insects parasitic on Phalaenoides glycine. Among these are several species of flies and wasps. Parasites have been found of the larval and pupal stages but not of the egg and adult stages.

6.2.1 Tachinid Flies

(i) Species and Life history: There are two species of Tachinid flies parasitic on the larval stages of the vine moth. These are Winthemia sp. and Exorista sp. cf. sorbillans (Wied.). They are large, bristly, grey and white flies, very similar in appearance, but Winthemia sp. has a grey head whilst Exorista sp. has a yellow head. Both are internal parasites. The eggs are laid on the external surface of the host larva around the head and on the body (Figure 6.7). The eggs are white and oval in shape. On hatching the parasite larvae burrow through

Figure 6.7 Sixth instar larva killed by Tachinid fly parasites. Arrows show Tachinid eggs.



the egg shell straight into the host. Here they feed until the host is ready to pupate. Then they either pupariate inside the larva (thereby killing it) or more usually emerge and pupariate nearby. Several parasites may emerge from one host.

The eggs are usually laid on 6th instar larvae and less frequently on 5th instars. If eggs are laid on 5th instars, the larvae do not moult to the 6th. The adult flies differ markedly in size depending on the amount of food they consume as larvae. If several emerge from one host often one is very big and the others tiny (sizes range from 4 mm. to 10-11 mm. in length).

Flies are present in the vineyard when the numbers of large larvae are at a peak. This is usually about late November, early December in the first generation and from late February through to the end of April or early May in the second generation. They overwinter as pupae in cells constructed by the host larvae.

Another species of fly, Rutilia speciosa Er., is mentioned by Fenner (1961) as a parasite of vine moth larvae but was not found in this study.

(ii) Abundance: Fifth and sixth instar larvae of P. glycine were collected at Langhorne Creek at weekly intervals during the second generation each year. They were brought back to the laboratory where they were reared through to pupation. The number of parasites that emerged was noted. These larvae were collected from the leaves. In the 1974-75 and 1975-76 seasons larvae were collected from the posts where they pupate. In 1975-76 some were also collected from the soil together with prepupae found wandering on the ground.

Results are given in Table 6.3. The total % parasitism by both Tachinid species in 1974-75 (i.e. in all sites) was 62%. That in 1975-76 was 33%. The data shows that parasitism followed the same general trends

TABLE 6.3 % parasitism at different sampling sites.

Sampling site	Generation	Total no. larvae sampled	No. larvae parasitized	% parasitism
leaves	(2) 1972-73	200	26	13
	(2) 1973-74	51	17	33
	(2) 1974-75	76	44	58
	(2) 1975-76	181	48	27
posts	(2) 1974-75	112	72	64
	(2) 1975-76	78	23	29
soil	(2) 1975-76	222	73	33
ground	(2) 1975-76	83	42	51

as predation i.e. increasing when the larval population increased and decreasing following a decrease in larval numbers. Winthemia sp. was more abundant than Exorista sp. Some larvae were parasitized by both (Table 6.4). Usually there was only one parasite/host but up to 4 have been found in a single larvae (Table 6.5).

The above discussion has been concerned with parasitism at Langhorne Creek. Tachinid parasites were also found at the Waite Institute, North Adelaide and Oakbank where samples were taken on a few occasions only. Four percent of larvae collected at Oakbank at the end of the 1972-73 season were parasitized by Tachinids. At the Waite Institute in 1973-74, 41.7% of larvae collected were parasitized and at North Adelaide in 1975-76, 17% were parasitized by these flies. All these collections were from vines in home gardens. Winthemia sp. again was most common (60% of parasitized larvae contained this species, 33% Exorista sp. and 7% both).

6.2.2 Hymenopterous parasites

(i) Species and Life history: There are four species of Hymenoptera that have been found parasitizing Phalaenoides glycine. One is a Eulophid wasp, one is a Eurytomid and the other two are Ichneumonids.

The Eulophid wasp, Euplectrus agaristae, is very small (approximately 2.5 mm long), and is an external parasite of the larval stage. Detailed descriptions of the wasp and its biology are given by Noble (1936, 1938). It attacks only 4th, 5th and 6th instar larvae, laying more eggs on the larger larvae. The eggs are laid in batches on the back of the host and beside each egg the female wasp pierces a hole in the host integument. When the egg hatches it begins feeding through this hole. The parasites remain fixed in the one position throughout their larval life. The host,

TABLE 6.4 % of parasitized larvae parasitized by two species of Tachinid flies.

Generation	% of parasitized larvae parasitized by		
	Winthemia sp.	*Exorista* sp.	Both
(2) 1973-74	71.1	21.1	7.8
(2) 1974-75	75.0	25.0	0.0
(2) 1975-76	83.3	11.1	5.6

TABLE 6.5 Number of larvae with 1 or more parasites.

Number of parasites x	No. of larvae with x parasites	
	1973-74	1975-76
1	11	18
2	4	5
3	2	1
4	0	1

when first parasitized moves and behaves normally but gradually all movement and feeding cease. The parasite larvae continue to grow in a compact mass (Figure 6.8). By the time they are ready to pupate the host larva is dead and they crawl underneath and pupate in a rough cocoon. Later tiny wasps emerge.

The two Ichneumonid parasites, Ecthromorpha intricatoria and Lissopimpla semipunctata, are large red and black species approximately 20 mm long. They are pupal parasites and are able to probe through wood and soil with their large ovipositors to deposit their eggs. If more than one egg is laid in a host, only one survives. Females observed ovipositing in the laboratory always successfully found the host even when it was embedded under bark. They usually attacked the anterior end of the pupa. If the pupa was turned around, they searched until they again found the head end before continuing oviposition. Adult wasps emerge straight from the pupa through a hole in the anterior end.

Eurytoma sp. is a minute (approximately 3mm. in length), Eurytomid parasite of the pupal stage. Up to 60 parasites emerged from each host pupa.

The literature mentions a small Chalcid wasp parasitic on the egg stage of Phalaenoides glycine (Anon., 1938, 1943), however no such parasite was found in this study.

(ii) Abundance: Euplectrus agaristae was never found at Langhorne Creek. Neither was it found in the Southern Vales District. However it is prevalent in commercial vineyards in the Coonawarra area at certain times. It was found around Adelaide in home gardens though even here it was not common, (approximately 3% of larvae collected in 1974-75 and 4% in 1975-76 were parasitized by this wasp).

Ecthromorpha intricatoria and Lissopimpla semipunctata were both

Figure 6.8 Sixth instar larva parasitized by *Euplectrus agaristae*

(a) parasite larvae in early stages of development.

(b) mature parasite larvae.

(c) parasite larvae pupating beneath the dead caterpillar.


a
b
c

recorded at Langhorne Creek. The incidence of parasitism by these species was very low, 3.3% in 1973-74 and 1.4% in 1975-76.

Only three specimens of P. glycine were found parasitized by Eurytoma sp.. These were all found at Langhorne Creek in the 1975-76 second generation. In all 175 of these wasps emerged from the three pupae.

6.2.3 Importance of Parasites

The incidence of parasitism by wasps was low in vineyards (and in home gardens) and it is unlikely that they would have a large effect on population numbers. Thus they are not considered important in the mortality of Phalaenoides glycine.

Tachinid flies have a greater influence. The proportion of larvae killed by these parasites was quite high in some years, and while they are not as effective as Oechalia schellenbergii, the predator discussed earlier, they are important in reducing population numbers. Combined with O. schellenbergii they have a considerable effect on the population.

6.3 Disease

A disease caused by a granulosis virus has been found in Phalaenoides glycine in the field. The virus was isolated from dead larvae in the late 1960's by Carl Reinganum of the Victorian Department of Agriculture (pers. comm.). However, beyond diagnosis, no further work has been done on the virus.

Symptoms of the disease are typical of virus diseases. The infected larva initially goes through a period of lethargy when it ceases to feed and movement becomes slow and finally stops. By the time death occurs the body contents are completely liquified and milky-brown in colour due to high concentrations of the viral particles. The characteristic posture

of an infected larva is hanging suspended by the prolegs from a leaf or stem with the anterior part of the body dangling below. This pose however is also characteristic of other diseases such as nuclear polyhedrosis viral diseases, (Steinhaus, 1948), and confirmation of a granulosis disease must be made with the electron microscope although a phase contrast microscope can be used to make a tentative diagnosis first.

In laboratory cultures this disease was a great problem but by ensuring cleanliness in the rearing containers and eventually by keeping each larva in a separate container the problem was partially overcome. However if larvae were at all stressed (i.e. starved or handled roughly) they succumbed. It is thought the disease may be latent and only become active when larvae are stressed. The symptoms exhibited by larvae all indicated a viral disease but its identification was not confirmed.

Any disease found in pest populations is of great potential importance. However in the field only one (possibly two) larva was diagnosed as having died from this disease. Population numbers varied from very low to very high but diseased larvae were not found. Thus it was concluded that disease is not important in the mortality of Phalaenoides glycine in the field.

6.4 Other Causes of Mortality

6.4.1 Flooding

The vineyards at Langhorne Creek are deliberately flooded in winter (and often accidentally at other times) each year. At such times the ground surface is covered with water and often the vines and posts are submerged. Flooding usually lasts for 2-3 days but can last for longer periods when rainfall is excessive. When flooding occurs in winter Phalaenoides glycine is in diapause in the pupal stage, buried in the soil or in fence posts.

An experiment was conducted in the laboratory to determine the effect of flooding on diapausing pupae. Pupae were collected in mid-winter and brought back to the laboratory where they were placed in various treatments at 7°C in the dark. The treatments were:

(1) submerged in water.

(2) in flooded soil.

(3) in damp soil.

(4) in dry soil.

Each day they were examined and their survival noted. They were then placed at 20°C where development was completed and emergence occurred.

This experiment was initially set up in 1975 with 40 diapausing pupae. They were placed in the four treatments at 7°C for four days before being transferred to 20°C. All subsequently emerged. In the winter of 1976, 80 pupae were collected and placed in the treatments at 7°C for 3 weeks. Results are given in Table 6.6. All pupae survived the three weeks at 7°C. Those that died did so when placed in 20°C. This was surprising because it was thought that they would not be capable of surviving for long periods completely submerged in water.

Thus flooding is not as important as first thought as a cause of mortality, at least not in diapausing pupae. It may have a greater effect if it occurred at a time when the pupae were not in diapause.

6.4.2 Temperature

All stages are able to survive in a wide range of temperatures. In the laboratory temperature is important in rearing insects, particularly when they are kept at constant temperatures. Table 6.7 shows the survival of eggs, larvae and pupae at different constant temperatures. Mortality is high at high temperatures - 100% at 35°C (LD_{50} = 4.9 days (see Appendix 3)). In the field temperatures higher than this are often encountered

TABLE 6.6 Results of an experiment on the effects of flooding on diapausing pupae.

Treatment	No. of pupae* alive	dead	% survival
water	12	8	60
flooded	20	0	100
damp soil	17	3	85
dry soil	17	3	85

* after 3 weeks at 7°C and 5 weeks at 20°C.

TABLE 6.7 % survival of different stages at several temperatures.

Stage	% survival at completion of stage at 10°C	15°C	20°C	25°C	27°C	30°C	35°C
egg	0	100	100	100	100	90	0
larva	0	95	100	100	80	70	0
pupa	*	100	100	100	100	90	0

* = survived indefinitely

particularly in the second generation during summer. However in the field they are maintained for short periods only and thus are not lethal to the insects.

Thus, in the field, temperature is not considered to be an important cause of mortality. Nevertheless it does influence activity and rate of development (Section 8.2).

6.4.3 Rain

This has little effect on mortality except in the early larval stages. First instar larvae particularly are easily drowned in droplets of water that form on the leaves and in the leaf axils. They may also be washed off the leaves. However they are usually found on the underside of leaves and are thus protected from rain.

6.4.4 Mortality of eggs in the field

Leaves on vines carrying large numbers of eggs in the second generation of the 1973-74 season were tagged and the position of the eggs marked. Their subsequent development was followed until they either hatched or were classified as dead or infertile. Of 519 eggs examined, 393 (76%) hatched, 126 (24%) died and none were infertile. Eggs classified as 'dead' all began development (i.e. turned brown) but failed to complete development and died without hatching. These eggs were all dry in appearance and although eggs take on such an appearance when about to hatch, none hatched. It was thought that this may be due to desiccation as moisture has been shown to be important in hatching in many species (Uvarov, 1931). No eggs were infertile. In fact infertile eggs have never been observed in the field (if eggs are fertile they turn brown within 24 hours of being laid; infertile eggs remain green).

Thus it was concluded that there was some mortality in the egg

stage and that death was probably due to desiccation.

6.4.5 Miscellaneous causes

These include failure to emerge successfully from the pupa, failure to pupate and failure to moult successfully from one larval stage to another. None of these is an important cause of mortality because they rarely occurred.

Ploughing may cause death but it was not considered important because so few pupae were found in the soil and those that were were in areas not covered by the plough e.g. down beside posts and vine stems.

When larvae pupate in cracks in posts they often pupate one on top of the other so that the last to pupate is nearest the entrance to the crack. Larvae that pupate first thus are deepest in the crack and because they will probably emerge first they may be unable to reach the outside. Some half-emerged moths were found dead in fence posts but it was impossible to tell if they had pupated in the same season as those on top and thus died because they could not emerge to the outside.

Such a cause of death would have a considerable effect on population numbers because most larvae pupate in cracks in posts (see Section 2.4.4).

CHAPTER 7

INSECT - PLANT RELATIONSHIPS

The grape vine, Vitis vinifera, was introduced into Australia early last century. Since then Phalaenoides glycine, a native insect, has become more associated with it, until now it is the major foodplant of this species. Early literature such as that of Lewin (1822) described Glycine bimaculata as being the main foodplant in New South Wales, but stated that occasionally larvae were found on grape vines. McCoy (1885) stated that in Victoria, before the introduction of the grape vine, larvae fed on Gnaphalium luteoalbum which was very common. However when vines were introduced and vineyards set up, Phalaenoides glycine abandoned this plant for the grape vine and increased enormously in numbers. It was never later found on Gnaphalium luteoalbum. French (1893, 1916) also refers to the shift from native foodplants to grape vines.

Glycine bimaculata and Gnaphalium luteoalbum were not the only native foodplants mentioned. Others were Hibbertia sp. and Glycine clandestina (French, 1916; Jones, 1967). Larvae are now also found on Fuchsia sp. and ornamental creepers such as Glory vine, Vitis kaempferi, and Virginia Creeper, Vitis quinquefolia, (Anon., 1943, 1952, 1965; Fenner, 1961; French, 1916; Jones, 1967).

Experiments were conducted in the laboratory to determine if Phalaenoides glycine would accept and survive on its original native foodplants and if adult females would oviposit on them.

7.1 Survival of Larvae on Different Foodplants

The following plants were used in an experiment to test the survival of larvae on different foodplants:

(1) Vines (old leaves)

(2) Vines (new leaves)

(3) *Fuchsia* sp.

(4) *Hibbertia sericea*

(5) *Hibbertia stricta*

(6) *Hibbertia scandens*

Other native foodplants were not available. *H. sericea* and *H. stricta* are native to the Adelaide hills area and *H. scandens* is native to New South Wales but is commonly grown in gardens in Adelaide. Old and young vine leaves were used because they differ in nutritive value and larvae were usually found on new leaves when these were available.

On hatching, first instar larvae were placed in containers with a fresh leaf of the appropriate foodplant. At the beginning of the experiment, when larvae were very small, they were all placed in one container but as they grew they were separated into smaller groups and by the fourth instar all were kept singly. This reduced the possibility of death due to disease which was a major problem when large numbers of larvae were reared together. Larvae were kept at 23^{o}C with a light regime of 14 hours light, 10 hours dark. Fresh food was given and the containers cleaned every second day or more often if necessary. Each day larvae were examined and their survival noted. Results are given in Table 7.1.

The survival of larvae fed on old vine leaves was low compared with that on young vine leaves. Survival on *Fuchsia* sp. was high although lower than on new vine leaves. After vines, *Fuchsia* sp. is the most common foodplant of vine moth larvae in the field.

Of the three species of *Hibbertia*, only *H. scandens* supported *Phalaenoides glycine* larvae throughout their larval life. Survival on this species was high. When newly hatched larvae (that had not fed) were placed on *Hibbertia* leaves they readily fed on them but if given a choice

TABLE 7.1 Survival of *Phalaenoides glycine* larvae on different foodplants.

Food	Total no. larvae	No. of larvae surviving to end of instar						% of total surviving to pupation
		1	2	3	4	5	6	
Old vines	20	20	18	15	14	12	2	10
New vines	20	20	20	20	20	20	19	95
Fuchsia	20	15	15	15	15	13	13	65
H. sericea	20	1	1	1	1	1	0	0
H. stricta	20	0	0	0	0	0	0	0
H. scandens	20	16	16	16	16	16	15	80

between Hibbertia and vine leaves, they always chose vine leaves. In a home garden where a plant of H. scandens was growing close to a grape vine, no larvae were found on the Hibbertia while several hundred were on the vine. In another situation where there was no grape vine near the Hibbertia, larvae were found on the Hibbertia.

A factor which complicates the issue is the possibility of the influence of the foodplant of the parent moth (when it was a larva) on the food preferences of the larvae. It is well known that not only will moths tend to oviposit on the foodplants they themselves fed on as larvae but their larvae will also show a preference for that foodplant (Jermy, 1968; Yamamoto, 1969; Hovanitz, 1969; Hovanitz and Chang, 1963). This factor was not considered in the above experiment. It is examined in Section 7.3.

7.2 Rate of Development on Different Foodplants

New and old vine leaves, Fuchsia sp. leaves and H. scandens leaves were used as foodplants in an experiment to examine the influence of food on the rate of development of larvae. This experiment was conducted under the same conditions as that in Section 7.1. Larvae were examined daily and their instars noted. Results are in Table 7.2.

Development was fastest on new vine leaves and slowest on old leaves however differences between the rates on different plants were not significant and it was concluded that the foodplant is not an important influence on the rate of development of larvae.

7.3 Oviposition on Different Foodplants

To test the ovipositional responses of female moths to different larval foodplants, an experiment was set up in an outdoor field cage with four species of plants. These were:

TABLE 7.2 Rate of development of Phalaenoides glycine larvae on different foodplants.

Instar	Average no. days in instar on			
	New vine leaves	Old vine leaves	Fuchsia	Hibbertia
1	4.0	4.5	4.7	5.7
2	2.8	3.5	2.8	7.5
3	2.2	3.2	3.5	5.3
4	3.4	4.1	4.8	4.9
5	5.5	8.5	7.4	5.1
6	10.7	11.5	11.1	7.9
TOTAL	28.6	35.3	34.3	34.3

(1) Grape vines

(2) *Fuchsia* sp.

(3) *Hibbertia scandens*

(4) *Citrus* sp. (orange)

Phalaenoides glycine larvae are known to feed on the first three species. *Citrus* seedlings, on which larvae do not feed, were included to see if the moths would oviposit on plants unacceptable to larvae.

The four species were arranged in a 4 x 4 Latin square design. Three plants (approximately the same size) of the particular species were placed at each position. The grape vines and *Citrus* seedlings were growing in pots and the *Fuchsia* and *Hibbertia* were cut and placed in water because no potted plants of these species were available.

Field-caught moths were collected at Langhorne Creek flying over vines. It was hoped to use a large number of females but on the day the experiment was set up, only 3 females were caught. These were released into the cage late in the afternoon of the day they were collected. They remained there for 3 days. Then all plants were examined and the number of eggs counted and recorded. Results are given in Table 7.3. The distribution of eggs among the plants is shown in Figure 7.1. Unfortunately the total number of eggs laid in the experiment was low even though the female moths collected appeared to be young (and thus not at the end of their reproductive life). However weather conditions during the experiment were not favourable for oviposition, with showers of rain and temperatures which were low for that time of year.

There was a definite preference for grape vines over all the other species. It is known and has often been observed that females lay eggs readily on *Fuchsia* plants and that larvae will survive through to

TABLE 7.3 Oviposition preferences of *Phalaenoides glycine* moths reared on vine leaves as larvae.

Species	No. eggs laid by ♀'s fed on Vine leaves
Vine	96
Fuchsia	2
Hibbertia	0
Citrus	0

Figure 7.1 Latin square design for oviposition preference experiments.

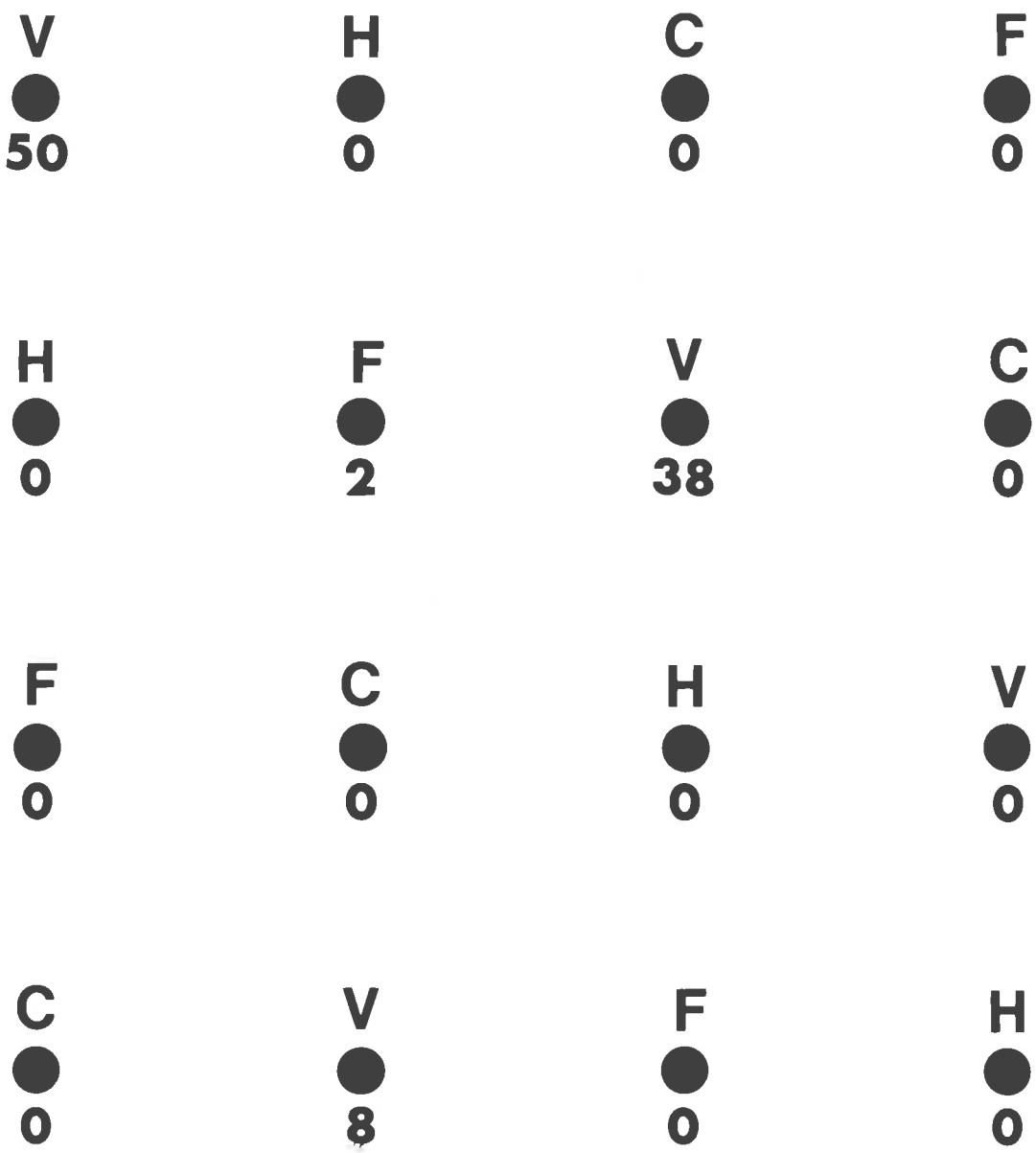
V = vines

C = *Citrus* sp.

H = *Hibbertia* sp.

F = *Fuchsia* sp.

The numbers show the distribution of eggs laid in the experiment.


V
50
H
0
C
0
F
0
H
0
F
2
V
38
C
0
F
0
C
0
H
0
V
0
C
0
V
8
F
0
H
0

pupation on them (Section 7.2). Thus it was surprising that more eggs were not laid on these plants. It seems that although moths will oviposit readily on Fuchsia if nothing else is present, they prefer vines.

It is well documented that in many species moths show an oviposition preference for the plants on which they were reared (Hovanitz, 1969; Yamamoto, 1969). The females used in the above experiment had fed on vines as larvae and this may have determined their preference for vines for oviposition. So the experiment was repeated with moths which had been reared on Hibbertia in the larval stages. Unfortunately weather conditions during the experiment were unsuitable for oviposition and no eggs were laid. It was not possible to repeat the experiment.

7.4 Native Populations

Some early literature (McCoy, 1885; French, 1893) states that once Phalaenoides glycine was established on grape vines it never returned to its native foodplants. However the above studies showed that larvae will still accept the native plants as food, (even though their survival on them may be reduced), and moths will oviposit on them. Thus it seemed likely that there would be populations of Phalaenoides glycine still feeding on these plants in the wild.

Hibbertia is the only genus which is native to the Adelaide area and so several areas where this grows were searched for P. glycine. These included the Southern Vales and Clare districts which are wine-growing areas, and the Adelaide hills and the Fleurieu Peninsula, south of Adelaide. H. sericea and H. stricta grew together in all areas except at Clare where only H. sericea occurred. Altogether several hundred plants were searched for eggs and larvae. In some cases Hibbertia was growing alongside vineyards where P. glycine larvae were present but none were ever found

on these Hibbertia plants, or on Hibbertia in areas where there were no vines.

Around Adelaide another species Hibbertia scandens is grown in home gardens. Many plants were searched but larvae were only found on one plant of this species. The larvae survived to pupation on the plant and later emerged successfully as adults. This particular plant was in a small courtyard surrounded by tall buildings in the grounds of Adelaide University. There were no grape vines nearby. In another situation H. scandens plants were growing alongside grapevines. In this case no P. glycine eggs or larvae were ever found on the Hibbertia even though there were several hundred on the vines. Thus it seems that moths will oviposit on H. scandens only in the absence of grape vines. Similarly in home gardens larvae were often found on Fuchsia bushes, but if the Fuchsia was near a grape vine, larvae were always on the vine and never on the Fuchsia.

Hibbertia scandens and Fuchsia are only found in home gardens in South Australia so it was concluded that populations of Phalaenoides glycine do not occur on native foodplants in the wild - at least not in South Australia. They may occur naturally in other parts of Australia but this has not been investigated.

In the above work two related species were found. These were Phalaenoides tristifica and Eutrichopidia latina. P. tristifica larvae were found feeding on Epilotium and Ludwigia peploides ssp. monte videnses. These larvae survived through to pupation on grape vine leaves but P. glycine would not feed on either species. Adults of E. latina were flying around Hibbertia. It is known that larvae of this species feed on Hibbertia (Common, 1966) but no larvae were found.

Thus vine moth larvae were able to survive on H. scandens though

not on other Hibbertia species. When adult moths were given a choice of plants on which to oviposit they chose vines. When vines were not present, they would oviposit on H. scandens. This is discussed in more detail in Chapter 9.

CHAPTER 8

MISCELLANEOUS STUDIES

During the course of this study several aspects of the biology of Phalaenoides glycine were studied that were "off shoots" of the main theme of the thesis. These included a study of prepupal wandering behaviour and the rate of development of larvae with respect to temperature. These are discussed in this chapter.

8.1 Prepupal Wandering

Prepupae, (i.e. 6th instar larvae that have ceased feeding prior to pupation), leave the vines and wander for approximately 2 days. Little work has been done on pre-pupal wandering but it is a phenomenon exhibited by many Lepidoptera and other insects e.g. Porthetria dispar (Doane & Leonard, 1975), Choristoneura fumiferana (Wellington, 1948) and Hyphantria textor (Wellington et al., 1954). Most work has been concerned with reactions to light and temperature e.g. Wellington (1948, 1955), Wellington et al. (1951), Madge (1964 a & b) and Sullivan & Wellington (1953). Dethier (1959) describes the dispersal of larvae to new food plants. This is not pre-pupal wandering but the behaviour pattern is similar.

Some of the factors that influence pre-pupae in the 'wandering' phase were investigated in this study.

8.1.1 Field observations

The wandering behaviour of prepupae was observed at Langhorne Creek. Prepupae usually travelled in straight lines. They crawled along the rows of vines on the ridge between vines. Few were ever seen between the rows of vines. They travelled mainly in the shade of the vines but did not avoid patches of sunlight. If obstacles were placed in their path they

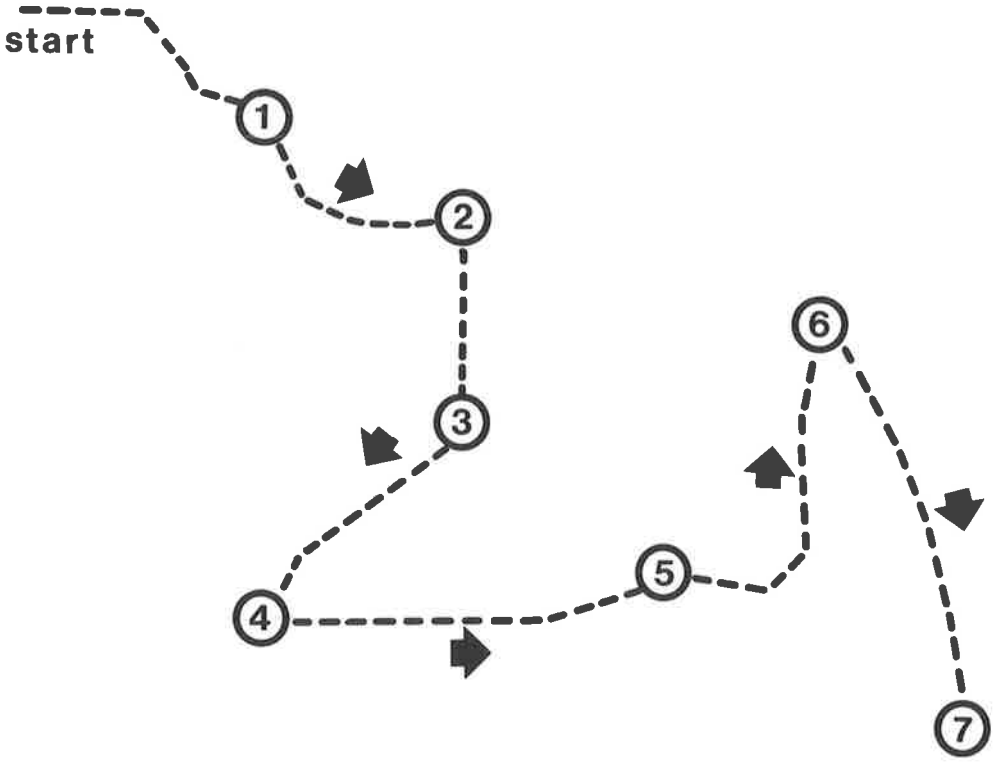
climbed them and continued in the same direction. When they encountered a vine trunk they often climbed up a short distance then descended and continued in the original direction of travel. They ignored vine branches or leaves touching the ground in their path. On coming to the end of a row they either climbed up the large end post or continued onto the bare ground around the edge of the vineyard. Those that continued onto bare ground invariably turned back after approximately 1 metre and returned to the end post.

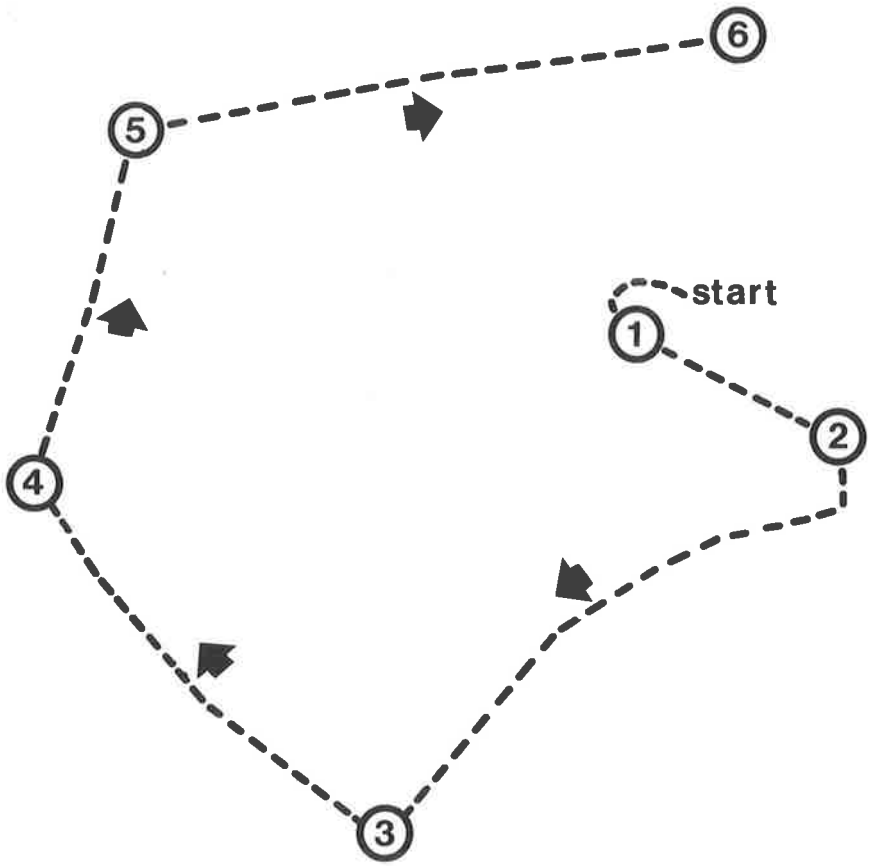
During these observations I noticed that preupae seemed to be attracted towards me. On reaching me they climbed up as far as my shoulders (when I removed them). On several occasions I deliberately stood to one side of prepupae and endeavoured to make them change direction, which they invariably did. It was possible to make them walk in circles by moving position. Figure 8.1 shows the results of some trials carried out in the field. Standing behind a prepupa had no effect on its direction of travel. Similar observations were made by Doane & Leonard (1975) on Porthetria dispar.

8.1.2 Attraction to Upstanding Objects

Experiments were conducted to investigate the attraction of prepupae to upstanding objects and to determine over what distances this attraction operated. A large arena, approximately 2.5 metres in diameter, was constructed out of corrugated cardboard (smooth side inwards). Prepupae were placed in the middle of this arena and their reactions to various objects over various distances were noted. The 'upstanding objects' were constructed out of black plastic. They ranged in height from 10-100 cm. and in width from 2.5-30 cm. Attraction to each object was tested over 3 distances, 30, 60 and 100 cm. The objects were placed at less than 90° from the path of travel and slightly in front of the

Figure 8.1 Prepupal wandering: attraction of prepupae to an observer in the vineyard. Arrows show direction of travel. Numbers show successive positions of the observer.


start
1
2
3
4
5
6
7


6
5
start
1
2
4
3

prepupa. The response was recorded as positive if the prepupa changed direction and came towards the object. A negative response was recorded if the prepupa did not change direction or if it came towards the object for a few steps only and then returned to its original path. A negative response was recorded only if the prepupa waved its head in the air so that the stemmata could be used (see Doane and Leonard, 1975).

Results are given in Table 8.1. They indicate that at a distance of 1 metre prepupae were not attracted to objects smaller than 100 cm. high and 20 cm. wide. At distances of 60 cm. they were attracted to all objects except those 10 cm. or less high, regardless of width, and those 2.5 cm. wide (regardless of height). At distances of 30 cm. prepupae responded to all objects except those 2.5 cm. wide (regardless of height).

Thus prepupae are attracted to large upstanding objects at a distance of 1 metre. At closer distances they are attracted to a range of shapes and sizes, but objects 2.5 cm. or less wide and 10 cm. or less high are not attractive.

The angles subtended by these objects in both the horizontal and vertical planes were calculated and are shown together with the responses of the prepupae in Table 8.2. They did not respond to horizontal angles of less than approximately 5° or to vertical angles of less than approximately 18°. Table 8.2 shows that both horizontal and vertical angles and their interactions are important in determining the response of prepupae to upstanding objects.

8.1.3 Light and Temperature

Most of the studies on wandering have been concerned with the reactions to light, particularly polarized light. These have mainly been on larvae, not on prepupae e.g. Wellington (1948, 1955), Wellington *et al*.

TABLE 8.1 Response of prepupae to upstanding objects at different distances.

Object		Size (cm) width	Size (cm) height	% Response at 1 metre	% Response at 60 cm.	% Response at 30 cm.
XL	1	30	100	87	100	100
	2	20	100	20	80	100
	3	10	100	0	73	93
	4	5	100	0	60	67
	5	2.5	100	0	0	0
L	1	30	70	0	100	100
	2	20	70	0	100	100
	3	10	70	0	53	100
	4	5	70	0	47	87
	5	2.5	70	0	0	0
M	1	30	50	0	100	100
	2	20	50	0	67	100
	3	10	50	0	80	53
	4	5	50	0	27	47
	5	2.5	50	0	0	0
S	1	30	30	0	100	100
	2	20	30	0	60	100
	3	10	30	0	20	80
	4	5	30	0	7	80
	5	2.5	30	0	0	0
XS	1	30	10	0	0	93
	2	20	10	0	0	13
	3	10	10	0	0	40
	4	5	10	0	0	7
	5	2.5	10	0	0	0

TABLE 8.2 % Response of prepupae to the angles subtended by upstanding objects.

Vertical Subtended Angle	Horizontal Subtended Angle											
	1.4	2.4	3	5	6	10	11	16	19	28	37	53
6	0		0		0		0	0				
10		0		0		0			0	0		
17	0		0		0		0	0				
18				0		7			40		13	93
27	0	0	0	7	0	20	0	0	60	100		
35	0		0		0		0	0				
40		0		27		80			67	100		
45	0		0	0	0	80	20	87	80		100	100
49		0		47		53			100	100		
59		0		60 0		73 47			80 53	100	100	100
67				0		87			100		100	100
73				0		67			93		100	100

(1951) and Sullivan & Wellington (1953).

The response of prepupae to polarized light was not investigated in this study. However an attempt was made to study the reactions of prepupae in the wandering phase to temperature and sunlight.

Larvae were placed on a large flat concrete area, in bright sunlight, in mid-afternoon, and their direction of travel noted. They were each given 10 trials i.e. were placed in the middle of the area on a large sheet of paper and when they reached the edge of the paper they were replaced in the middle for the next trial and so on. Their tracks were traced on graph paper. The ground temperature was also recorded.

The results showed that in the first few trials each time, the prepupae walked in the opposite direction to that of the sun. They walked in approximately straight lines. The trials were carried out in summer when ground temperatures were between 40 and 44^{o}C. As the number of trials increased the paths of the prepupae become more and more erratic with changes of direction every few centimetres. When placed in the shade, these prepupae immediately stopped walking. Thus the longer they were in the sun, the hotter they became (prepupae are mainly black in colour) and the more erratic their wandering became.

8.1.4 Speed and Distance

Several trials were conducted in the field to determine the speed at which prepupae travel. Individual prepupae were tracked over periods of up to 1 hour and the distance travelled in each 5 minute period recorded. The results showed that the mean speed was 0.64 m/minute (range for 10 individuals, 0.25-1.53 m/min.).

In the laboratory prepupae wander for approximately 2 days (at 25^{o}C) before pupating. They do not walk continuously nor are they active at night. Thus in this time they could travel as far as 0.9 km.

8.2 Influence of Temperature on Rate of Development

The effect of temperature on the rate of development of eggs and larvae was studied in the laboratory. Within 24 hours of being laid, eggs were placed on moist filter paper in petri dishes and transferred to either 10, 15, 20, 25, 27, 30 or 35°C. The resulting larvae remained at these temperatures through to their emergence as adults. Development was noted daily. Table 8.3 shows the mean duration of each stage at the various temperatures. At 10°C and 35°C all eggs developed but failed to hatch. Larvae placed at 10° and 35°C failed to survive beyond the first instar.

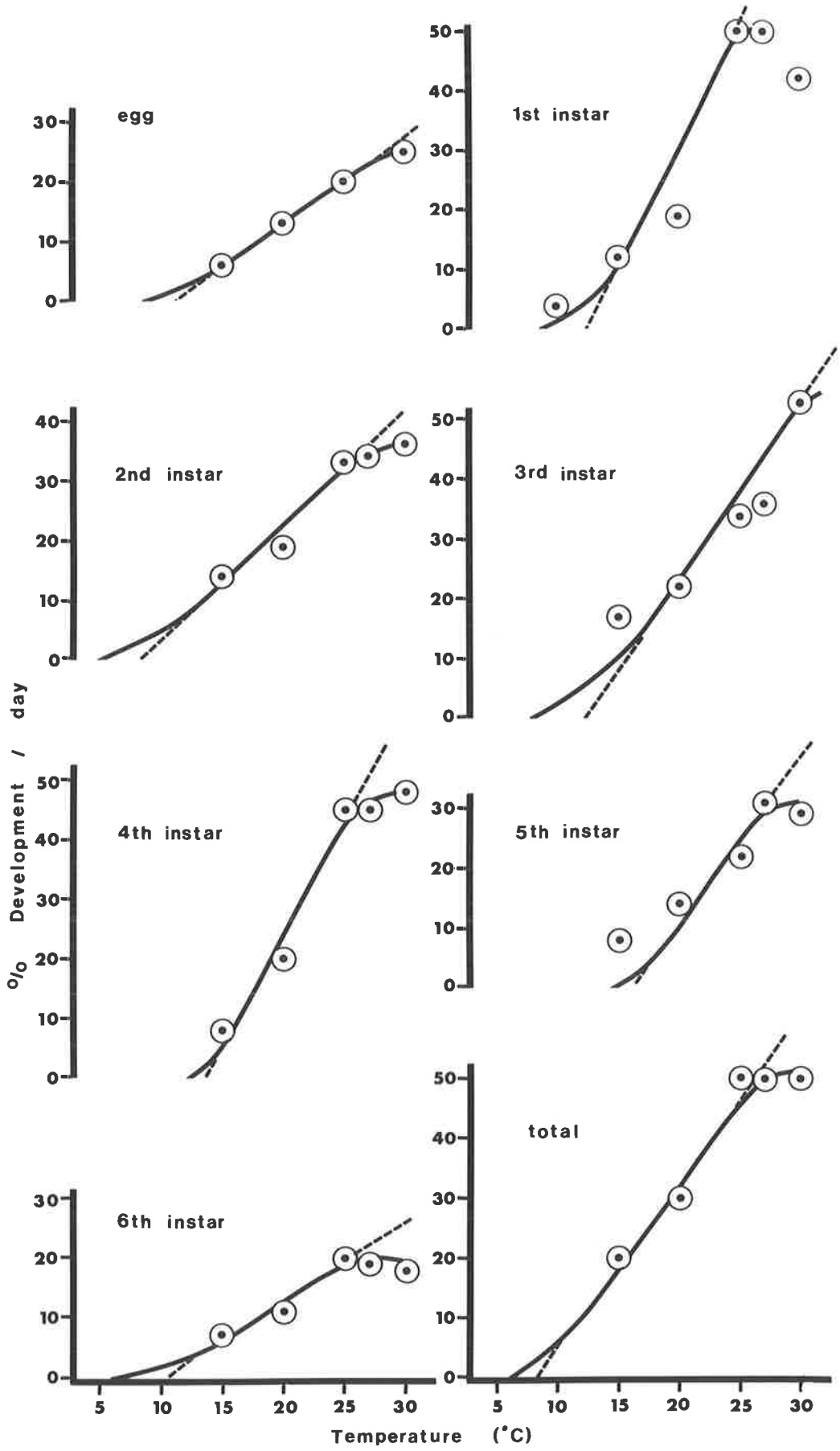
The rate of development, (as measured by the reciprocal of the duration of development), when plotted against time, may be approximated by a straight line. Davidson (1942) stated that the rate approximates a straight line only over a restricted median range of temperatures within which development occurs. He proposed (Davidson, 1944), that a better approximation was a sigmoid curve. However Varley et al. (1973) found that it was simpler and accurate enough (for their purposes) to fit a straight line to the graph of rate of development against temperature. If this line is extrapolated, the point at which it cuts the temperature axis gives an approximation of the threshold temperature for development.

Figure 8.2 shows the rate of development/day (as a percentage) for each stage at different temperatures. Straight lines and curves were fitted to the data. However as Andrewartha (1970) stated, the concept of the point where the straight line cuts the temperature axis as the threshold of development is unrealistic. The inappropriatness of fitting a straight line to the data and estimating the threshold of development from extrapolation of this is well demonstrated by Figure 8.2

TABLE 8.3 Duration of development for eggs and larvae at different temperatures.

Temp. °C	Duration of development (days)							
		Instar						Larval
	Egg	1	2	3	4	5	6	Total
10	-	26.7	-	-	-	-	-	-
15	13.5	8.2	6.9	5.8	12.6	13.0	15.1	61.6
20	7.5	5.2	5.4	4.5	5.1	7.4	8.9	36.5
25	5.0	2.0	3.0	2.9	2.2	4.6	5.1	19.8
27	-	2.0	2.9	2.8	2.2	3.2	5.4	18.5
30	4.0	2.4	2.8	1.9	2.1	3.5	5.7	18.4
35	-	3.0	-	-	-	-	-	-

Figure 8.2 Percentage development/day of eggs and larvae at various temperatures.


egg
1st instar
2nd instar
3rd instar
4th instar
5th instar
6th instar
total
% Development / day
Temperature (°C)
0
10
20
30
40
50
5
10
15
20
25
30

(1st instar). If the straight line fitted is extended it cuts the temperature axis at approximately 12.6°C. It is usually assumed that all development ceases at temperatures lower than this. But some larvae at 10°C survived through the first instar. They developed very slowly (mean duration = 26.7 days) but development did proceed. When the threshold of development is calculated (see below) it is found to be 8.8°C. Thus this is a better estimate of the temperature at which development really stops.

The threshold of development can be calculated using the formula

$$K = \frac{dt - DT}{d - D}$$

(Matteson & Decker, 1965), where K = threshold of development, t and T = constant temperatures within the optimum range of development and d and D = the respective durations of the stage at the constant temperatures t and T. This formula has been used by several workers e.g. Dumbleton (1939), and Muggeridge (1942). The threshold of development for each stage as calculated by this formula is given in Table 8.4.

A more realistic way of examining the effect of temperature on the rate of development is to look at it in terms of the number of 'day-degrees' necessary for the completion of each stage of development. A day-degree is defined as a unit of one degree operating for one day. For example, at 30°C development in the egg stage takes 4 days. The threshold of development for eggs was calculated to be 8.68 (Table 8.4). Thus at 30°C there are 21.32 degrees/day above this threshold. Since development at this temperature takes 4 days, there are 4 x 21.32 = 85.28 day-degrees needed for egg development. The numbers of day-degrees necessary for development at each stage are given in Table 8.5. Once the number of day-degrees necessary for development has been calculated, the theoretical durations of development can be estimated

TABLE 8.4 Thresholds of development as calculated by the formula of Matteson & Decker (1965) for each developmental stage.

Stage	Calculated threshold of development
egg	8.68
1st instar	8.79
2nd "	4.76
3rd "	7.69
4th "	12.00
5th "	9.47
6th "	5.90
Total (larval)	8.61

TABLE 8.5 The number of day-degrees necessary to complete development at each stage.

Stage	No. of day-degrees necessary to complete development
egg	85.28
1st instar	50.90
2nd "	70.67
3rd "	42.39
4th "	37.80
5th "	71.86
6th "	137.37
Total	410.99

for other temperatures. These are given in Table 8.6. There was good agreement between calculated and observed durations of development (Table 8.3) in most cases.

In general the rate of development increases with increase in temperature up to approximately 27°C and then decreases. The optimum range of temperature for development is from 15 to 27°C. Larvae and pupae are able to survive outside this range but survival is reduced. In natural situations the temperature fluctuates well outside this range but is not constant for long periods and so the ability to survive is greater than it would appear from constant temperature experiments.

Eggs will develop at 10° and 35°C but hatching does not occur at either temperature. Thus the range of temperatures within which hatching occurs is narrower than for general development.

The durations of development for different stages were used to estimate the number of generations per season at Langhorne Creek and in Adelaide. The thresholds of development for eggs, larvae and pupae were calculated using the formula given above. They are shown in Table 8.7 together with the number of day-degrees necessary for development. The overall threshold of development (i.e. from egg to adult) was taken as 10.1°C (the mean of egg, larval and pupal figures). The mean monthly temperatures from September to April and the number of day-degrees available for development above the threshold temperature, at Langhorne Creek and in Adelaide are given in Table 8.8.

At Langhorne Creek the total number of day-degrees available for development per season is approximately 1744.7. The number of day-degrees necessary for development from egg to adult (from Table 8.7) is 817.4. Thus the expected number of generations at Langhorne Creek is 1744.7/817.4 = 2.1. In Adelaide the number of day-degrees available is 2262.7 and thus the expected number of generations in Adelaide is 2.8.

TABLE 8.6 Calculated duration of development for eggs and larvae at different temperatures.

Temperature	Duration of development (in days)							Larval Total
	Egg	1	2	3	4	5	6	
10	-	42.1	-	-	-	-	-	-
15	13.5	8.2	6.9	5.8	12.6	13.0	15.1	61.6
20	7.5	4.5	4.6	3.4	4.7	6.8	9.7	34.6
25	5.3	3.1	3.5	2.5	2.9	4.6	7.2	24.0
27	-	2.8	3.2	2.4	2.5	4.1	6.5	21.4
30*	-	-	-	-	-	-	-	-
35	-	1.9	-	-	-	-	-	-

* Figures for 30°C not included as these were used to calculate the day-degrees.

TABLE 8.7 Calculated thresholds of development and the number of day-degrees necessary for development.

Stage	Threshold of development	No. day-degrees necessary for development
eggs	8.7	85.3
larvae	8.6	411.0
pupae	13.1	321.1
	Total	817.4

TABLE 8.8 Mean temperatures and number of day-degrees available for development each month.

Month	Langhorne Creek		Adelaide	
	Mean temp.	no. day-degrees available	Mean temp.	no. day degrees available
September	11.7	48.0	14.0	117.0
October	14.6	139.5	16.5	198.4
November	15.1	150.0	19.1	270.0
December	18.2	251.1	21.4	350.3
January	21.9	365.8	23.0	399.9
February	19.7	268.8	23.0	361.2
March	21.1	341.0	21.0	337.9
April	16.1	180.0	17.7	228.0
TOTAL		1744.2		2262.7

These estimates for the number of generations per season agree with the observations made in Chapter 2 that at Langhorne Creek there were only 2 generations while in Adelaide there was a partial third generation.

8.3 Diapause

Phalaenoides glycine has a facultative diapause in the pupal stage which carries it over the winter period when the vines are not in leaf. One publication by an anonymous author (Anon., 1966) refers to the egg as being the overwintering stage but this is incorrect.

Diapause usually occurs only the second (or third) generation i.e. the last generation before winter. However it has been known to occur in the first (or spring) generation also. Monro (1957) found that, in 1955 and 1956, a proportion of first generation larvae collected in the field, (and brought back to the laboratory and reared at 25°C), entered diapause. He concluded that spring diapause was correlated with cold weather. In this study no first generation larvae collected in the field went into diapause.

Diapause in Phalaenoides glycine is very variable (see later). Monro (1957) classified P. glycine pupae as having been in diapause if they took longer than 30 days to develop into adults. The same classification was used in this study.

8.3.1 Induction of Diapause

Monro (1957) states that the onset of diapause in Phalaenoides glycine is probably connected with low temperatures. He also thought that daylength may be important although it might be masked by the influence of temperature (i.e. Phalaenoides glycine is a typical "long-day" species - see Lees, 1955; Beck, 1968). Daylength and

temperature have been found to be important in diapause induction in many species e.g. Grapholitha molesta (Oriental Fruit moth) (Dickson, 1949). Bursell (1970), Lees (1955) and de Wilde (1969) regard day-length as the most important factor because they say that unlike temperature, photoperiod varies predictably with the seasons.

To test the influence of photoperiod on the induction of diapause in P. glycine, larvae were reared at 25°C on young vine leaves at several different photoperiods:

24	hours	light,	0	hours	dark
16	"	"	8	"	"
12	"	"	12	"	"
8	"	"	16	"	"
0	"	"	24	"	"

However none of the resulting pupae entered a diapause state i.e. all emerged within 30 days of pupating.

The effect of temperature on the induction of diapause was also investigated. Larvae were reared on fresh vine leaves, in a photoperiod of 16 hours light : 8 hours dark, at 12°, 15°, 20°, 25°, 27° and 30°C. Below 12°C development was very slow and none of the larvae survived to pupation. Results showed that no pupae entered diapause at temperatures of 25°C or higher. At 20°C, 7 out of 20 (35%) pupae entered diapause while at 15°C and 12°C all pupae entered diapause.

The induction of diapause may also be influenced by food (Andrewartha, 1952; Lees, 1956; Prokopy, 1968; de Wilde, 1969). Andrewartha et al. (1974) suspected that the onset of diapause in Phalaenoides glycine might be influenced by the quality of food, (spring leaves are young and succulent while autumn leaves are mature and fibrous).

They were unable to test their hypothesis because they could not produce spring foliage in autumn and spring larvae fed on mature leaves all died from disease. In the present study grape vines were grown from cuttings in pots in glasshouse conditions. These could be planted so as to produce foliage at any time of the year. Thus autumn foliage could be obtained in spring and spring foliage in autumn.

An experiment was conducted to determine the influence of food on the induction of diapause. Larvae were kept at approximately 25^{o}C and a photoperiod of 16 hours light : 8 hours dark. They were fed either new spring foliage or mature autumn foliage. However none of the resulting pupae entered diapause.

Thus in this study food and light alone were not factors that influenced the induction of diapause. Temperature was an important factor. However it should be realized that the above factors do not act independently of one another. Food and light may, in combination with temperature, reinforce the stimulus to enter diapause. It was not possible to carry out more complex experiments to investigate such combinations.

Andrewartha et al. (1974) stated that diapause in Phalaenoides glycine is caused by a hormone secreted by the suboesophageal ganglion. They suggested that the intensity of diapause may depend on the concentration of this hormone and that the amount of hormone present depends on the temperature and light regime experienced in the larval stages.

8.3.2 Stage of Induction of Diapause

Factors which influence the onset of diapause, such as light, temperature and food, often influence the onset long before diapause actually occurs. Lees (1955) states that the period when the developing

insect is most responsive to diapause stimuli is characteristic of the species. He states that this period of sensitivity may or may not extend over several instars.

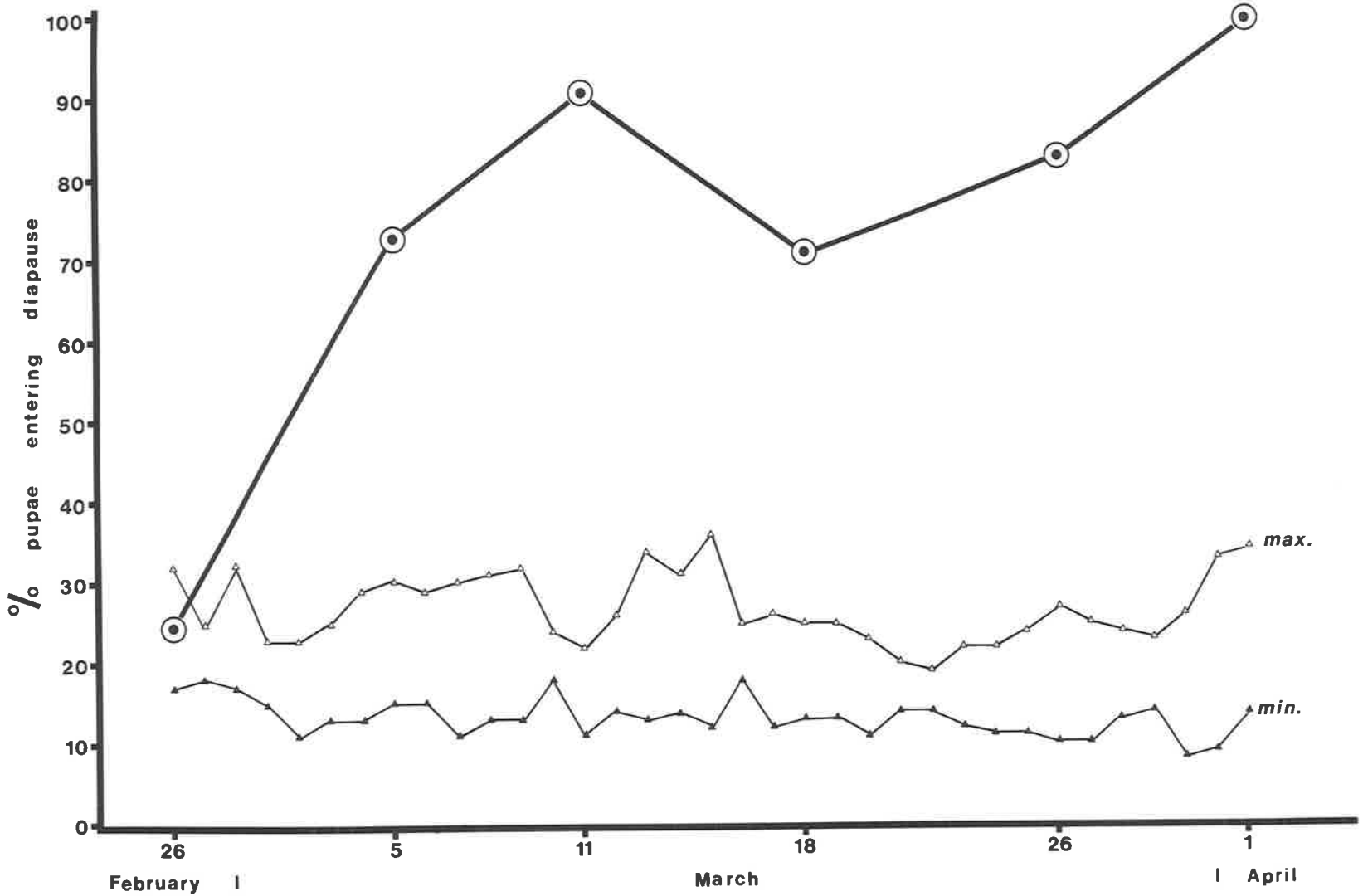
An experiment was conducted in the laboratory to investigate the stage or stages during which Phalaenoides glycine larvae are sensitive to diapause stimuli. Larvae were reared at 25°C and a photoperiod of 16 hours light : 8 hours dark. They were exposed to diapause conditions in either the 1st, 2nd, 3rd, 4th, 5th or 6th instars. Unfortunately all the larvae died due to disease before pupation occurred. However larvae of different ages were collected throughout the 1975-76 second generation at Langhorne Creek, brought back to the laboratory and reared through to adults under the temperature and light conditions mentioned above. Results showed that larvae collected in the field as early as the third instar entered diapause. None of the larvae collected in first and second instars survived through to pupation.

8.3.3 Proportion of the Population Entering Diapause

Both Andrewartha et al. (1974) and Monro (1957) found that in Phalaenoides glycine the incidence of diapause increased towards autumn.

No larvae were collected in the first generations but during the 1975-76 second generation larvae were collected at weekly intervals in the field (20 larvae/week). They were brought back to the laboratory and reared at 25°C and a photoperiod of 16 hours light : 8 hours dark. The number of larvae that subsequently entered diapause was noted (Figure 8.3). By the end of the second generation, all larvae collected entered diapause. From the 26/2/76 to 11/3/76 there was a steady increase in the number of individuals entering diapause. From 11/3/76 to 18/3/76 the number entering diapause decreased, to rise again later. This decrease coincided with a peak in temperature in the preceeding

Figure 8.3 Percentage of pupae entering diapause in the second generation 1975-76. Maximum and minimum temperatures are also given.


% pupae entering diapause
100
90
80
70
60
50
40
30
20
10
0
max.
min.
26
February
5
11
18
26
1
March
April

weeks (Figure 8.3).

8.3.4 Intensity of Diapause

The duration of diapause may be used as a measure of the intensity of diapause (Andrewartha, 1952). In Phalaenoides glycine the duration of the pupal stage is variable. Some pupae spend as little as 15 days (at 25°C) in pupation and others well over 100 days. In the field in emergence traps a few individuals that pupated at the end of the first generation in the 1973-74 season, did not emerge until the beginning of the first generation the following season (1974-75).

Monro (1957), in 1954-55, collected 6th instar larvae from the field and kept them at 25°C until they emerged as adults. He recorded the duration of the pupal stage. He regarded pupae that took longer than 30 days to develop into adults as having been in diapause. He found that some pupae developed with no diapause while others had a very definite diapause (and many were intermediate between these extremes).

The present study confirmed that the duration of the pupal stage is very variable. Field collected larvae were brought back to the laboratory and kept at 25°C. The length of the pupal stage was noted for each larva. Results are given in Table 8.9. These confirm Monro's conclusion that there was a continuous gradation between the non-diapause and diapause states and that some pupae appeared to be in a state of quiescence rather than diapause.

Andrewartha et al. (1974) states that Phalaenoides glycine pupae that are not intensely in diapause will eventually complete development without being exposed to cold. This was also confirmed in the present study. In the field some moths were found to emerge in mid-winter (when there was no food and temperatures were low). This also indicates that some pupae are in a state of quiescence.

TABLE 8.9 Intensity of diapause as measured by the duration of pupation. (Pupae that took more than 30 days to develop to adults were classified as having been in diapause).

No. days in pupation	No. of pupae
<20	3
20-30	11
31-40	5
41-50	1
51-60	3
61-70	3
>100	25

Andrewartha et al. (1974) also found that wounding tends to intensify diapause if the diapause already exists.

8.3.5 Rate of Development of Diapause Larvae

The rate of development of larvae that were destined to diapause in the pupal stage was compared with the rate of development of larvae that did not enter pupal diapause. To induce diapause, larvae were kept at low temperatures and short daylengths for the first 3 instars. In the 4th instar they were placed at 25^{o}C and a photoperiod of 16 hours light : 8 hours dark. Non-diapause larvae were kept in these conditions throughout their larval life. Development was recorded daily. Results are given in Table 8.10. There were no significant differences between the rate of development in the larval stage of diapausing and non-diapausing individuals.

TABLE 8.10 Rate of development of larvae destined to diapause in the pupal stage and those destined to develop without diapause.

Instar	Mean no. days in instar		Mean rate of development	
	Diapause	Non Diapause	Diapause	Non Diapause
4	7.5	5.5	0.13	0.18
5	7.0	6.6	0.14	0.15
6	10.1	10.2	0.10	0.10
Prepupa	6.5	6.5	0.15	0.15

CHAPTER 9

DISCUSSION

The main theme of this thesis was a study of the basic biology of *Phalaenoides glycine*, the factors that influence its population dynamics and the relationships between *P. glycine* and the environment. *P. glycine* has not previously been studied in detail.

A characteristic of *P. glycine* populations is that population numbers were always much lower in the first generation each season than in the second generation. Numbers fluctuated from season to season and the numbers in the first generation reflected those of the previous second generation e.g. a large second generation in 1973-74 was followed by a relatively large first generation the following season (1974-75) even though the numbers were much lower in the first generation. (In this study moths that emerged from overwintering pupae were termed 'first generation' moths, while moths that emerged in January and February were termed 'second generation' moths).

There are several explanations as to why numbers in the first generations were always much lower than in the second generations. Emergence trap data (Chapter 8) showed that some second generation pupae (which overwinter in diapause) did not emerge the following spring (first generation) but remained in diapause until the following second generation, in autumn, i.e. they remained in diapause for at least a year. This confirms Monro's (1957) findings that some pupae remain in diapause for a year or more.

Larvae were not collected in the first generations so it is not known if any of these larvae entered diapause but Monro found that some larvae of the first or spring generation entered diapause. Monro makes no mention of second generation pupae, (which always diapause), remaining in diapause

until the following second generation.

The obvious conclusion to reach if the first generation is always much smaller than the second generation is that there is a large amount of mortality over winter. But results showed that in the laboratory pupae survived at 10°C for well over 100 days, so prolonged cold has little effect on the survival of pupae. Results also showed that the death-rate due to the flooding of the vineyards in winter was low.

The rate of parasitism was generally high (Chapter 6) in the second generation but because larvae were not collected in the first generations, no figures for rates of parasitism in this generation are available. Therefore it is not known if there is more parasitism in the first generation than in the second generation.

Predation by Oechalia schellenbergii is an important factor influencing population numbers but results of population studies on these bugs indicate that bug population numbers followed more or less the same trends as larval population numbers and did not account for the consistent difference in numbers between first and second generations. For example in the second generation in 1973-74 (see Table 9.1), bug numbers were low. If predation was the factor causing the difference in numbers in first and second generations, then the first generation in 1974-75 would be expected to be large; however numbers were very low (lower than at any time during the study). So predation is not the cause of low numbers in the first generation each season.

It is not known what proportion of pupae remain in diapause from one second generation to the next in the field, but, if the amount of parasitism is similar in both generations, this is the most likely cause of the differences in numbers between first and second generations.

Within each generation, population numbers fluctuated from year to year. For example, numbers in the second generation in 1974-75 were much

TABLE 9.1 Summary of larval and bug population fluctuations. (mean nos. given in brackets).

Season	Larval numbers	Bug numbers
1972-73		
Gen. (2)	very high	-
1973-74		
G (1)	small (0.33)	high (1.18)
G (2)	small (2.80)	small (0.74)
1974-75		
G (1)	small (0.29)	small (0)
G (2)	very large (14.65)	large (2.81)
1975-76		
G (1)	small but larger than previous 1st gen. (0.59)	small (0.64)
G (2)	large but smaller than previous 2nd gen. (7.96)	large (1.92)

higher than in either 1973-74 or 1975-76. Several factors influenced these changes, the main ones being parasites, predators and weather conditions.

It was shown in Chapter 6 there were enough bugs present in the vineyard in both 1st and 2nd generations to completely destroy the larval population. But this did not happen because the peaks of the two populations occurred at different times. The generation time for the two species was also different - approximately 4 weeks for P. glycine and 2-3 weeks for the bugs. Bug numbers began building up when larval numbers were at a peak and by the time bug numbers had reached a peak, the larvae had almost disappeared. Bugs also feed on other species and when numbers of Phalaenoides glycine become low, bugs will feed either on other more abundant species in the vineyard or move to other areas. Several other studies have revealed that when prey population numbers are low, predators may feed on other prey species or move out of the area. Dixon (1959) found with Adalia decempunctata (a predatory coccinellid beetle) that adults tended to leave an area when the return for the amount of effort expended in catching prey reached a certain critical level. Errington (1946) spoke of "compensatory" predation, in which predators consume prey provided the density of the prey species exceeds a certain threshold. He claimed that this threshold was largely determined by the ability of the prey to get away from predators by hiding in niches inaccessable to the predators. Huffaker and Kennett (1956) thought this idea of secure habitats was debatable and suggested that all populations have certain low levels of density which represent security from predation. This security may merely be the unlikelihood of an encounter between predator and prey as the numbers of prey become lower and lower. Thus as the P. glycine larval population declines the chances of being found by a bug decrease and the population survives.

Oaten & Murdoch (1975) studied the situation of a single predator hunting two prey species. A switching mechanism occurs in this situation if the predator's preference for one or other of the prey species is affected by past experiences. For example, as one particular prey species decreases in number the chances of a member of that species being eaten previously, (i.e. in the last meal of the predator), decrease and therefore at the next meal the predator is more likely to choose the more abundant species as prey. Thus switching (Murdoch, 1969) means that the predator attacks the prey species in response to prey frequency, concentrating on the more abundant prey. This ensures the survival of the species when numbers are low.

So the concept of a certain lower limit to population numbers below which the chances of a larva of P. glycine being found by a bug, together with the fact that bugs will feed on other species, ensures the survival of P. glycine.

As mentioned earlier bug population numbers usually followed a similar pattern to those of the caterpillars (see Chapter 6 and Table 9.1). However on some occasions large numbers of bugs were not followed by a small number of caterpillars the following generation. This is because bug numbers usually reached a peak after caterpillars had disappeared (pupated) and were therefore not available as food. [i.e. the prey species decreased as the predator species increased and vice versa. Volterra called this the "law of the periodic cycle" (Andrewartha & Birch, 1954)]. The earlier in the season the bugs are present, the more effective they will be in reducing larval population numbers.

Thus Oechalia schellenbergii has a profound effect on the population numbers of P. glycine. There is much scope for further detailed study of the interactions between this predator and P. glycine.

Tachinid flies also cause considerable mortality to the larval stages

of P. glycine (see Chapter 6). This mortality does not have an effect on the numbers of P. glycine until the following generation because parasitized larvae are not killed until they stop feeding and construct a pupal cell.

Weather conditions act to regulate population numbers also, in particular wind and temperature. If winds are stronger than approximately 12 km/hour, moths do not fly and this in turn affects population numbers because if flight ceases, oviposition ceases.

Wind also influences the places in which the eggs are laid. In Chapter 5 it was shown that moths "prefer" to oviposit in sheltered areas. This behaviour on the part of the female moth increases the chances of the egg surviving the effects of adverse weather conditions, such as rain and wind, which could wash or blow eggs or young larvae off the vines, (also, because the eggs are laid on the undersides of the leaves, they are sheltered from direct sunlight which, if too hot, would kill them (fertile eggs are dark brown and thus absorb heat very quickly)). Therefore wind is an important factor influencing changes in population numbers.

Temperature also influences population numbers. Laboratory studies showed that the optimum temperature for oviposition was about 25°C. At temperatures lower and higher than this oviposition was reduced. Thus as temperatures fluctuate throughout the season, so does the rate of oviposition and in cold or very hot weather, oviposition is reduced and therefore population numbers are reduced.

The survival of eggs and larvae is also affected by temperature. There is a decrease in survival at very high and very low temperatures, the optimum temperature for larval development being 25-27°C. At lower temperatures (15 or 20°C) survival is high but the duration of development is much longer (Chapter 8) and so larvae are present for longer periods in

the vineyard, thereby increasing the chances of death by predation or parasitism.

Temperature also influences the number of pupae entering diapause. Lower temperatures result in a greater proportion of pupae entering diapause and this affects the numbers emerging in the following generation.

So, temperature influences population numbers by influencing survival and rate of development of eggs, larvae and pupae and the oviposition rate of female moths. Other causes of death are not considered important in the population dynamics of P. glycine. They are discussed in Chapter 6.

Thus there are four main factors that affect population numbers; predation by O. schellenbergii, parasitism by Tachinid flies, wind and temperature. P. glycine has an almost unlimited food supply but population numbers are so low that very little of this resource is utilized. This is because P. glycine is kept well in control by a combination of these four factors, particularly by predators and parasites. Therefore they do not expand in numbers to the stage where their food supply is limiting.

In Chapter 3, the distribution of larvae and eggs in the vineyard in the second generations was shown to be aggregated. However there was no evidence to suggest that the distribution was aggregated in the first generations when population numbers were very low, i.e. the distribution in the first generations did not differ from a random distribution. There are several explanations for this change or apparent change in distribution from the first to the second generation each season.

The distributions may be similar but appear to be different only because of the very low numbers present in the first generation. Such an apparent change in distribution has been observed in many other insects e.g. in Pieris rapae (Harcourt, 1961).

In Chapter 5, results showed that more eggs were laid on trailing

canes than on non-trailing canes and therefore vines with trailing canes had more eggs than other vines. It was also shown that vines sheltered from the prevailing winds and rain had more eggs. These findings led to the conclusion that female moths do not lay eggs at random but actively "choose" oviposition sites, laying more eggs in sheltered sites close to the ground. Therefore the behaviour of the female moth plays a part in determining the distribution of eggs and larvae in the vineyard.

It was expected that the vines with trailing canes would be more heavily damaged than other vines. The distribution of trailing canes in the vineyard is shown in Figure 9.1. Analysis, using Morisita's Index to measure the dispersion, showed that vines with trailing canes are distributed more or less evenly (Table 9.2). However the distribution of trailing canes was examined at the end of the season and by this time vine growth had reached its maximum extent. Earlier in the season, when moths were flying and ovipositing, vine growth would be less and thus may have been patchy. Also vine growth was mapped in the season following that of vine damage (it was not possible to examine both vine damage and vine growth in the same season). No conclusions could be drawn from the data available but it is likely that vine growth does influence the choice of oviposition site, which in turn influences the distribution of larvae (and damage), by providing shelter on those days in the season when oviposition occurs only in sheltered sites.

Vine growth, however, is likely to influence oviposition only in the second generations because in the first generations all the vines are just bursting into leaf and they do not grow sufficiently during the first generation to provide sheltered sites and trailing canes. Consequently in the first generation female moths may lay at random because they do not have a choice of oviposition sites. This would lead to a random distribution

Figure 9.1 Map of vine growth (●) and damage (■).

one ● = ¼ vine with trailing canes

two ●'s = ½ " " " "

three ●'s = 3/4 " " " "

four ●'s = whole " " " "

See Figure 3.2 for explanation of damage ratings.

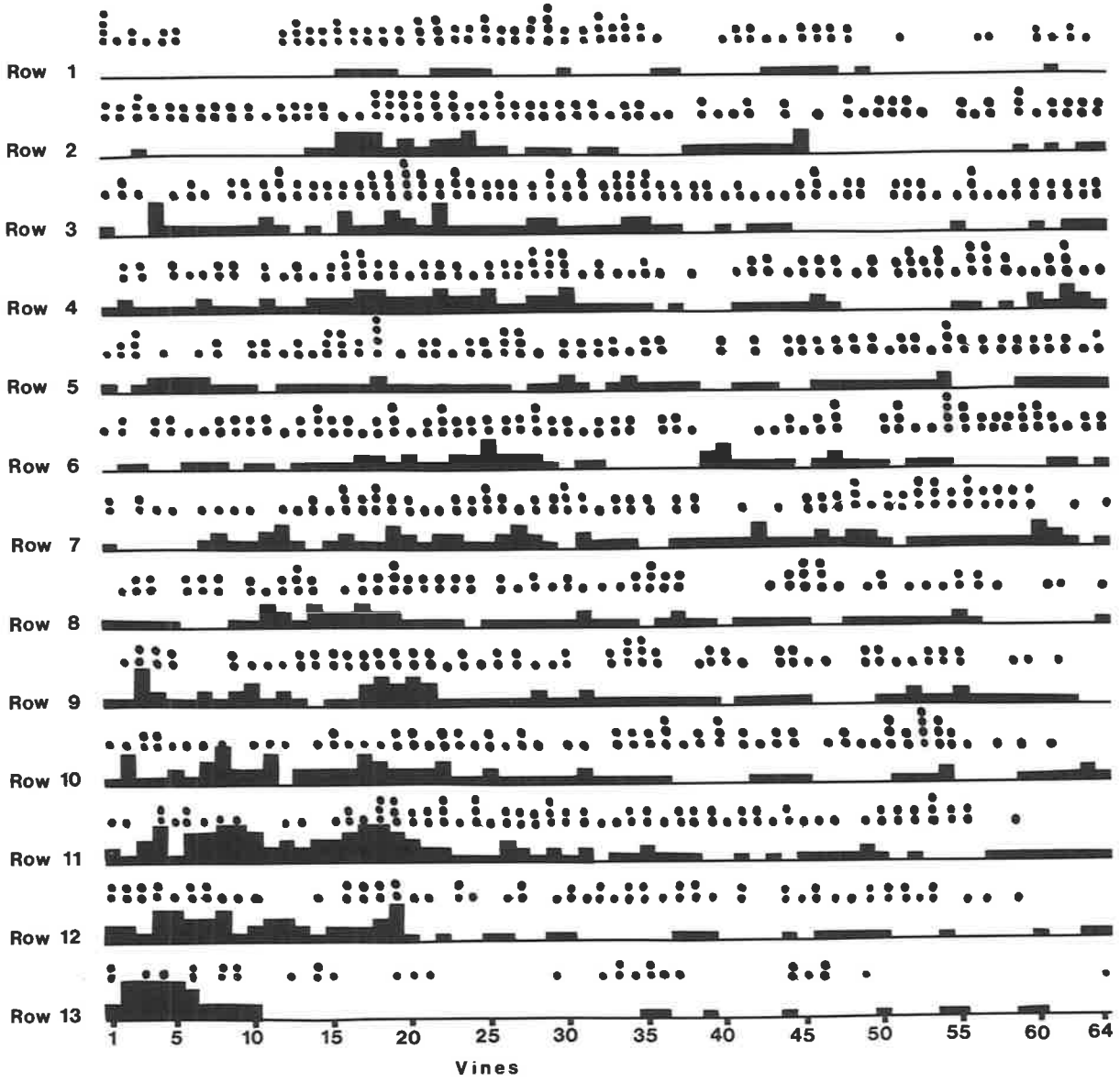

Row 1
Row 2
Row 3
Row 4
Row 5
Row 6
Row 7
Row 8
Row 9
Row 10
Row 11
Row 12
Row 13
1 5 10 15 20 25 30 35 40 45 50 55 60 64
Vines

TABLE 9.2 Morisita's Index for the distribution of trailing vines in the vineyard.

[F (variance ratio) (5% probability) for $n_1 = 63$, $n_2 = \infty$ is approximately 1.0]

Row	I_δ	F_o
1	0.91	0.86
2	0.65	0.38
3	0.67	0.36
4	0.68	0.47
5	0.70	0.49
6	0.72	0.52
7	0.72	0.57
8	0.75	0.68
9	0.71	0.64
10	0.71	0.63
11	0.72	0.62
12	0.64	0.60
13	1.09	1.05

of eggs in the first generation.

Weather also plays a part in influencing the distribution. Windy conditions either stop moths flying or cause them to seek sheltered sites as described above.

Figure 3.2 shows that in the second generation in 1973-74 not only were there vines that were completely defoliated in the vineyard, but almost all vines had some damage even if only a few chewed leaves. Similar damage occurred in other season. Therefore almost every vine had larvae present on it in the 2nd generation. This can also be explained in terms of the behaviour of the female moth. The presence of a larva or larvae on almost every vine occurs because on calm days with no wind, shelter does not influence the oviposition site and on such days, moths lay at random in the vineyard. Wind speed records for the flight seasons at Langhorne Creek show that there are approximately 5 days/month with no wind, during which time moths may oviposit anywhere, and approximately 20 days which are too windy for flight, and therefore oviposition. This leaves approximately 5 days/month when the wind is not strong enough to prevent activity, but is strong enough to cause the moths to seek sheltered oviposition sites. Though even on days that are too windy for flight, there are periods when flight can occur. Moth behaviour in windy conditions probably accounts for the patches of vines with large numbers of larvae, so overall the distribution pattern would be aggregated even though there were larvae on most vines.

So the distribution of Phalaenoides glycine eggs and larvae is determined by the behaviour of the female moth which in turn is influenced by weather conditions and the growth of the vines. The behaviour of the female moth can also account for the apparently random distribution in the first generations and the aggregated distribution in the 2nd generations

(though this may be a statistical accident of differences in population numbers).

P. glycine is a native insect that has become a pest on introduced grape vines. Early literature mentioned P. glycine as feeding on native plants in the eastern states of Australia. After the introduction of vines into Australia, P. glycine spread to them and was found wherever grape vines were grown. Much work has been done on introduced species becoming pests, [e.g. the European corn borer, Ostrinia nubilalis, (Univ. Missouri Bull, 1961); the gypsy moth, Porthetria dispar (Bess, 1961); the pea moth Laspeyresia nigricana (Wright & Geering, 1948); the manuka scale, Eriococcus orariensis, (Cumber, 1961) and the codling moth, Cydia pomonella (Geier, 1963, 1964)], and on native species that are pests on introduced plants (see below), but no work has been done on the actual switching over of a native species from native to introduced foodplants.

Perhaps the most well known example of a native insect that is a pest on introduced plants is the Light Brown Apple Moth, Epiphyas postvittana, native to Australia. Its natural hosts are native evergreens but it has become a pest on apple, grape, lemon and other fruit crops. It still occurs on its native hosts to which it returns in winter when hosts such as apple shed their leaves. It was introduced into New Zealand where it has also become a pest (MacLellan, 1973). Goeden (1975) describes a cerambycid, Ipochus fasciatus, previously known to exist on native host plants in southern California, as adopting the recently introduced milk thistle, Silybum marianum, as a foodplant. He states that this represents a radical departure from the normal host-plant range of Ipochus fasciatus. (The adaptation of I. fasciatus to S. marianum however is not complete. Larvae are unable to complete development to the adult stage because they become trapped in the flower-

heads). Goeden states that this is perhaps a transitional stage in the process of adaptation to a new food niche. This is a similar situation to that of Phalaenoides glycine adapting to grape vines.

Another example is that given by Wheeler (1975) who found several plant feeding insects breeding on the introduced ginkgo tree, Ginkgo biloba. Hall (1974) reported that a native foodplant of Papilio canopus canopus had been found. Thus this species must also have spread to an introduced species, Citrus.

Gupta (1974) found that Bemisia gossypiperda survived on Justicia betonica, a non-host plant, if its normal host-plants were not available. He thought this was due to the chemical nature, texture and micro-climatic conditions of the leaves of J. betonica. A similar situation may exist in P. glycine. Grape vines may well contain chemical substances similar to those in its native foodplants, but no information is available on this.

No native populations of P. glycine were found in S. Aust. in this study. But the only native foodplants that grow in S. Australia are Hibbertia sp. (H. sericea and H. stricta) and these are different species from those that grow in Eastern Australia (although they do grow in parts of the south-east). P. glycine larvae would feed on the S. Australian species of Hibbertia but none survived. They did survive however on H. scandens, a native of New South Wales, which is often grown in gardens in South Australia. Larvae were found naturally occurring on this species in South Australia. Thus native populations of P. glycine may still occur in eastern Australia where H. scandens is found.

It was also noted that larvae were not found on H. scandens in South Australia when this was growing beside vines. Experiments showed that moths which were reared in their larval stages on vine leaves preferred to oviposit on vine leaves. Unfortunately it is not known if

moths reared on Hibbertia prefer to oviposit on Hibbertia, but if they do then it is likely that there are 2 races of P. glycine - one which feeds on vines and another which feeds on Hibbertia. However moths that were reared on vines will oviposit on Hibbertia if vines are not available.

Therefore it seems likely that P. glycine is native to the eastern part of Australia and only spread to other areas with vines. If this is so, native populations would not be found in the wild in South Australia. Shields (1974) suggests that variations in plant resistance occur in nature and that this may account for the discontinuous distribution of species and explain why a species is absent in an area containing its normal food-plant.

Jermy et al. (1968) suggested 3 mechanisms that could cause a transition from feeding on one foodplant to another: (i) olefactory conditioning of the larval stages, (ii) natural or artificial selection of forms with different feeding behaviour, (iii) modification of feeding behaviour by the induction of specific food preferences. These mechanisms could also interact to produce changes. Examples of (i) are given by Hovanitz & Chang (1963(b)), of (ii) by Hovanitz & Chang (1962, 1963(a)) and of (iii) by Stride & Straatman (1962). Any of these mechanisms could operate in P. glycine. For example, P. glycine moths do not always lay eggs on their foodplant. They sometimes lay on nearby inanimate objects (Chapter 5). If only one or two of the resulting larvae climbed a nearby grape vine then, assuming vines contain some substance that stimulates feeding, (Thorsteinson, 1960), these larvae would feed and survive. If as adults they then "prefer" to lay eggs on vines, a new strain would develop on grape vines.

Hovanitz & Chang (1963, a & b) have carried out experiments on the genetic inheritance of foodplant selection in Pieris rapae. They found

that selection of genes for food preferences occurred over several generations when strains were maintained on particular foodplants for many generations.

Many studies have been done on the ability of larvae to find food e.g. Dethier (1959(b)). If a larva of P. glycine walked off a native foodplant (perhaps after defoliating the plant) and by chance came upon a grape vine, crawled onto it, fed and survived then as above, a new strain may well develop feeding on grape vines. By whatever mechanism vine moths came to feed on grape vines, they are now well adapted to the grape vine cycle, (larvae that fed on Hibbertia still entered diapause over winter), and are kept under control by natural enemies.

Life history studies showed that in some areas there were three generations per season while in others there were only 2. Populations emerged earlier in Adelaide than at Langhorne Creek and similarly bud-burst was earlier in Adelaide. These differences are thought to be due to temperature differences between the two areas and the same stimuli probably operate to induce bud-burst and break diapause. Temperatures in Adelaide over summer are approximately 1-2^{o}C higher than at Langhorne Creek. The rate of development of P. glycine was shown in Chapter 8 to be very dependent on temperature and thus in Adelaide, since emergence is earlier and temperatures are higher over summer, there is time for more generations than at Langhorne Creek.

P. glycine often seemed to be a more serious pest in home gardens, where it attacks fuchsias and ornamental creepers, than in vineyards. Certainly the numbers of larvae/vine are much greater in home gardens, where up to 500 larvae have been collected from one vine. There are two reasons for this. One is that in home gardens vines are usually much larger than vines in a vineyard, and are often grown over a verandah

or carport, thus presenting a very large area to the moths for oviposition. The second reason is that in home gardens there is usually only one or two vines and oviposition is concentrated on these vines whereas in a vineyard there are many more vines on which to oviposit.

It became very apparent during this study that several aspects of the ecology of P. glycine need further study. In particular there is much scope for work on the interactions between P. glycine and its predator, O. schellenbergii. Other aspects include the oviposition preferences of moths and the influence of vine growth on oviposition in the vineyard. The aim of the study was to provide a broad background knowledge of the biology of Phalaenoides glycine and the factors that influence its ecology. (I hope that this has been achieved).

BIBLIOGRAPHY

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 animal populations.
2nd edition.
Chapman & Hall Ltd. 283 pp.

ANDREWARTHA, H.G. and BIRCH, L.C. (1954). The distribution and abundance of animals.
Univ. of Chicago Press. 782 pp.

ANDREWARTHA, H.G., MIETHKE, P.M. and WELLS, A. (1974). Induction of diapause in the pupa of Phalaenoides glycinae by a hormone from the suboesophageal ganglion.
J. Insect Physiol. 20: 679-701.

ANON., (1934). The Grape-Vine Moth.
Agric. Gaz. N.S.W. 45: 515.

ANON., (1938). The Grape-Vine Moth.
Agric. Gaz. N.S.W. 48: 515.

ANON., (1943). The Grape-Vine Moth.
Agric. Gaz. N.S.W. 54: 371.

ANON., (1945). The Grape-Vine Moth.
Agric. Gaz. N.S.W. 56: 355.

ANON., (1947). Predacious shield bugs (Pentatomidae).
Agric. Gaz. N.S.W. 58: 308-309.

ANON., (1952). The Grape-Vine Moth.
Agric. Gaz. N.S.W. 63: 663.

ANON., (1960). Vine moths overwhelmed by natural enemies.
J. Dep. Agric. S. Aust. 63: 312.

ANON., (1965). Vine Moth.

Agric. Gaz. N.S.W. 76 (8) Back cover.

ANON., (1966). Pest of Grape Vines.

Fr. Mark. Grow. 67: 12-13.

ANON., (1967). Vine moth (Phalaenoides glycine).

N.S.W. Dept. Agric. Div. Sci. Serv. Bull. 1P 132C.

ANSCOMBE, F.J. (1949). The statistical analysis of insect counts based on the Negative Binomial distribution.

Biometrics 5: 165-173.

ANSCOMBE, F.J. (1950). Sampling theory of the Negative Binomial and Logarithmic series distributions.

Biometrika 37: 358-382.

APLIN, R.T. and BIRCH, M.C. (1968). Pheromones from the Abdominal Brushes of Male Noctuid Lepidoptera.

Nature 217: 1167-1168.

BAILEY, N.T. (1959). Statistical methods in biology.

Lond. Eng. Univ. pr. 200 pp.

BECK, S.D. (1968). Insect photoperiodism.

N.Y. Acad. pr. 288 pp.

BECKWITH, R.C. (1970). Influence of host on larval survival and adult fecundity of Choristoneura conflictana (Lepidoptera:Tortricidae).

Can. Ent. 102: 1474-80.

BENGSTON, M. (1961). Grape pest control in the granite belt.

Qd. agric. J. 87: 225-26.

BESS, H.A. (1961). Population ecology of the gypsy moth Porthetria dispar L. (Lepidoptera:Lymantridae).

Connecticut Agric. Expt. Station Bull. No. 646.

BIRCH, M.C. (1970). Structure and function of the pheromone-producing brush-organs in males of Phlogophora meticulosa (L.). (Lepidoptera:Noctuidae).
Trans. R. ent. Soc. Lond. 122: 277-292.

BIRCH, M.C., GRANT, G.G. and BRADY, V.E. (1976). Male scent Brush of Peridroma saucia : Chemistry of Secretion.
Ann. ent. Soc. Am. 69: 491-492.

BLISS, C.I. and FISHER, R.A. (1953). Fitting the Negative Binomial Distribution to Biological Data and Note on the efficient fitting of the Negative Binomial.
Biometrics 9: 176-200.

BLISS, C.I. (1958). The Analysis of Insect Counts as Negative Binomial Distributions.
Proc. 10th Int. Congr. Ent. 2: 1015-1032.

BURSELL, E. (1970). An introduction to Insect Physiology.
Academic Press 276 pp.

CALLAHAN, P.S. and CHAPIN, J.B. (1960). Morphology of the reproductive systems and mating in two representative members of the family Noctuidae, Pseudaletia unipuncta and Peridroma margaritosa, with comparison to Heliothis zea.
Ann. ent. Soc. Am. 53: 763-782.

de CASTELLA, F. (1927). Sulphuring and spraying vines.
J. Agric. Vict. 25: 734-735.

CHENG, H.H. (1972). Oviposition and Longevity of the Dark-sided Cutworm, Euxoa messoria (Lepidoptera:Noctuidae), in the Laboratory.
Can. Ent. 104: 919-925.

CHISHOLM, E.C. (1933). Useful Coccinellidae found on the Comboyne Plateau.
Proc. Linn. Soc. N.S.W. 58: 405-407.

COMMON, I.F.B. (1966). Australian Moths.
Jacaranda Press 131 pp.

CULLEN, J.M. (1969). The reproduction and survival of Heliothis punctigera Wallengren in South Australia.
Ph.D. Thesis. University of Adelaide.

CUMBER, R.A. (1961). The interaction of native and introduced insect species in New Zealand.
Proc. N.Z. Ecol. Soc. 8: 55-60.

DAVEY, K. (1965). Reproduction in the Insects.
Edin. Oliver & Boyd. 96 pp.

DAVIDSON, J. (1942). On the speed of development of insect eggs at constant temperatures.
Aust. J. exp. Biol. med. Sci. 20: 233-239.

DAVIDSON, J. (1944). On the relationship between temperature and rate of development of insects at constant temperatures.
J. Anim. Ecol. 13: 26-38.

DETHIER, V.G. (1959). Egg-laying Habits of Lepidoptera in Relation to Available Food.
Can. Ent. 91: 554-561.

DETHIER, V.G. (1959b). Food-Plant Distribution and Density and Larval Dispersal as Factors Affecting Insect Populations.
Can. Ent. 91: 581-596.

DICKSON, R.C. (1949). Factors governing the induction of Diapause in the Oriental Fruit Moth.
Ann. ent. Soc. Am. 42: 511-537.

DIXON, A.F.G. (1959). An experimental study of the searching behaviour of the predatory coccinellid beetle Adalia decempunctata (L.)
J. Anim. Ecol. 28: 259-281.

DOANE, C.C. and LEONARD, D.E. (1975). Orientation and dispersal of late-stage larvae of Porthetria dispar (Lepidoptera: Lymantriidae).
Can. Ent. 107: 1333-1338.

DROOZ, A.T. (1975). Larval diet and Adult Longevity in the Elm Spanworm.
Environ. Entomol. 4: 847-848.

DUMBLETON, L.J. (1939). Contribution to the physical ecology of Tortrix postvittana, Walk. (Lep.).
Bull. ent. Res. 30: 309-319.

EDGAR, J.A. and CULVENOR, C.C.J. (1974). Pyrrolizidine ester alkaloid in Danaid butterflies.
Nature 248: 614-615.

ELTRINGHAM, H. (1925). On the Abdominal Brushes in certain male Noctuid Moths.
Trans. ent. Soc. Lond. 73: 1-5.

ERRINGTON, P.L. (1946). Predation and vertebrate populations.
Quart. Rev. Biol. 21: 144-177.

FENNER, T.L. (1961). Vine Moth.
J. Dep. Agric. S. Aust. 65: 73.

FINNEY, D.J. (1941). Wireworm populations and their effect on crops.
Ann. appl. Biol. 28: 282-295.

FISHER, R.A. (1941). The negative binomial distribution.
Ann. Eugen. 11: 182-187.

FISHER, R.A., CORBET, A.S. and WILLIAMS, C.B. (1943). The relation between the number of species and the number of individuals in a random sample of an animal population.
J. Anim. Ecol. 12: 42-58.

FISHER, R.A. and YATES, F. (1970). Statistical Tables for biological, agricultural and medical research. 6th edition. Oliver and Boyd. 146 pp.

FRENCH, C. (1893). A Handbook of the destructive insects of Victoria. Part II: 101-107. Govt. Printer Melbourne 222 pp.

FRENCH, C. (1916). Insect pests of the fruit, flower and vegetable garden. J. Agric. Vict. 14: 433-438.

FROST, S. (1959). Insect life and insect natural history. N.Y. Dover 526 pp.

GALUN, R. et al. (1975). Sensory Physiology and Behaviour. Plenum New York.

GEIER, P.W. (1963). The Life history of codling moth, Cydia pomonella (L.) (Lepidoptera:Tortricidae), in the Australian Capital Territory. Aust. J. Zool. 11: 323-367.

GEIER, P.W. (1964). Population dynamics of codling moth, Cydia pomonella (L.) (Tortricidae), in the Australian Capital Territory. Aust. J. Zool. 12: 381-416.

GIVEN, B.B. (1944). Longevity of Diamond-back Moth (Plutella maculipennis) Adults in Relation to Nutrition. N.Z. Jl. Sci. Technol. 26: No. 4. (Sec. A),:192-194.

GOEDEN, R.D. (1975). A Noteworthy Host-Plant Record for Ipochus fasciatus. Ann. ent. Soc. Am. 63: 493-494.

GREEN, W.Q. (1974). An antagonistic insect/host plant system: the problem of persistence. Ph.D. Thesis. Dept. of Zoology. Univ. of British Columbia 247 pp.

GROSS, G.F. (1975). Plant feeding and other bugs (Hemiptera) of South Australia. Heteroptera Part I. Govt. Printer South Australia 250 pp.

GUPTA, P.C. (1974). Preference of oviposition in Bemisia gossypiperda M & L. (Homoptera:Aleyrodidae) on different nonhost plants. Zool. Beitr. 20: 497-499.

HALL, M.C. (1974). A native foodplant of Papilio canopus canopus Westwood (Lepidoptera:Papilionidae). Aust. Entomol. Mag. 2: 6.

HARCOURT, D.G. (1960). Distribution of the Immature Stages of the Diamondback Moth, Plutella maculipennis (Curt.) (Lepidoptera: Plutellidae) on Cabbage. Can. Ent. 92: 517-521.

HARCOURT, D.G. (1961). Spatial pattern of the Imported Cabbageworm, Pieris rapae (L.) (Lepidoptera:Pieridae), on Cultivated Cruciferae. Can. Ent. 93: 945-952.

HOLT, G.G. and NORTH, D.T. (1970). Effects of Gamma Irradiation on the mechanisms of sperm transfer in Trichoplusia ni. J. Insect Physiol. 16: 2211-2222.

HOVANITZ, W. (1969). Inherited and/or conditioned changes in host-plant preference in Pieris. Entomologia exp. appl. 12: 729-735.

HOVANITZ, W. and CHANG, V.C.S. (1962). Three factors affecting larval choice of foodplant. J. Res. Lepid. 1: 51-61.

HOVANITZ, W. and CHANG, V.C.S. (1963). Ovipositional preference tests with Pieris. J. Res. Lepid. 2: 185-200.

HOVANITZ, W. and CHANG, V.C.S. (1963a). Change of food plant preference by larvae of Pieris rapae controlled by strain selection, and the inheritance of this trait.
J. Res. Lepid. 1: 163-168.

HOVANITZ, W. and CHANG, V.C.S. (1963b). Ovipositional preference tests with Pieris.
J. Res. Lepid. 2: 185-200.

HUFFAKER, C.B. and KENNETT, C.E. (1956). Experimental studies on predation: Predation and Cyclamen-Mite. Populations on Strawberries in California.
Hilgardia 26: 191-222.

ISELY, D. (1938). Codling moth oviposition and temperature.
J. econ. Ent. 31: 356-359.

JACOBSON, M. (1974). Insect Pheromones
in The Physiology of Insecta Vol. III ed. M. Rockstein.

JERMY, T., HANSON, F.E. and DETHIER, V.G. (1968). Induction of specific food preference in Lepidopterous larvae.
Entomologia exp. appl. 11: 211-230.

JOHNSON, N.L. and KOTZ, S. (1969). Discrete Distributions.
Houghton Mifflin Co. Boston. 328 pp.

JONES, E.L. (1967). Pests of the grape vine.
Agric. Gaz. N.S.W. 78: 708.

LATHEEF, M.A. and HARCOURT, D.G. (1972). A quantitative study of food consumption, assimilation, and growth in Leptinotarsa decemlineata (Coleoptera:Chrysomelidae) on two host plants.
Can. Ent. 104: 1271-1276.

LEES, A.D. (1955). The Physiology of diapause in arthropods.
Cambridge University Press 151 pp.

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

LEWIN, J.W. (1822). Natural History of the Lepidopterous insects of New South Wales.
Lond. J.H. Bohte 19 pp & 19 plates.

McCOY, F. (1885). Agarista glycine (Lewin sp.). The vine day-moth.
Prodromus Zool. Vict. 1 Decade I: 30-32.

McCUBBIN, C. (1971). Australian Butterflies.
Thomas Nelson Ltd. 206 pp. (Aust.).

McKEOWN, K.C. (1942). Australian Insects, an introductory handbook.
Syd. Royal Zool. Soc. N.S.W. 304 pp.

McLACHLAN, R.A. (1968). A dipping trial with larvae of the grape-vine moth (Phalaenoides glycine Lew.).
Queensl. J. Agric. & Animal Sci. 25: 255-258.

MACLELLAN, C.R. (1973). Natural enemies of the light brown apple moth, Epiphyas postvittana, in the Australian Capital Territory.
Can. Ent. 105: 681-700.

MACAULAY, E.D.M. (1973). Tocopherol: Egg production and Migration by Plusia gamma.
Entomologia exp. appl. 16: 48-52.

MADGE, D.S. (1964a). The light reactions and feeding activity of larvae of the cutworm Tryphaena pronuba L. (Lepidoptera:Noctuidae).
Part I. Laboratory Investigations.
Entomologia exp. appl. 7: 47-61.

MADGE, D.S. (1964b). The light reactions and feeding activity of larvae of the cutworm Tryphaena pronuba L. (Lepidoptera:Noctuidae).
Part II. Field Investigations.
Entomologia exp. appl. 7: 105-114.

MARTYN, E.J. (1965). Studies on the ecology of Oncopera intricata Walker (Lepidoptera:Hepialidae). I. Fecundity of the Female Moth. Aust. J. Zool. 13: 801-805.

MATTESON, J.W. and DECKER, G.C. (1965). Development of the European Corn borer at controlled constant and variable temperatures. J. econ. Ent. 58: 344-349.

MEINWALD, J., MEINWALD, Y.C. and MAZZOCCHI, P.H. (1969). Sex pheromone of the Queen Butterfly: Chemistry. Science 164: 1174-1175.

MEINWALD, J., MEINWALD, Y.C., WHEELER, J.W. EISNER, T. and BROWER, L.P. (1966). Major components in the Exocrine Secretion of a Male Butterfly (Lycorea). Science 151: 583-585.

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

MILLER, C.D.F., MUKERJI, M.K. and GUPPY, J.C. (1972). Notes on the spatial pattern of Hypera postica (Coleoptera:Curculionidae) on alfalfa. Can. Ent. 104: 1995-1999.

MILLER, D. (1940). The Australian grape-vine moth Phalaenoides glycine Lew. Cawthron Instit. Public. No. 41.

MILNE, A. (1964). Biology and ecology of the garden chafer, Phyllopertha horticola (L.). IX. Spatial Distribution. Bull. ent. Res. 54: 761-795.

MONRO, J. (1957). The Physiology of moulting, metamorphosis and diapause in insects. Ph.D. Thesis. University of Adelaide.

MORISITA, M. (1959). Measuring of the Dispersion of Individuals and Analysis of the Distributional Patterns.
Mem. Fac. Sci. Kyusha Univ. Ser. E. (Biol.) 2: 215-235.

MORISITA, M. (1962). I_δ-Index, a measure of dispersion of individuals.
Researches Popul. Ecol. IV: 1-7.

MORISITA, M. (1964). Application of I_δ-index to sampling techniques.
Researches Popul. Ecol. 6: 43-53.

MUGGERIDGE, J. (1942). The White Butterfly (Pieris rapae L.)
I. Its establishment, spread and control in New Zealand.
N.Z. Jl. Sci. Technol. (A) 24: 107-129.

MUKERJI, M.K. and GUPPY, J.C. (1970). A quantitative study of food consumption and growth in Pseudaletia unipuncta (Lepidoptera:Noctuidae).
Can. Ent. 102: 1179-1188.

MUKERJI, M.K. and HARCOURT, D.G. (1970). Spatial pattern of the immature stages of Hylemya brassicae on cabbage.
Can. Ent. 102: 1216-1222.

MURDOCH, W.W. (1969). Switching in general predator: experiments on predator specificity and stability of prey populations.
Ecol. Monogr. 39: 335-354.

MYERS, J.H. and CAMPBELL, B.J. (1976). Indirect measures of larval dispersal in the Cinnabar moth, Tria jacobaeae (Lepidoptera:Arctiidae).
Can. Ent. 108: 967-972.

NOBLE, N.S. (1936). Euplectrus agaristae Craw., a parasite of the Grape Vine Moth - Phalaenoides glycine Lew.
J. Aust. Inst. agric. Sci. 2: 165-168.

NOBLE, N.S. (1938). Euplectrus agaristae Craw., a parasite of the Grape Vine Moth (Phalaenoides glycine Lew.). Sci. Bull. Dep. Agric. N.S.W. No. 63.

NORRIS, M.J. (1932). Contributions toward the study of insect fertility. I. The structure and operation of the reproductive organs of the Genera Ephestia and Plodia (Lepidoptera:Phycitidae). Proc. zool. Soc. Lond. Pts. 3 & 4: 595-611.

OATEN, A. and MURDOCH, W.W. (1975). Switching, Functional response, and stability in predator-prey systems. Amer. Natur. 109: 299-318.

PAHL, P.J. (1969). On testing for goodness-of-fit of the negative binomial distribution when expectations are small. Biometrics 25: 143-151.

PETERSEN, W. (1904). Die morphologie der generationsorgane der schmetterline und ihre bedeutung fur die artbildung. Mem. Acad. Sciences de St. Petersburg Serie VIII, Classe Physico-Mathematique XVI (8): 1-84.

PIELOU, E.C. (1969). Introduction to mathematical ecology. N.Y. Wiley 286 pp.

PLISKE, T.E. and EISNER, T. (1969). Sex pheromone of the Queen Butterfly: Biology. Science 164: 1170-1172.

PROKOPY, R.J. (1968). Influence of photoperiod, temperature and food on initiation of diapause in the apple maggot. Can. Ent. 100: 318-329.

QUENOUILLE, M.H. (1949). A relation between the Logarithmic, Poisson and negative binomial series. Biometrics 5: 162-164.

ROCKSTEIN, M. (1974) ed. The Physiology of Insecta Vol. III. 2nd edition. Academic Press 517 pp.

SALT, G. and HOLLICK, F.S.J. (1946). Studies on wireworm populations II. Spatial distribution. J. exp. Biol. 23: 1-46.

SCHNEIDER, D. (1975). Pheromone communication in moths and butterflies. in Sensory Physiology and Behaviour (1975) eds. R. Galun et al. Plenum New York pp 173-193.

SHIELDS, O. (1974). Resistance in butterfly foodplants [Lep.]. J. Lep. Soc. 28: 288.

SHOREY, H.H. (1963). The Biology of Trichoplusia ni (Lepidoptera: Noctuidae). II. Factors affecting Adult Fecundity and Longevity. Ann. ent. Soc. Am. 56: 476-480.

SMITH, J.H. (1938). Pests of the grape vine. Qd. agric. J. 50: 700-707.

SNEDECOR, G.W. (1962). Statistical methods applied to experiments in agriculture and biology. 5th edition. Ames. Collegiate pr. 341 pp.

SOUTHWOOD, T.R.E. (1966). Ecological methods, with particular reference to the study of insect populations. Lond. Methuen. 391 pp.

STEINHAUS, E.A. (1948). Polyhedrosis ("Wilt Disease") of the Alfalfa Caterpillar. J. econ. Ent. 41: 859-865.

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.

STRIDE, G.O. and STRAATMAN, R. (1962). The hostplant relationship of an Australian swallowtail Papilio aegeus, and its significance in the evolution of hostplant selection.
Proc. Linn. Soc. N.S.W. 87: 69-78.

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. pluviale (Dyar). (Lepidoptera: Lasiocampidae).
Can. Ent. 85: 297-310.

THORSTEINSON, A.J. (1960). Host selection in phytophagous insects.
A. Rev. Ent. 5: 193-218.

UNIVERSITY OF MISSOURI, (1961). Populations of European Corn Borer, Ostrinia nubilalis (Hbn.) in Field Corn, Zea mays (L.).
Agric. Expt. Station. Univ. of Missouri. Bull. No. 776.

UVAROV, B.P. (1931). Insects and Climate.
Trans. R. ent. Soc. Lond. 79: 1-247.

VARLEY, G.C., GRADWELL, G.R. and HASSELL, M.P. (1973). Insect Population Ecology - an analytical approach.
Blackwell 212 pp.

WADLEY, F.M. (1950). Notes on the form of distribution of insect and plant populations.
Ann. ent. Soc. Am. 43: 581-586.

WATERS, W.E. (1959). A quantitative measure of aggregation in insects.
J. econ. Ent. 52: 1180-1184.

WATERS, W.E. and HENSON, W.R. (1959). Some sampling attributes of the negative binomial distribution with special reference to forest insects.
Forest Sci. 5: 397-412.

WELLINGTON, W.G. (1948). The light reactions of the Spruce Budworm Choristoneura fumiferana Clemens (Lepidoptera:Tortricidae). Can. Ent. 80: 56-82.

WELLINGTON, W.G. (1955). Solar heat and plane polarized light versus the light compass reaction in the orientation of insects on the ground. Ann. ent. Soc. Am. 48: 67-76.

WELLINGTON, W.G., SULLIVAN, C.R. and GREEN, G.W. (1951). Polarized light and body temperature level as orientation factors in the light reactions of some hymenopterous and lepidopterous larvae. Can. J. Zool. 29: 339-351.

WELLINGTON, W.G., SULLIVAN, C.R. and HENSON, W.R. (1954). The light reactions of larvae of the Spotless Fall Webworm, Hyphantria textor Havr. (Lepidoptera:Arctiidae). Can. Ent. 86: 529-542.

WHEELER, A.G. (1975). Insect associates of Ginkgo biloba [Ginkgoaceae]. Entomol. News 86: 37-44.

de WILDE, J. (1969). Hormones and insect diapause. Mem. Soc. Endocr. No. 18: 487-514.

WILLIAMS, C.B. (1944). Some applications of the logarithmic series and the index of diversity to ecological problems. J. Ecol. 32: 1-44.

WILLIAMS, C.B. (1947). The logarithmic series and its application to biological problems. J. Ecol. 34: 253-272.

WILLIAMS, J.L. (1946). Vine pests and diseases. J. Dep. Agric. S. Aust. 49: 441-447.

WRIGHT, D.W. and GEERING, Q.A. (1948). The biology and control of the pea-moth Laspeyresia nigricana, Steph.
Bull. ent. Res. 39:. 57-84.

YAMAMOTO, R.T., JENKINS, R.Y. and McCLUSKY, R.K. (1969). Factors determining the selection of plants for oviposition by the tobacco hornworm Manduca sexta.
Entomologia exp. appl. 12: 504-508.

ZECK, E.H. (1955). The Grape-Vine Moth.
Agric. Gaz. N.S.W. 66: 552.

APPENDIX 1 Observed and expected frequencies for a Poisson distribution of larvae in the first generation each season.

1973-74

Date	x	O(f)	E(f)
11/10/73	0	29	28.26
	1	2	3.53
	2	1	0.22
16/10/73	0	39	37.11
	1	0	2.78
	2	0	0.10
	3	1	0.00
23/10/73	0	26	22.55
	1	7	12.97
	2	6	3.73
	⩾2	1	0.75
30/10/73	0	21	16.25
	1	7	14.62
	2	8	6.58
	3	3	1.97
	4	1	0.44
8/11/73	0	21	20.35
	1	13	13.74
	2	4	4.64
	3	2	1.04
13/11/73	0	38	37.11
	1	1	2.78
	>1	1	0.11
20/11/73	0	35	34.43
	1	4	5.16
	2	1	0.31
29/11/73	0	39	38.99
	1	1	0.97

APPENDIX 1 continued

1974-75

Date	x	O(f)	E(f)
31/10/74	0	15	12.76
	1	3	5.74
	2	1	1.29
	4	1	0.02
19/11/74	0	11	10.45
	1	6	6.80
	2	2	2.21
	3	1	0.48
28/11/74	0	15	13.42
	1	3	5.37
	2	1	1.07
	3	1	0.14
1975-76			
27/10/75	0	6	5.17
	1	2	2.87
	3	1	0.15
4/11/75	0	10	7.73
	1	6	7.35
	2	2	3.49
	3	1	1.11
	>6	1	0.31
11/11/75	0	10	8.56
	1	3	5.35
	2	2	1.67
	3	1	0.35
18/11/75	0	8	8.61
	1	4	2.87
25/11/75	0	11	9.70
	1	3	4.85
	2	1	1.21
	3	1	0.20

APPENDIX 2(a) Observed and expected frequencies for a Negative Binomial distribution of eggs in the second generation each season.

1973-74

Date	x	O(f)	E(f)*
5/2/74	0	22	24.64
	1	7	3.75
	2	2	2.07
	3	2	1.42
	4	1	1.07
	5	1	0.85
	6	1	0.69
	>11	4	4.93
12/2/74	0	25	18.29
	1	1	4.37
	2	2	2.61
	5	2	1.18
	6	2	0.99
	9	1	0.64
	>14	7	5.92
21/12/74	0	14	17.29
	1	9	5.38
	2	3	3.30
	3	2	2.36
	4	5	1.80
	5	2	1.43
	8	1	0.81
	>14	4	3.72
1/3/74	0	20	13.91
	1	2	4.63
	2	1	2.97
	3	1	2.22
	4	5	1.77

* expectancies <0.5 pooled.

APPENDIX 2(a) continued

1973-74

Date	x	O(f)	E(f)*
1/3/74	7	2	1.07
	8	1	0.93
	>17	8	6.46
7/3/74	0	31	28.19
	1	3	5.07
	2	1	2.44
	4	2	0.90
	>5	3	1.40
1974-75			
20/2/75	0	7	15.78
	2	1	0.41
	3	4	0.28
	4	1	0.21
	>5	7	2.37
27/2/75	0	2	0.57
	2	2	0.81
	6	1	0.80
	8	1	0.73
	9	1	0.69
	10	2	0.65
	12	1	0.57
	>13	6	6.01
6/3/75	0	2	0.55
	2	2	1.13
	3	1	1.23
	5	1	1.22
	7	3	1.07
	9	1	0.88
	11	1	0.69
	12	1	0.61
	>14	4	3.00

APPENDIX 2(a) continued

1974-75

Date	x	O(f)	E(f)*
13/3/75	0	13	12.11
	1	1	1.92
	3	1	0.45
	>4	1	0.68
20/3/75	0	14	11.97
	1	0	1.03
	2	0	0.54
	>4	2	2.46
1975-76			
3/2/76	0	11	10.11
	1	2	2.51
	3	1	0.73
	>3	2	1.40
12/2/76	0	2	1.44
	1	1	0.79
	4	1	0.41
	>4	4	4.29
19/2/76	0	2	2.66
	1	3	1.46
	3	1	0.87
	4	1	0.73
	>4	6	5.03
26/2/76	0	2	1.48
	1	1	1.85
	2	3	1.78
	4	1	1.28
	5	1	1.02
	6	2	0.79
	7	1	0.60
	>11	1	1.65

* expectancies <0.5 pooled unless impractical in which case expectancies <0.15 pooled.

APPENDIX 2(a) continued

1975-76

Date	x	O(f)	E(f)*
4/3/76	0	7	6.72
	1	2	1.84
	2	1	1.01
	>4	2	1.78

* Expectancies <0.5 grouped where practical.

APPENDIX 2(b) Observed and expected frequencies for a Negative Binomial distribution of larvae in the second generation each season.

1973-74

Date	x	O(f)	E(f)
5/2/74	0	17	22.13
	1	7	5.65
	2	7	3.17
	3	5	2.10
	>3	4	6.96
12/2/74	0	20	15.51
	1	5	6.65
	3	4	3.00
	4	1	2.22
	5	3	1.69
	>5	7	6.70
21/2/74	0	5	7.87
	1	9	4.72
	2	3	3.58
	3	1	2.90
	4	4	2.43
	5	2	2.07
	6	3	1.79
	7	1	1.56
	>7	12	13.07
1/3/74	0	14	14.19
	1	4	5.04
	2	6	3.25
	3	2	2.41
	4	2	1.90
	>5	12	11.65

APPENDIX 2(b) continued

1973-74

Date	x	O(f)	E(f)
7/3/74	0	18	20.37
	1	8	5.84
	2	7	3.38
	3	1	2.29
	4	1	1.66
	>7	5	6.46
14/3/74	0	19	18.16
	1	7	7.05
	2	6	4.21
	3	1	2.81
	>4	7	5.81
21/4/74	0	28	28.44
	1	6	4.99
	2	2	2.39
	>2	4	4.18
1974-75			
20/2/75	0	3	1.92
	1	2	2.55
	2	2	2.61
	4	4	2.10
	5	4	1.77
	6	1	1.45
	10	2	0.58
	>12	2	1.79
27/2/75	<3	3	1.85
	5	1	0.52
	6	1	0.54
	10	1	0.55
	13	1	0.51
	>20	9	9.30

APPENDIX 2(b) continued

1974-75

Date	x	O(f)	E(f)
6/3/75	<8	4	2.83
	11	2	0.53
	13	1	0.53
	15	1	0.51
	>21	8	9.01
13/3/75	3	1	1.25
	8	1	0.66
	9	1	0.71
	12	2	0.77
	13	2	0.76
	14	1	0.75
	15	1	0.72
	17	2	0.66
	18	1	0.62
	>19	4	4.17
20/3/75	0	1	2.36
	1	1	1.22
	2	1	0.91
	5	3	0.56
	>7	10	9.07
27/3/75	4	1	0.98
	6	1	0.50
	7	1	0.61
	8	1	0.71
	10	1	0.84
	12	1	0.89
	16	2	0.80
	17	1	0.75
	18	1	0.69
	19	1	0.63

APPENDIX 2(b) continued

1974-75

Date	x	O(f)	E(f)
27/3/75	20	2	0.57
	21	1	0.52
	>21	2	3.26
10/4/75	0	2	1.14
	1	2	2.02
	2	3	2.38
	4	2	2.03
	6	3	1.29
	7	1	0.96
	8	1	0.70
	9	2	0.50
1975-76			
12/2/76	0	2	1.99
	1	2	1.13
	3	1	0.64
	>5	3	2.90
19/2/76	0	1	2.06
	1	2	1.21
	2	1	0.93
	3	2	0.77
	5	1	0.58
	>9	6	6.25
26/2/76	2	1	0.57
	4	1	0.43
	6	1	0.36
	8	1	0.31
	11	1	0.26
	>11	7	6.46

APPENDIX 2(b) continued

1975-76

Date	x	O(f)	E(f)
4/3/76	1	1	1.18
	2	3	1.03
	3	1	0.91
	4	2	0.80
	6	1	0.64
	8	1	0.51
	>17	3	4.28
11/3/76	0	1	1.79
	1	3	1.09
	2	1	0.85
	>7	7	6.43
18/3/76	2	2	0.61
	4	1	0.86
	5	2	0.91
	7	1	0.89
	8	1	0.83
	12	1	0.55
	>13	4	2.99
25/3/76	0	1	1.37
	1	2	1.58
	2	2	1.52
	3	1	1.36
	4	1	1.16
	5	1	0.98
	6	1	0.81
	>8	3	2.03

APPENDIX 2(c)

Generation 1 1973-74

Date	x	O(f)	E(f)
16/10/73	0	39	38.39
	1	0	0.95
	2	0	0.33
	>2	1	0.32

APPENDIX 3 Probit analysis to find LD_{50} at $35^{o}C$

(see Section 6.4.2)

x	n	r	p	Emp. prob.
1	10	0	0	-
2	10	0	0	-
3	10	0	0	-
4	10	2	0.2	4.16
5	10	6	0.6	5.25
6	10	8	0.8	5.84
7	10	10	1.0	8.72
8	10	10	1.0	8.72

x = duration of exposure

n = number of larvae exposed

r = number of larvae dead

p = proportion of larvae dead

Emp. prob. = Empirical Probit.

APPENDIX 4

During this study a parasite of the egg stage of *Oechalia schellenbergii* was found. It was identified as *Trissolcus* sp. (F. Scelionidae).

APPENDIX 5 Species mentioned in this thesis.

Insects:

Adalia decempunctata (L.)
Bemisia gossypiperda M & L
Cermatulus nasalis (Westw.)
Choristoneura fumiferana (Clem.)
Colias philodice eurytheme Boisduval
Cuspicona sp.
Cydia pomonella (L.)
Danaus gilippus berenice (Cram.)
Ecthromorpha intricatoria (Fabr.)
Epiphyas postvittana (Walk.)
Eriococcus orariensis Hoy
Euplectrus agaristae Crawf.
Eurytoma sp.
Eutrichopidia latina (Don.)
Exorista sp. of sorbillans (Wied.)
Grapholitha molesta (Busck)
Halyzia galbula Mulsant
Hyphantria textor Havr.
Ipochus fasciatus LeConte
Laspeyresia nigricana (Steph.)
Leucania sp.
Lissopimpla semipunctata Kby.
Lycorea ceres ceres (Cram.)
Oechalia schellenbergii (Guér-Men.)
Ostrinia nubilalis (Hbn.)
Papilio anactus W.S. Macleay
Papilio canopus canopus Westwood
Papilio troilus L.
Phalaenoides glycine Lewin
Phalaenoides tristifica (Hübn.)
Phylogophora meticulosa (L.)
Pieris rapae (L.)
Porthetria dispar (L.)
Rhyacionia frustrana (Comst.)
Rutilia speciosa Er.
Trissolcus sp.
Winthemia sp.
Xylophasia monoglypha Hüfner

Birds:

Acridotheres tristis (Linn.)
Chrysococcyx basalis (Horsfield)
Cuculus pallidus (Latham)
Gymnorhina tibicen (Latham)

Plants:

Citrus sp.
Echium plantagineum L.
Epilotium sp.
Foeniculum vulgare Mill.
Fuchsia sp.
Ginkgo biloba L.
Glycine bimaculata Curtis
Glycine clandestina Wendland
Gnaphalium luteoalbum L.
Hibbertia scandens Gilg
H. sericea Benth.
H. stricta R. Br.
Justicia betonica L.
Ludwigia peploides ssp. monte videnses (Raven)
Silybum marianum (L.) Gaertner
Vitis kaempferi (L.)
V. quinquefolia (L.)
V. vinifera L.