APPLIED ECOLOGY OF THE TASMANIAN LACEWING *Micromus tasmaniae* WALKER (NEUROPTERA : HEMEROBIIDAE)

A thesis submitted in fulfilment of
the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENTOMOLOGY

at

LINCOLN COLLEGE
UNIVERSITY OF CANTERBURY

D. M. Leathwick
1989

ABSTRACT

The Tasmanian lacewing (*Micromus tasmaniae* Walker) is one of the most common aphid predators occurring in lucerne crops in New Zealand. A comparison of sampling techniques, and the output from a simulation model, suggest that the abundance of this lacewing may have been significantly underestimated in the past. Although the occurrence of aphid predators was erratic *M. tasmaniae* occurred more often and in far greater numbers (up to 100 m^{-2}) than any other predator species.

A simulation model for lacewing development in the field indicated that the large adult populations which occurred could be accounted for on the basis of reproductive recruitment. Independent evidence that immigration was not involved in the occurrence of these large populations was gathered using directional flight traps around the field perimeter. The major factors influencing lacewing population dynamics were the availability of aphid prey and, in the autumn, parasitism. Otherwise, survival of all life-histoty stages was high with no evidence of egg or larval cannibalism. Several instances of high lacewing mortality were identified by the model and the lack of any obvious cause for these highlights inadequacies in the understanding of lacewing bionomics.

The model, which used a linear relationship (day-degrees) between development and temperature, was incapable of accurately predicting lacewing emergence under field temperatures which fluctuated outside the linear region of the development rate curve. Temperature thresholds and thermal requirements estimated under fluctuating temperatures similar to those in the field produced almost identical model output to those estimated under constant temperatures in the laboratory. Prey species was capable of influencing the rate of lacewing development.

M. tasmaniae has the attributes necessary to produce large populations in the short time available between lucerne harvests. The asymptote of the functional response curve is low but the efficiency at converting aphids to eggs is high. Therefore, the lacewing is able to attain maximun reproductive output at low prey densities. A low temperature threshold for development (4-5^{o}C), rapid development and short preoviposition period results in a short generation time (49 days at 15^{o}C). Long adult life, high fecundity and the absence of any form of estivation or diapause, results in complete overlap of generations and multiple generations per year.

M. tasmaniae's role as an aphid predator is restricted by its low appetite for prey and by the lucerne management regime currently practiced in New Zealand. Because it consumes relatively few aphids per day the lacewing's ability to destroy large aphid populations is limited. However, this may be offset by its ability to attack aphids early in the aphid population growth phase, and by the large numbers of lacewings which may occur. Under the present lucerne management schemes the large lacewing populations which do occur are forced out of the fields, or die, following harvest. A number of management options for increasing the lacewings impact as an aphid predator are briefly discussed.

CONTENTS

FIGURES

TABLES

List of alterations and corrections to thesis

Applied ecology of the Tasmanian lacewing *Micromus tasmaniae*.

D.M. Leathwick

1989

page 2	is unknown.
page 2	throughout
page 4	. However, severe drought
page 8	lycosid
page 9 para 3	lower
page 10	(nabids and syrphids)
page 24 line 7	females'
page 26 line 3	lacewing's
page 26	$P < 0.01$)
page 30 bottom line	of
page 31 line 3	insect's
page 32	segments
page 32	larva
page 38 line 2	sometimes
page 38 para 2 line 6	disproportionate
page 39 3 lines from bottom	separately
page 40 explanation of graph	95% confidence interval for To
	95% confidence interval for K
	a = regression of 3 estimates of To and K
page 4 para 2 line 4	of
page 50	Berlese
page 54 para 2 line 6	too late
page 54 para 3	precision
page 58 para 3	unexplained mortality not
page 58 2 lines from bottom	larva
page 59 line 1	larva
page 59 para 2 line 8	amending
page 59 para 2 last line but 1	intense competition
page 59 last line but 1	affected
page 60 heading	third instar
page 62 para 2 line 2	when
page 65 para 3 last line	affecting
page 67 4 lines from bottom	parasitism

page 71 para 2	bias
page 71 para 3 line 3	parasite's
page 72	preceding
page 74 Heading	Pattern of growth and number of prey killed for Micromus
page 76	15°C
page 80 para 4 line 2	smaller
	Leathwick unpubl.).
page 93 para 1 line 8	too late
line 9	to
para 3 line 7	occurrence
page 95 line 3	McDonald and Harper,1978;
page 99 line 1	lacewing's
page 99 para 3 line 6	lacewing's
page 120 flow chart	yes no

CHAPTER 1: Introduction

Lucerne (*Medicago sativa*) is an important forage crop in many parts of New Zealand, with up to 140,000 hectares grown annually for hay or silage (Dunbier *et al.*, 1982). Lucerne is particularly valuable to farmers in the drier areas of Canterbury and Otago because it offers high food value, drought tolerance and is resistant to feeding injury from grass grub (*Costelytra zealandica* White). Although a wide range of arthropod species can be found inhabiting lucerne, prior to the mid 1970's few species caused any appreciable damage (Macfarlane, 1970).

In 1975 the bluegreen lucerne aphid (BGLA) *Acyrthosiphon kondoi* Shinji was discovered in New Zealand, followed in 1977 by the pea aphid (PA) *Acyrthosiphon pisum* Harris. These species spread rapidly causing severe damage to lucerne crops (Kain *et al.*, 1977; Kain *et al.*, 1979) and contributed to a decline in the popularity of lucerne as a forage crop (Dunbier *et al.*, 1982). By 1982 the spotted alfalfa aphid (SAA) *Therioaphis trifollii* fm. *maculata* Monell had arrived in New Zealand, but it did not reach the epidemic levels observed overseas (Rohitha *et al.*, 1985). However, it is now an established component of the lucerne aphid fauna in most areas (Cameron and Walker, 1984; Rohitha *et al.*, 1985; Chapter 2) and, when coincident with BGLA and PA populations, may contribute to production losses.

A range of insecticides are effective against these aphids (Kain *et al.*, 1976; Syrett and Penman, 1980) but reinfestation can be very rapid (Sharma *et al.*, 1975). In more recent years damage caused by these aphids appears to have declined from the dramatic levels seen in the late 1970's. This may reflect either an increase in the number of aphid natural enemies and/or an increased use of advantageous management techniques such as winter grazing and resistant lucerne cultivars (Cameron *et al.*, 1983). The number of aphid natural enemy species occurring in lucerne crops in New Zealand is low compared with overseas (see Wheeler, 1977) and is generally restricted to four commonly occurring species; the 11-spotted ladybird *Coccinella undecimpunctata* L., the Pacific damsel bug *Nabis kinbergii* Germar, a syrphid *Melanostoma fasciatum* MacQuart, and the Tasmanian lacewing *Micromus tasmaniae* Walker (Cameron *et al.*, 1979). Several species of introduced parasites *Aphidius* spp. are also present. Of these *C. undecimpunctata* and *M. tasmaniae* are the species most often reported in New Zealand as being abundant and thought to be involved in suppressing aphid populations (Cameron *et al.*, 1983; Rohitha *et al.*, 1985).

Although natural enemies are capable of suppressing the growth of lucerne aphid populations (Henderson, 1979; Rohitha *et al.*, 1985; Bishop and Milne, 1986) their performance appears to be

limited by a lack of synchrony with the aphids (Cameron *et al.*, 1983). However, the role of beneficial organisms in suppressing pest populations forms a natural basis for the integration of all other control strategies (Bishop, 1979). In the long term, then, optimization of aphid control strategies will depend on a knowledge of the biologies of both the aphids and their natural enemies. Some work has been carried out on the biology of the aphids under New Zealand conditions (Rohitha, 1979) but very little information is available on the biologies of the predator species.

The larvae of Neuroptera are generally predaceous and in many species so too are the adults (New, 1975). Representatives of two Neuropteran families, the Chrysopidae or green lacewings, and the Hemerobiidae or brown lacewings, are frequently encountered in agro-ecosystems throughout the world and have proved important in the suppression of numerous pest species (for a review of these two families see New, 1975). However, while the available information on the Chrysopidae is vast (Canard *et al.*, 1984), studies involving the Hemerobiidae are few. In terms of number of species the New Zealand lacewing fauna is sparse (New, 1975) with only five species of Hemerobiidae and no Chrysopidae (Wise, 1963). By comparison Britain has 14 chrysopid and 29 hemerobiid species, while the Hawaiian islands have 25 and 28 species respectively (New, 1975).

Of the five hemerobiid species in New Zealand *M. tasmaniae* is by far the most common, being almost completely dominant in field crops. In the present study only occasional specimens of other hemerobiid species (*Drepanacra binocula* Newman and *Wesmaelius subnebulosus* Stephens) were recorded. Although the presence of *M. tasmaniae* in lucerne crops has been reported on numerous occasions with respect to its possible role as an aphid predator in New Zealand (Thomas, 1977; Cameron *et al.*, 1983; Rohitha *et al.*, 1985) and in Australia (Ting *et al.*, 1978; Bishop and Milne, 1986), few studies have looked at the insect's biology. Samson and Blood (1979) and Syrett and Penman (1981) established thermal coefficients for the species (Chapter 4), Syrett and Penman (1980) showed its very high tolerance to certain insecticides (Chapter 7), and Samson and Blood (1980) investigated its searching ability and voracity against eggs of *Heliothis* species. The major study on the species was done by Hilson (1964) but unfortunately much of his work was not quantitative. *M. tasmaniae* is known to be attacked by at least one hymenopteran parasite (*Anacharis zealandica* Dalman) but the extent to which parasitism influences lacewing bionomics is unknown.

The objectives of the present study were therefore;

1. To identify, and quantify, the major factors influencing lacewing population dynamics within the lucerne forage crop.

2. To investigate the predator/prey relationship between *M. tasmaniae* and the pest aphid species inhabiting lucerne.

3. To identify possible ways of augmenting the lacewing's effect on the aphids.

CHAPTER 2: Sampling techniques and predator abundance

INTRODUCTION

In order to gain insight into *Micromus tasmaniae's* role as a natural enemy of aphids it is necessary to establish its seasonal abundance, and hence its degree of synchrony with the aphid populations. The lacewings abundance relative to that of the aphids, and other species of aphid predators, will contribute to its importance as a biological control agent.

Some data are available on the abundance of lucerne aphid predators in New Zealand (Cameron *et al.*, 1979; Henderson, 1979; Bates and Miln, 1982). In the main, sampling for the estimation of predator abundance has been carried out using the sweep net. This is despite considerable literature which shows that the results of sweeping are influenced by a wide variety of factors (see Southwood, 1978 for a review) and that it is not a suitable technique for comparing the abundance of different species (Hodek *et al.*, 1972).

It was necessary, therefore, to evaluate the sweep net as a legitimate device for sampling lacewings from lucerne and in the light of this evaluation establish when and in what numbers lacewings occur in the field.

METHODS

Sites

During the spring and early summer of 1983-84 four lucerne fields were quantitatively sampled at approximately weekly intervals whenever the lucerne was actively growing. Sites were a 2.7 hectare field of Wairau lucerne on the Lincoln College research farm (site R.21), a 4.4 hectare field of WL318 on the Lincoln College Sheep Breeding Unit (site S.20), a 1.0 hectare field of Rere at Tai Tapu near Lincoln (site Tai Tapu) and an 0.2 hectare lucerne varieties trial at Henley Estate near Lincoln (site Henley). The latter site was a Plant Science Department trial which consisted of 16 plots (9 x 12 metres) of four lucerne cultivars ('Rere', 'Wairau', 'Saranac' and 'Matador').

Sampling was discontinued at Henley and Tai Tapu after January 1984 in order to allow more intensive sampling at the other two sites. In 1984-85 sampling was further restricted to that of site R.21 as part of the lacewing life-table study (Chapter 5). However, severe drought

throughout the summer prevented lucerne growth and no insect populations established. Sampling was successfully carried out at this site in the spring of 1985 and 1986 and in the autumn of 1986.

All sites were sampled using a D-vac motorized suction sampler while S.20, R.21 and the Tai Tapu site were also sampled with a sweep net in order to compare the two sampling techniques.

Sampling techniques

All samples were collected between 1000h and 1600h in order to minimize the effects of diel activity patterns.

D-vac samples

D-vac samples were taken in the manner considered most efficient by Southwood (1978). The nozzle of the D-vac was lowered vertically into the foliage and down to the ground surface, held in this position for approximately 30 seconds, and lifted vertically off. The populations from five such samples were pooled to give a single sample, except in the life-table study where sample size was increased (see Chapter 5). Since the D-vac nozzle covered an area of 850 cm^2, each sample represented 0.43 m^2.

The D-vac was modified to facilitate convenient use by a single operator. A Velcro^R strip was glued to the outside of the cone 25 mm from the open end. Corresponding strips of Velcro were sewn to the outside of mesh collecting bags. This enabled bags to be fitted quickly and easily while the machine was running, simply by inserting the bag and pushing the strips of Velcro together. After collecting a sample the bag was removed, sealed with a rubber band and left in the crop. In this way an operator working alone could easily collect up to ten samples without stopping the machine or leaving the crop. Sample bags were collected after all the samples had been taken and were returned to the laboratory for sorting.

Whenever time allowed samples were sorted by hand. Otherwise, the insects were extracted from the foliage and litter in Berlese funnels and stored in 70% alcohol until time was available to sort and count them.

Sweep samples

Sweep samples were taken using a 30 cm diameter sweep net with a 1.3 m long handle. One sample consisted of 20 sweeps through the foliage taken while walking through the crop sweeping in a 90^{o} arc alternately to the right and left. After 20 sweeps the contents of the net were emptied into a plastic bag for returning to the laboratory and sorting. All sweeping was carried out by the same person to avoid operator bias.

Stem samples

In 1985-86 quadrat stem samples were taken to estimate lacewing egg densities as part of the lacewing life-table study (Chapter 5). All the vegetation within a 0.625 m^2 quadrat was cut as close to ground level as possible and placed carefully into a plastic bag. Ten such samples were taken on each sampling occasion (3-5 day intervals). As the vegetation was carefully searched for lacewing eggs, the number of aphid mummies and any predators were recorded.

Pitfall traps

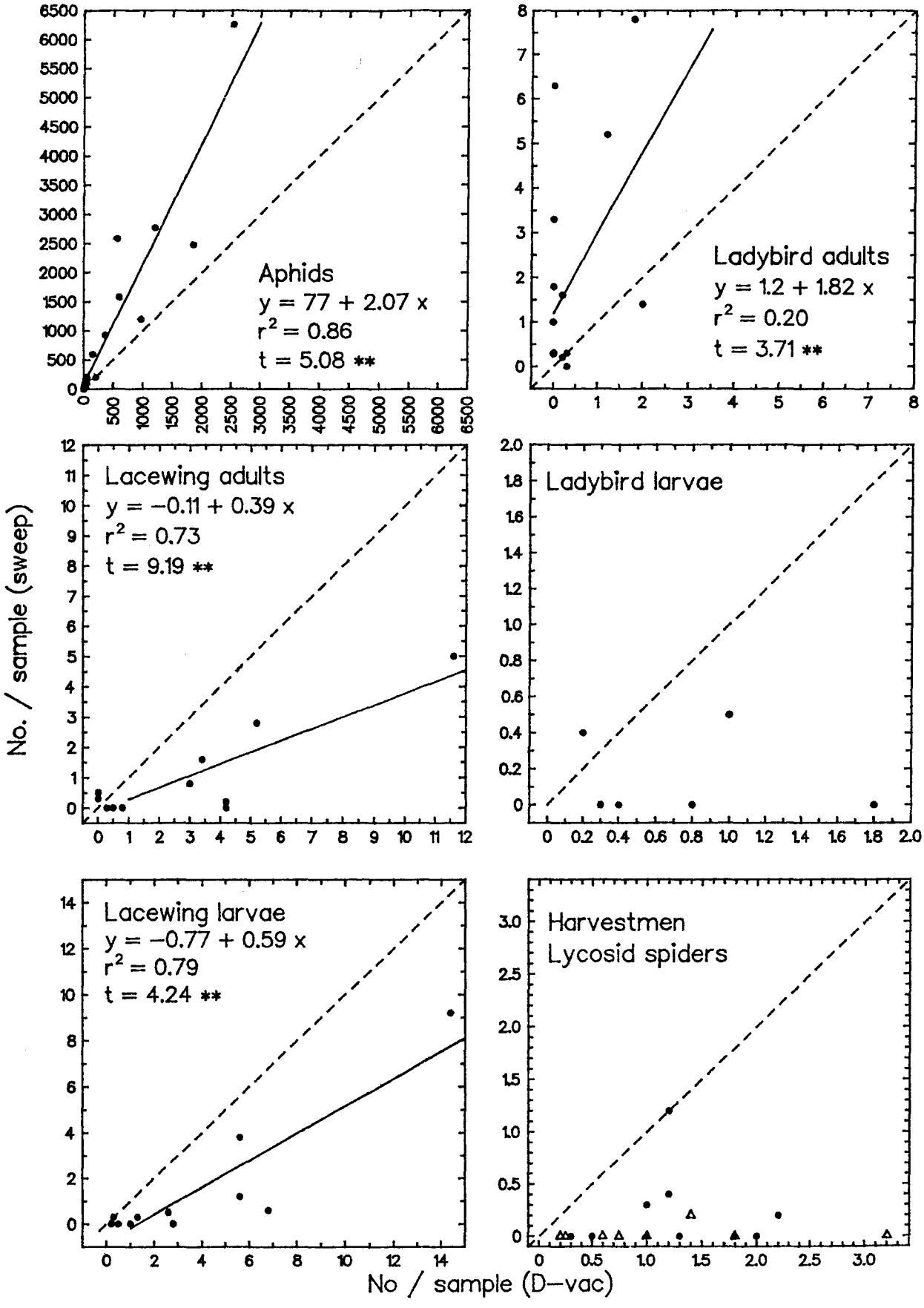
Pitfall traps were set out at site R.21 during spring 1985 and autumn 1986. Traps consisted of pieces of perspex in which a 60 mm diameter hole had been cut and a 250 ml plastic pottle fixed underneath. Five such traps were placed in the ground along a transect line running diagonally across the field. Traps were half filled with 70% alcohol and were emptied at 7-14 day intervals.

RESULTS

D-vac versus sweep samples

The relative efficiency of the D-vac and sweep net at catching different species was assessed by plotting the number of individuals collected by one technique against the number collected by the other (Fig.2-1). Each pair of data points represent samples taken from the same site on the same day. As care was taken to ensure that the areas sampled did not overlap, all samples were from the same population. Hence, when means from the two sampling techniques are plotted against one another a significant deviation from a slope of 1.0 indicates a bias in sampling efficiency between the techniques.

Fig. 2-1: Regression of the number of individuals caught by D-vac against the number caught by sweep net. ** indicates that the slope of the regression line (solid) deviates significantly from 1.0 (dashed) $P < 0.01$



All of the regression lines presented in Fig.2-1 have slopes which deviate significantly from 1.0. The sweep net showed a bias toward catching aphids and adult ladybirds while the D-vac caught more lacewing adults and larvae. There were too many zeros in the data to plot regressions for ladybird larvae, harvestmen and lycosid spiders, but the data show a clear trend towards a greater catching efficiency by the D-vac.

The sampling technique used can therefore have a considerable effect on the observer's impression of what is occurring within the crop. For example, data from sweep sampling at the Tai Tapu site on 4/1/84 indicated that adult ladybirds outnumbered adult lacewings by 6.5:1 and that the aphid:predator ratio was 11:1. However, D-vac samples from the same site on the same day indicated that adult lacewings outnumbered adult ladybirds by 7:1 and that the aphid:predator ratio was less than 2:1.

For reasons outlined below the D-vac was used for all sampling after January 1984.

Occurrence of different species

A summary of data on the abundance of aphids, the four major groups of aphidophagous insects, and the lacewing parasite, as estimated by D-vac sampling, are presented in Figs.2-2 to 2-7.

Aphids

In 1983-84 the aphid population was made up of two species, the bluegreen lucerne aphid (BGLA) *Acyrthosiphon kondoi* and the pea aphid (PA) *Acyrthosiphon pisum*. By 1985, however, the spotted alfalfa aphid (SAA) *Therioaphis trifolii f. maculata* was established in Canterbury and occurred at low levels throughout the rest of the sampling period. Time did not permit each aphid species to be considered separately and data are pooled under the heading 'Aphids'.
Peak aphid populations generally occurred in October/ November and on several occasions large predator populations coincided with them (at Henley in 1983; at R.21 in 1985, and again in 1986). In general, however, there was no consistent trend between the appearance of aphids and predators.

For logistical reasons only two sites were sampled through the summer. Aphid numbers were very low at the non-irrigated Henley site during the summer but a moderate population (6500 m^{-2}) occurred at S.20 where the field was irrigated. At two of the three sites which were sampled

during the autumn, populations were low, but a sizeable population occurred at R.21 in 1986 along with a noticeably reduced number of predators.

Aphid population crashes coincided with a high proportion of alates in the population, which along with flight trap catches (Chapter 5) suggests that emigration was a major cause of the fall in numbers. *Entomophthora* spp. was noted on occasions and may have contributed to aphid mortality.

The lucerne variety 'Rere' had noticeably lower aphid numbers at Tai Tapu and in the plots at Henley. This is the only variety reputedly resistant to BGLA (Dunbier, 1979; Farrell and Stufkens, 1981: for a contrary view see Rohitha *et al.*, 1985).

Predators

Significant predator populations seldom occurred before November, by which time aphid numbers were reaching, or had reached, their spring peak. Only in the spring of 1985 did large numbers of predators (lacewings and ladybirds) occur in September/October, but this was a particularly early season (following a very mild winter) and was probably atypical.

1. Lacewings

Lacewing adults and larvae were present in samples from August-May and could be found in the field during the remainder of the year. Since both immature and adult stages were present throughout the year there is, therefore, no suggestion of any form of winter hibernation or summer estivation.

None of the sampling techniques collected lacewing pupae. Although a few pupae did appear in samples these were all in the early stages of pupation (i.e., the larval shape still recognizable within the cocoon) suggesting that they were larvae which had pupated in the bag. The only potential pupation site not sampled was on or in the soil. Lacewing cocoons have been found in considerable numbers (up to 95 m^{-2}) in the top centimetre of soil in a lucerne field at Darfield near Christchurch (D. Gassen, pers. comm.). These cocoons were strongly fixed to the soil and were not removed by vacuum sampling.

M. tasmaniae was the most frequently occurring predator and was also present in the greatest numbers. From 102 sampling occasions, lacewing adults were present in 88 and larvae in 75. Densities greater than 60 m^{-2} occurred on five occasions and twice exceeded 100 m^{-2}.

Adults of the lacewing parasite *Anacharis zealandica* generally appeared in December/January and never occurred in any number until February/March. In the spring of 1985 *A. zealandica* was collected as early as October, but as mentioned above, this followed a particularly mild winter and spring temperatures were above normal.

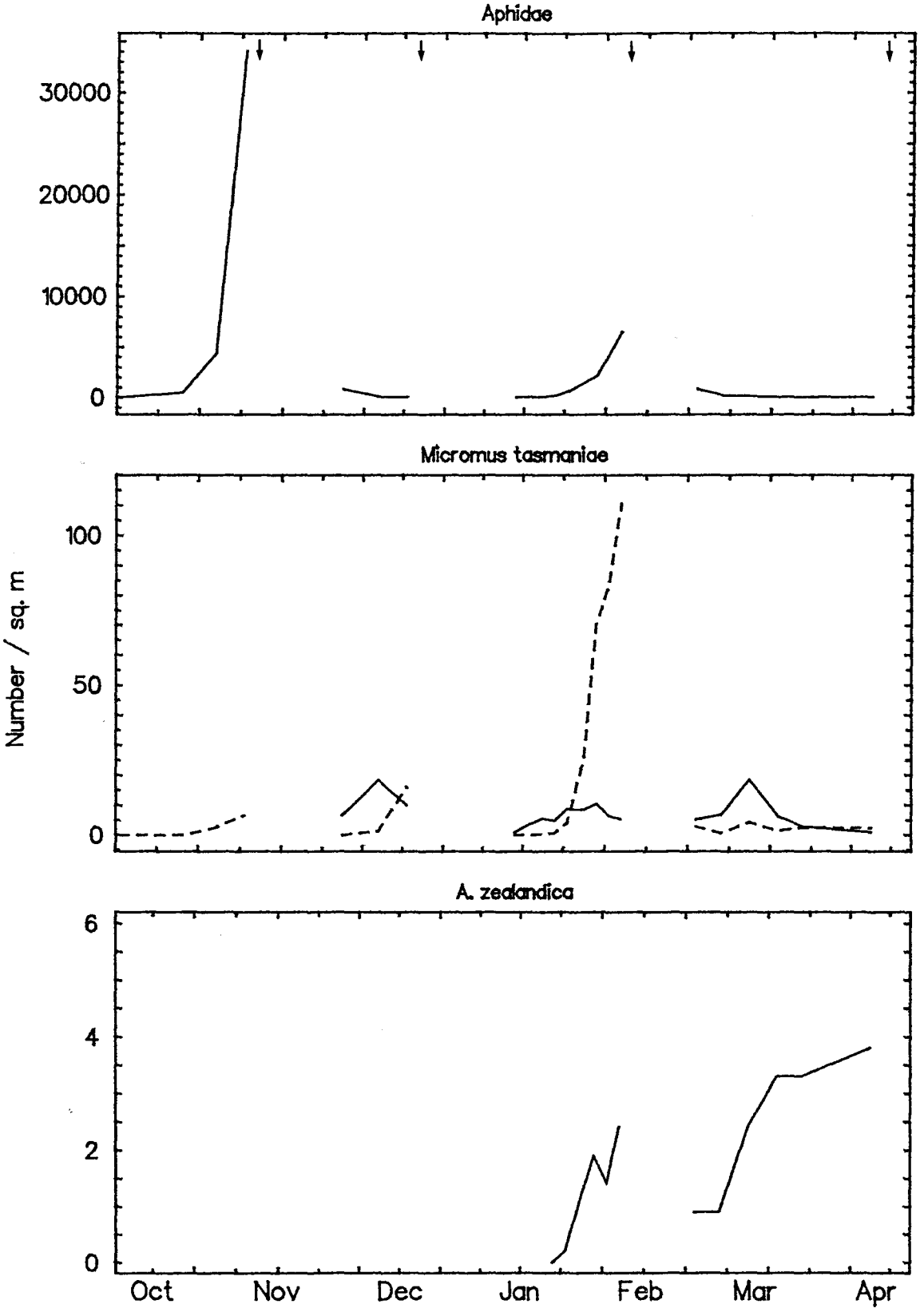
2. Other predators

The second most abundant predator group was the ladybirds (predominantly *Coccinella undecimpunctata*) occurring on 49 and 41 (adults and larvae respectively) of the 102 sampling occasions. Densities twice exceeded 20 m^{-2}. The other aphid predator groups common in New Zealand (nabids and syrphids) occurred only in low numbers. The European harvestman *Phalangium opilio* was more common and occurred in greater numbers in samples than either of these latter groups.

In the spring of 1986 syrphid larvae appeared in the stem samples in considerable numbers. Because they were taken primarily for the estimation of lacewing egg density, these stem samples were of less than optimum size for estimating predator numbers. Consequently the estimates of syrphid larval density varied widely. They did, however, show that syrphid larvae were present in much higher numbers than indicated by the D-vac samples. The D-vac, therefore, appears to be incapable of sampling these larvae with any degree of accuracy.

The predator most often caught in the pitfall traps (Fig.2-8) was the lycosid or wolf spider (identified as *Lycosa* spp., J.A. Wightman, pers. comm.). The number of these spiders in the pitfall traps indicates that they were far more abundant in the lucerne than predicted from the D-vac samples. For example, in November 1985 130 lycosids were caught in five pitfall traps over a ten day period, while none appeared in the D-vac samples. Aphids were also caught in the pitfall traps, along with harvestmen and adult and larval ladybirds (Fig.2-8). The relative occurrence of these species in the traps coincided with their presence in the D-vac samples. Only two lacewings (one adult and one third instar larvae) were caught in pitfall traps over the sampling period.

Fig. 2-2: Abundance of aphids, four groups of aphidophagous insects, and the lacewing parasite at site S.20 during 1983-84 Samples taken with D-vac suction sampler. Arrows indicate crop grazed or mown



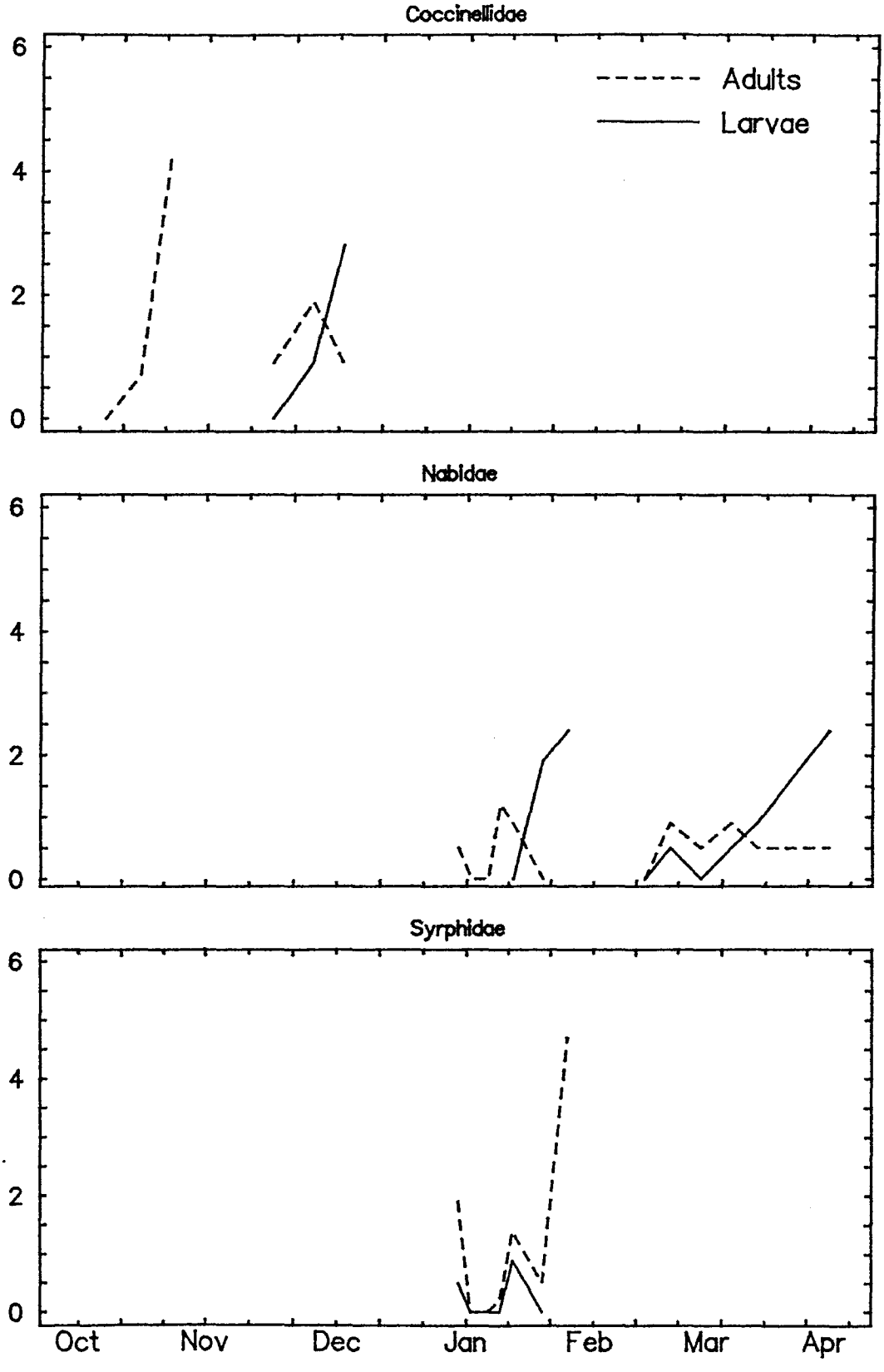
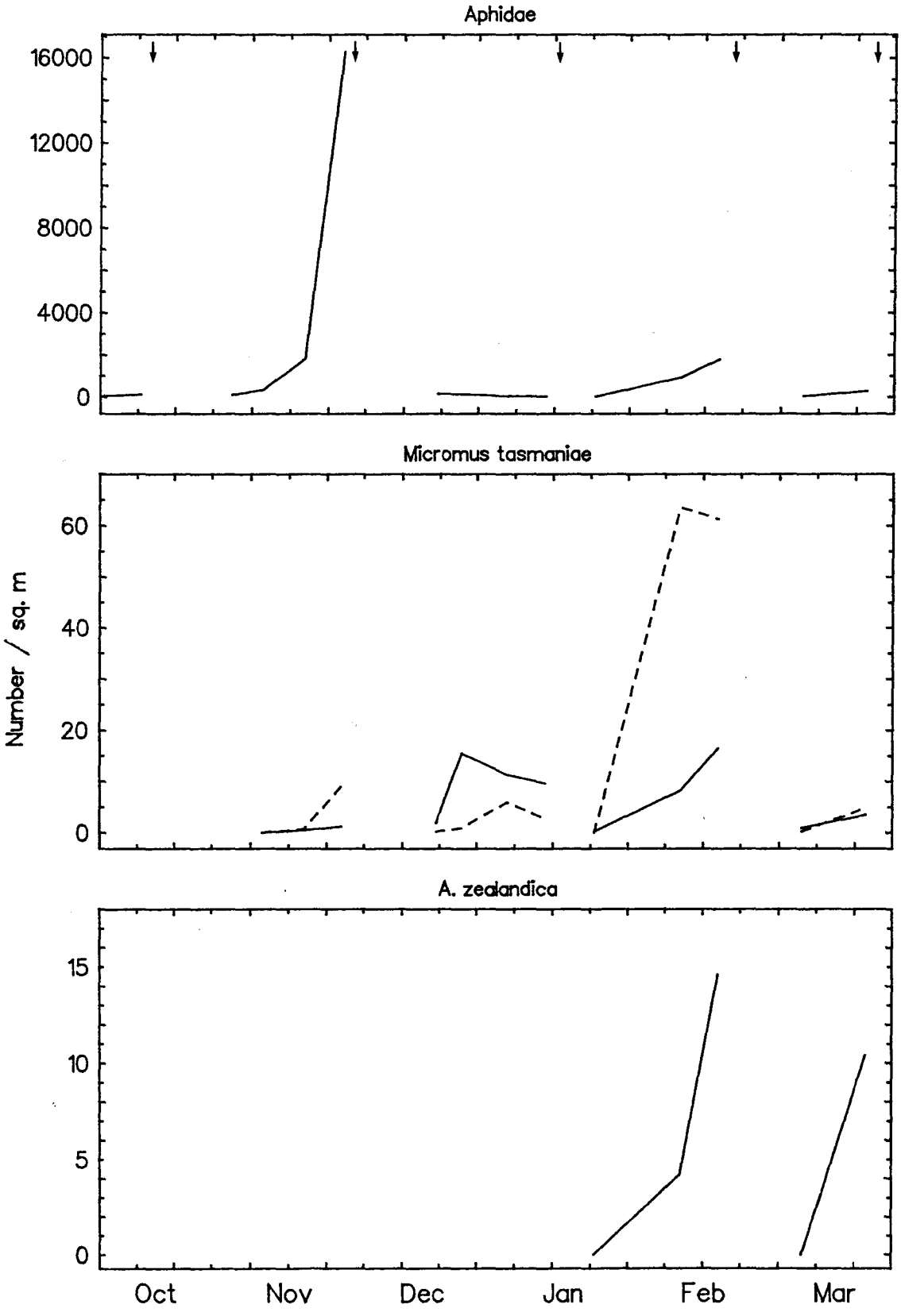

Coccinellidae
Adults
Larvae
6
4
2
0
Nabidae
6
4
2
0
Syrphidae
6
4
2
0
Oct
Nov
Dec
Jan
Feb
Mar
Apr

Fig. 2-3: Abundance of aphids, four groups of aphidophagous insects, and the lacewing parasite at site Henley during 1983-84. Samples taken with D-vac suction sampler. Arrows indicate crop grazed or mown.



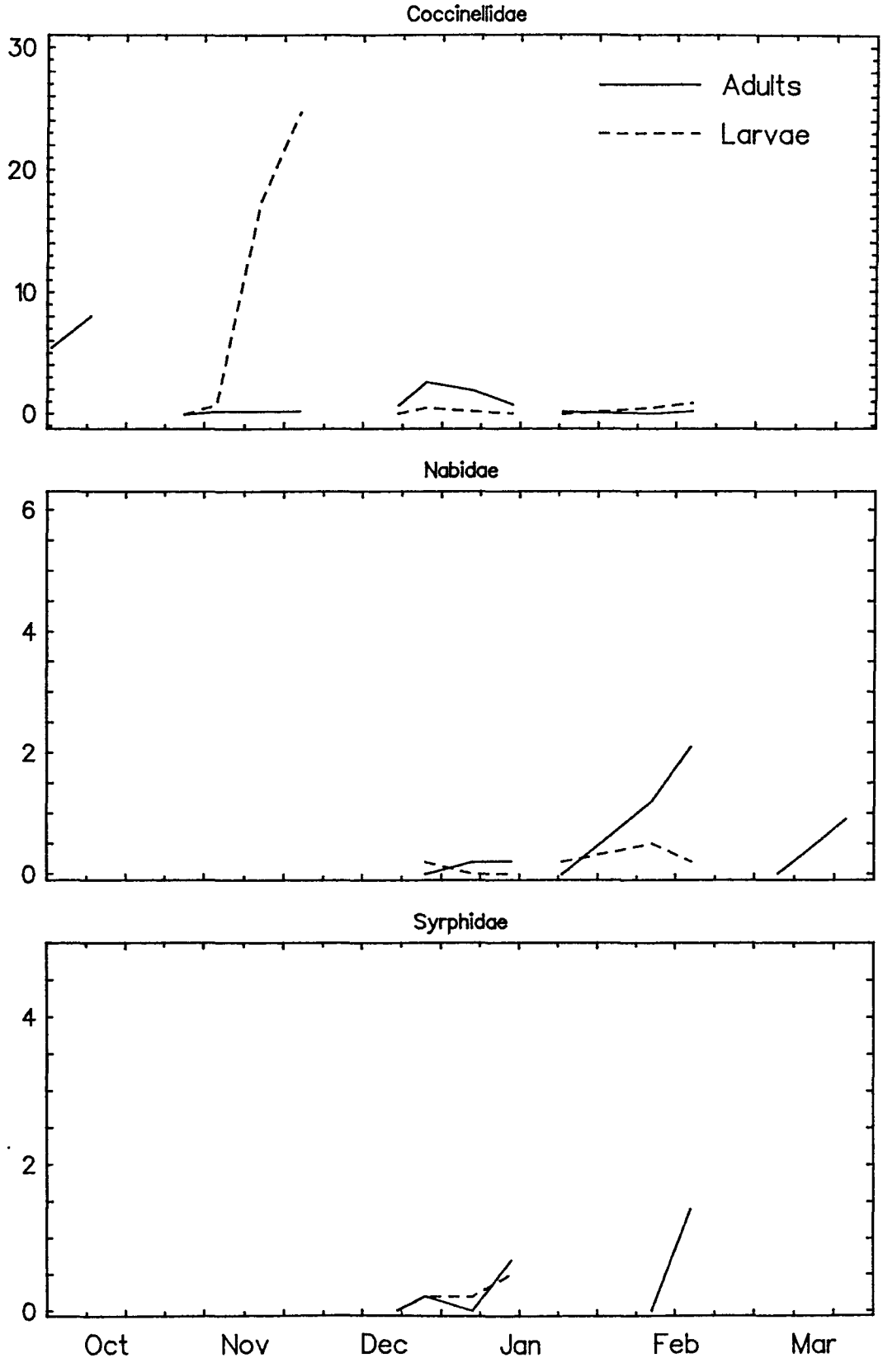
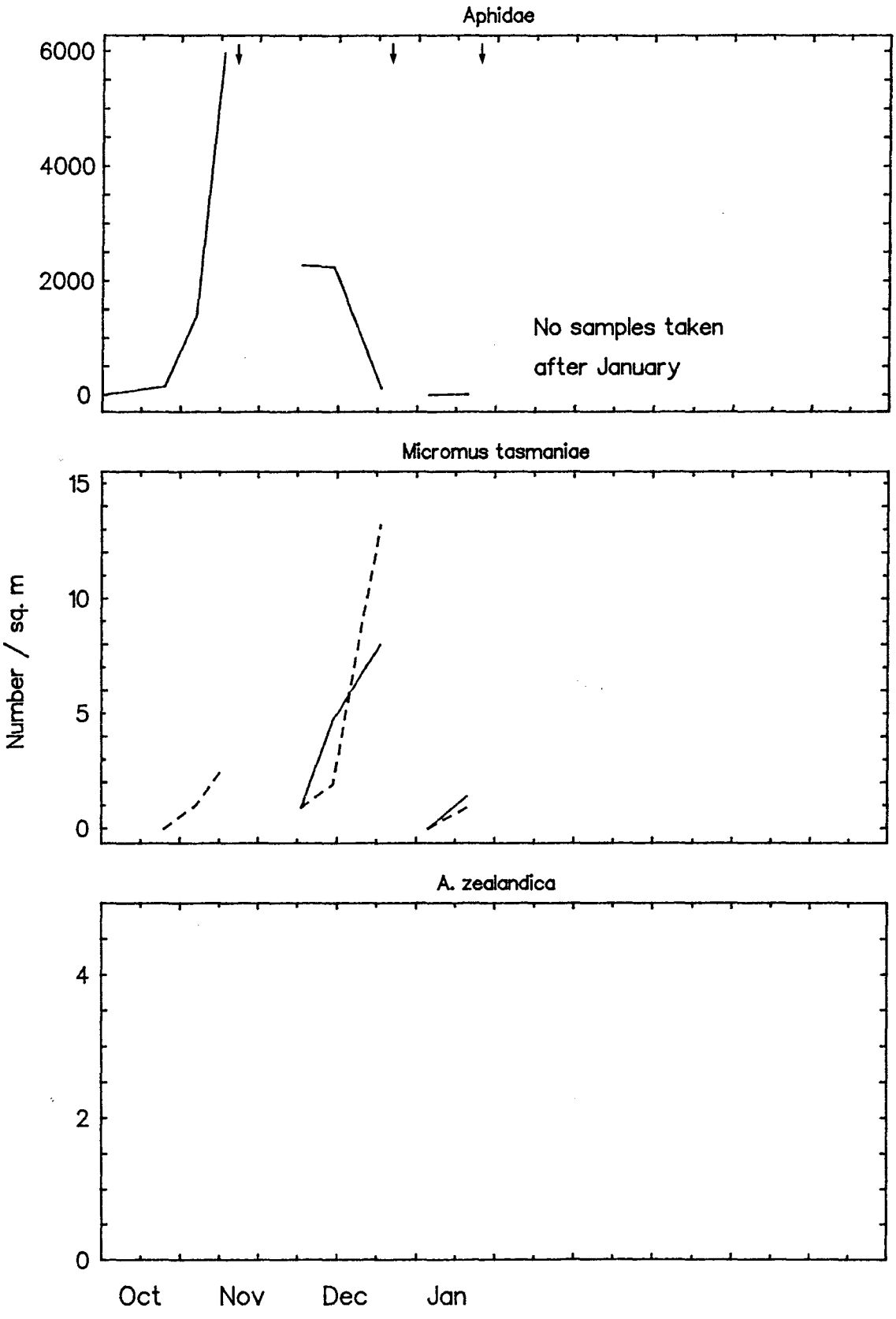

Coccinellidae
30
20
10
0
Adults
Larvae
Nabidae
6
4
2
0
Syrphidae
4
2
0
Oct
Nov
Dec
Jan
Feb
Mar

Fig. 2-4: Abundance of aphids, four groups of aphidophagous insects and the lacewing parasite at site R.21 during 1983-84. Samples taken with D-vac suction sampler. Arrows indicate crop Arrows indicate crop grazed or mown.



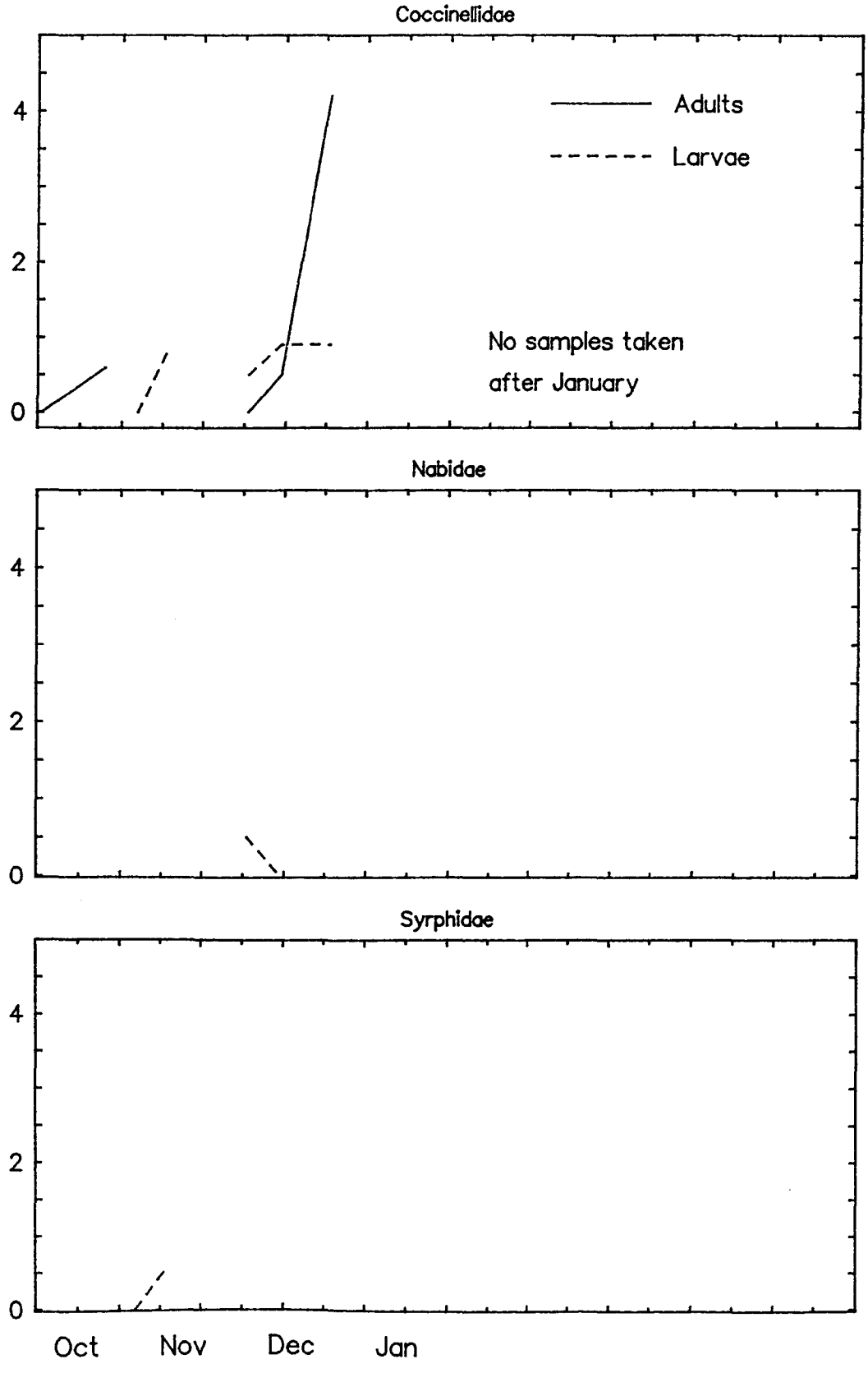
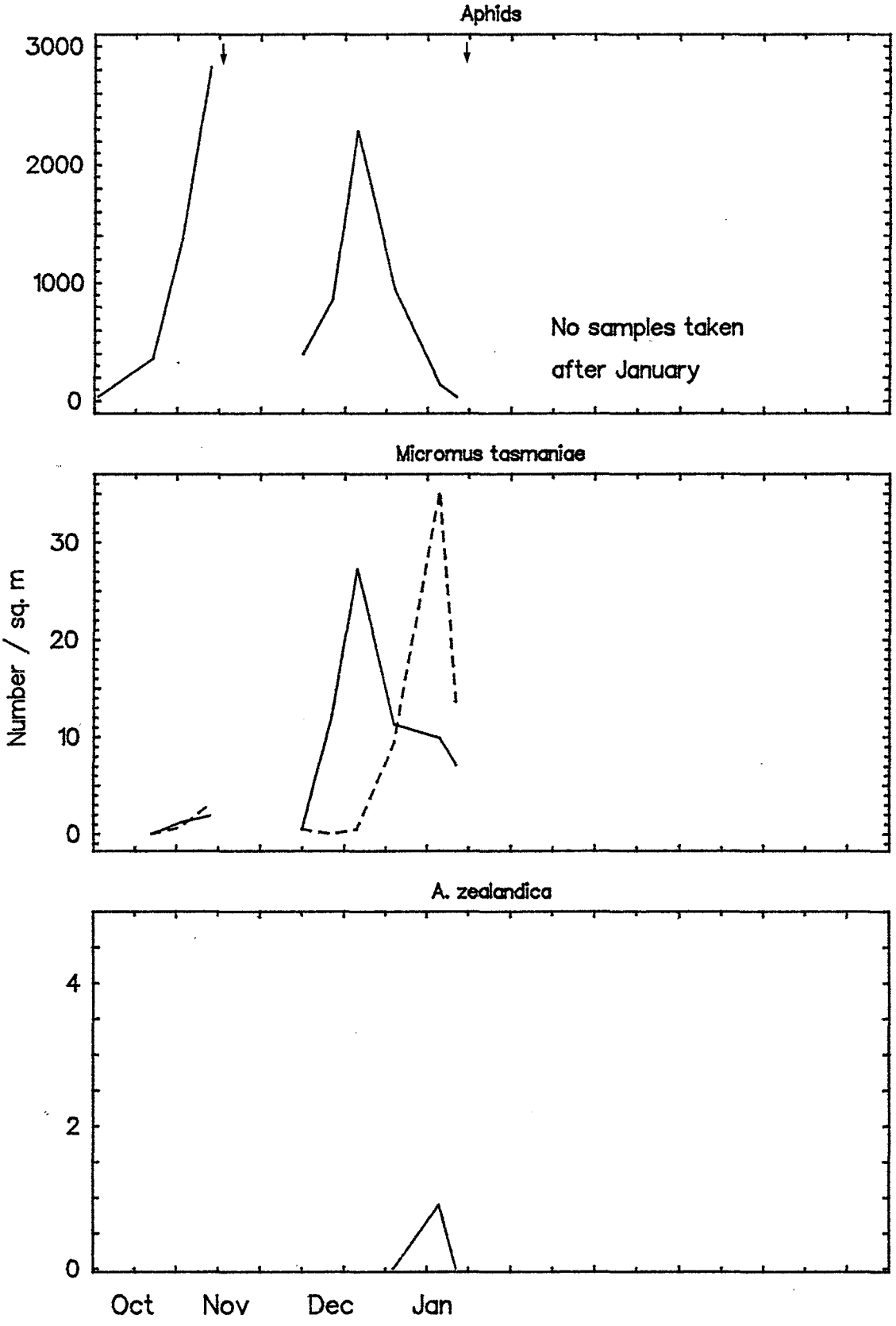

Coccinellidae
Adults
Larvae
No samples taken
after January
4
2
0
Nabidae
4
2
0
Syrphidae
4
2
0
Oct
Nov
Dec
Jan

Fig. 2-5: Abundance of aphids, four groups of aphidophagous insects and the lacewing parasite at site Tai Tapu during 1983-84. Samples taken with D-vac suction sampler. Arrows indicate crop grazed or mown.



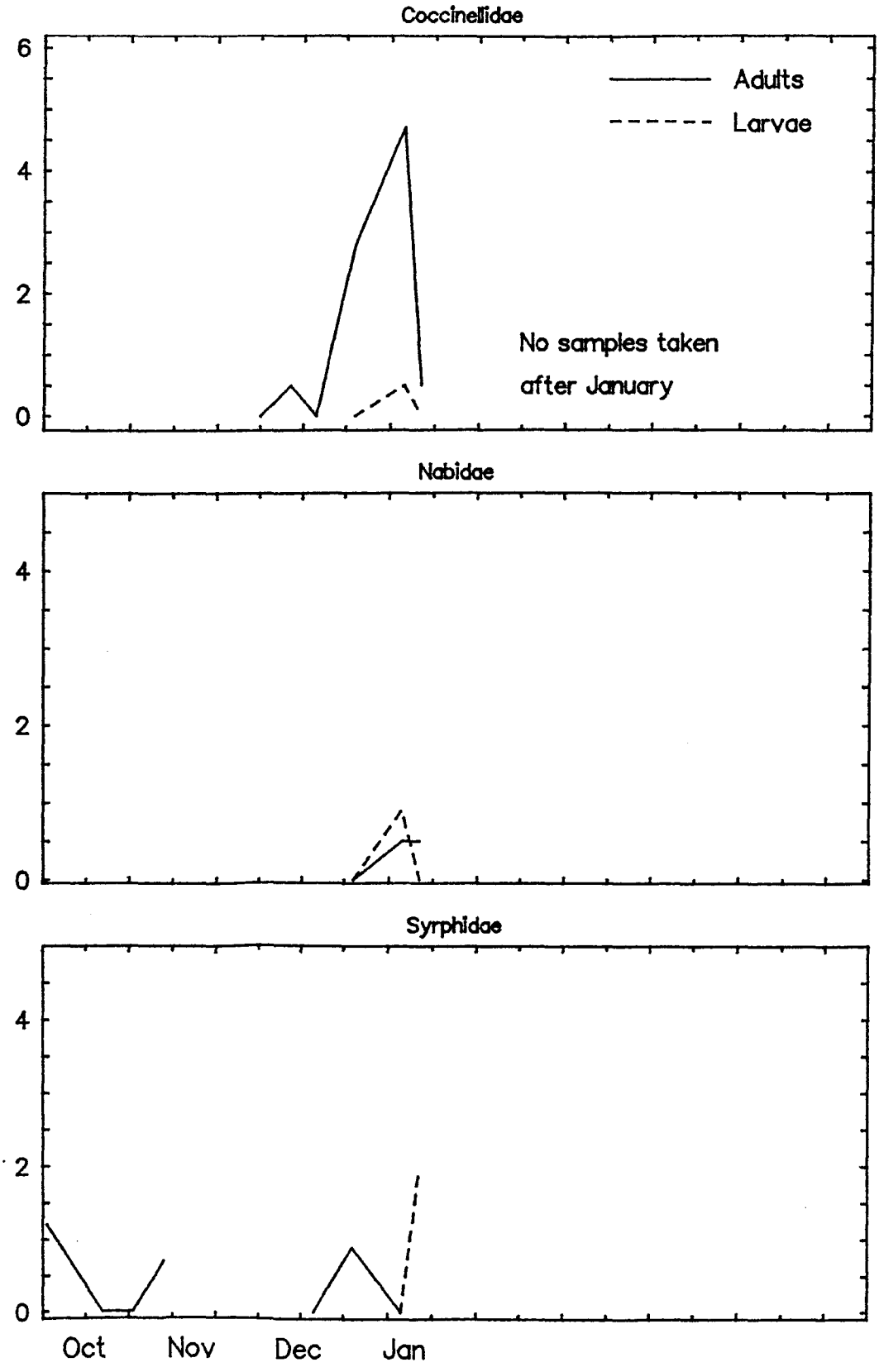
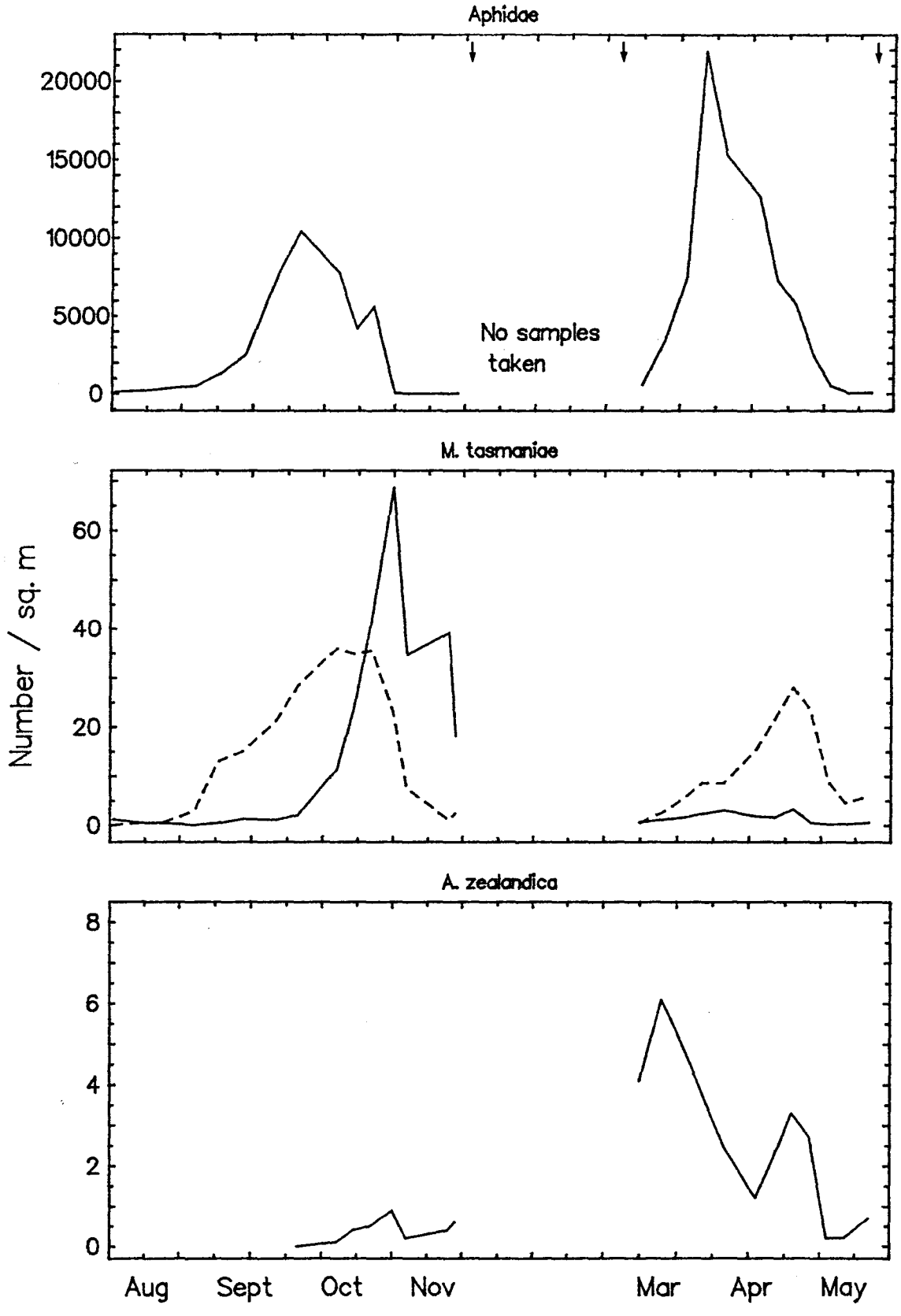

Coccinellidae
6
4
2
0
Adults
Larvae
No samples taken
after January
Nabidae
4
2
0
Syrphidae
4
2
0
Oct
Nov
Dec
Jan

Fig. 2-6: Abundance of aphids, four groups of aphidophagous insects and the lacewing parasite at site R.21 during 1985-86. Samples taken with D-vac suction sampler. Arrows indicate crop grazed or mown.



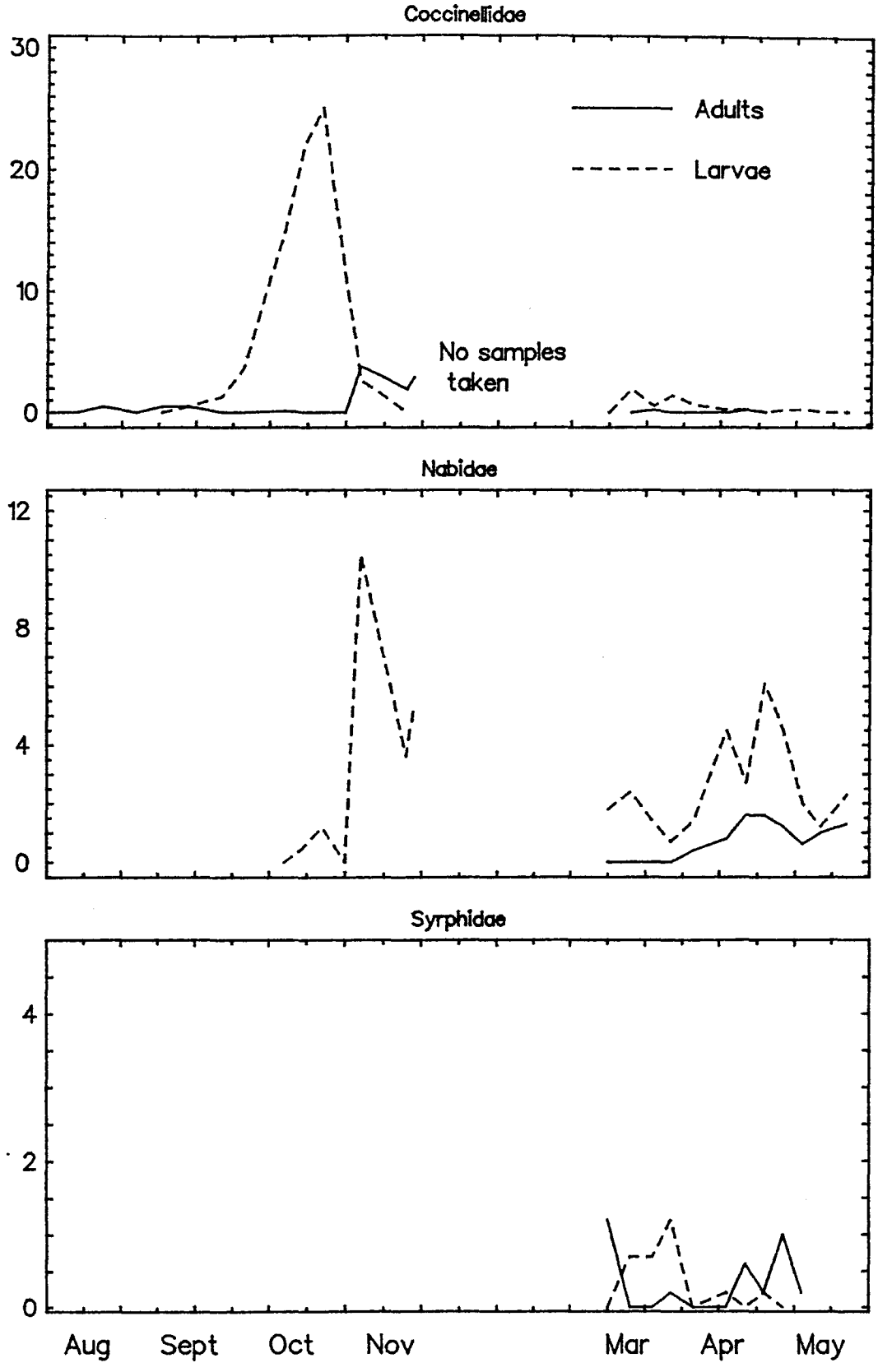
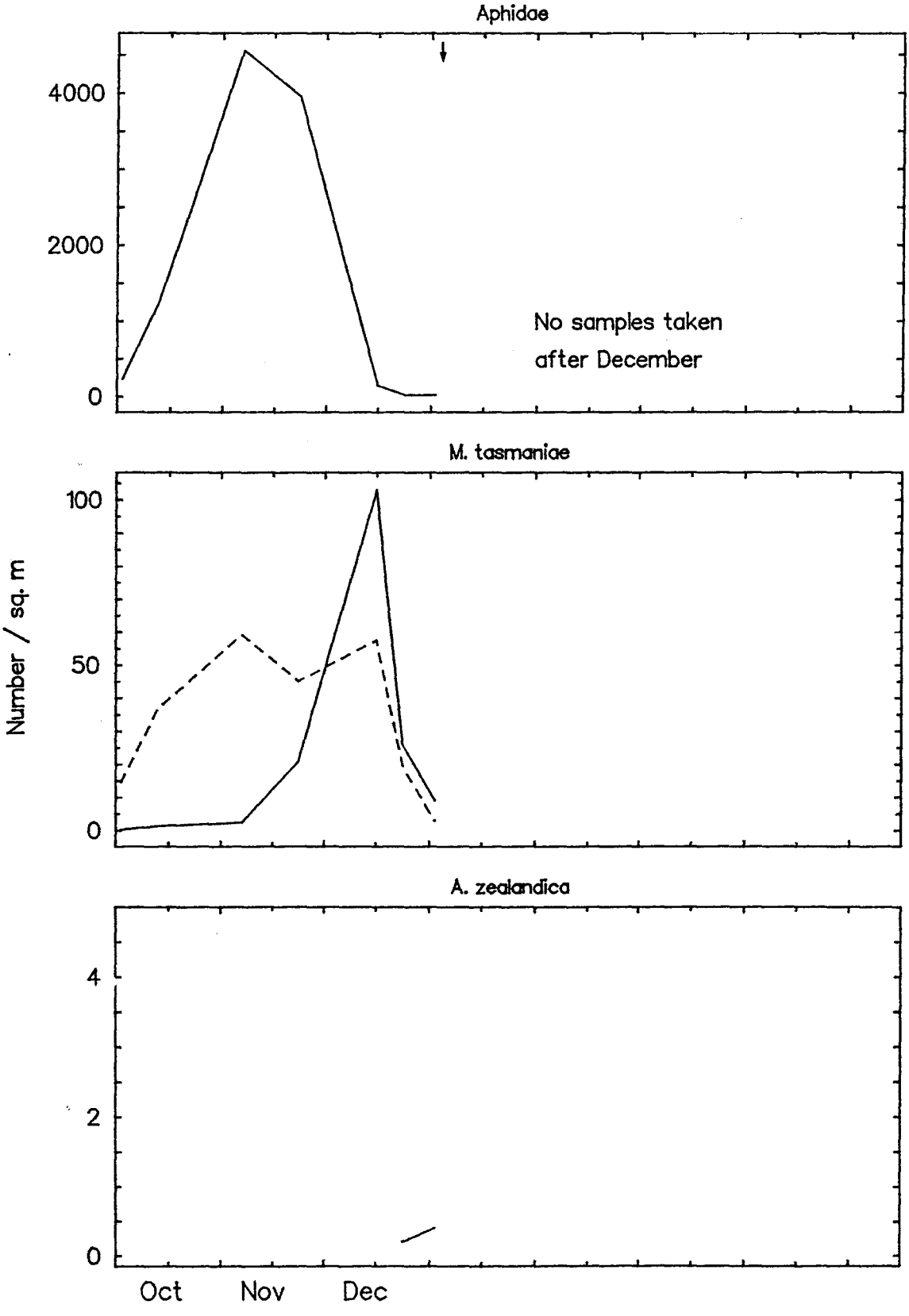

Coccinellidae
30
20
10
0
Adults
Larvae
No samples
taken
Nabidae
12
8
4
0
Syrphidae
4
2
0
Aug
Sept
Oct
Nov
Mar
Apr
May

Fig. 2-7: Abundance of aphids, four groups of aphidophagous insects and the lacewing parasite at site R.21 during 1986-87 Samples taken with D-vac suction sampler. Arrows indicate crop grazed or mown.



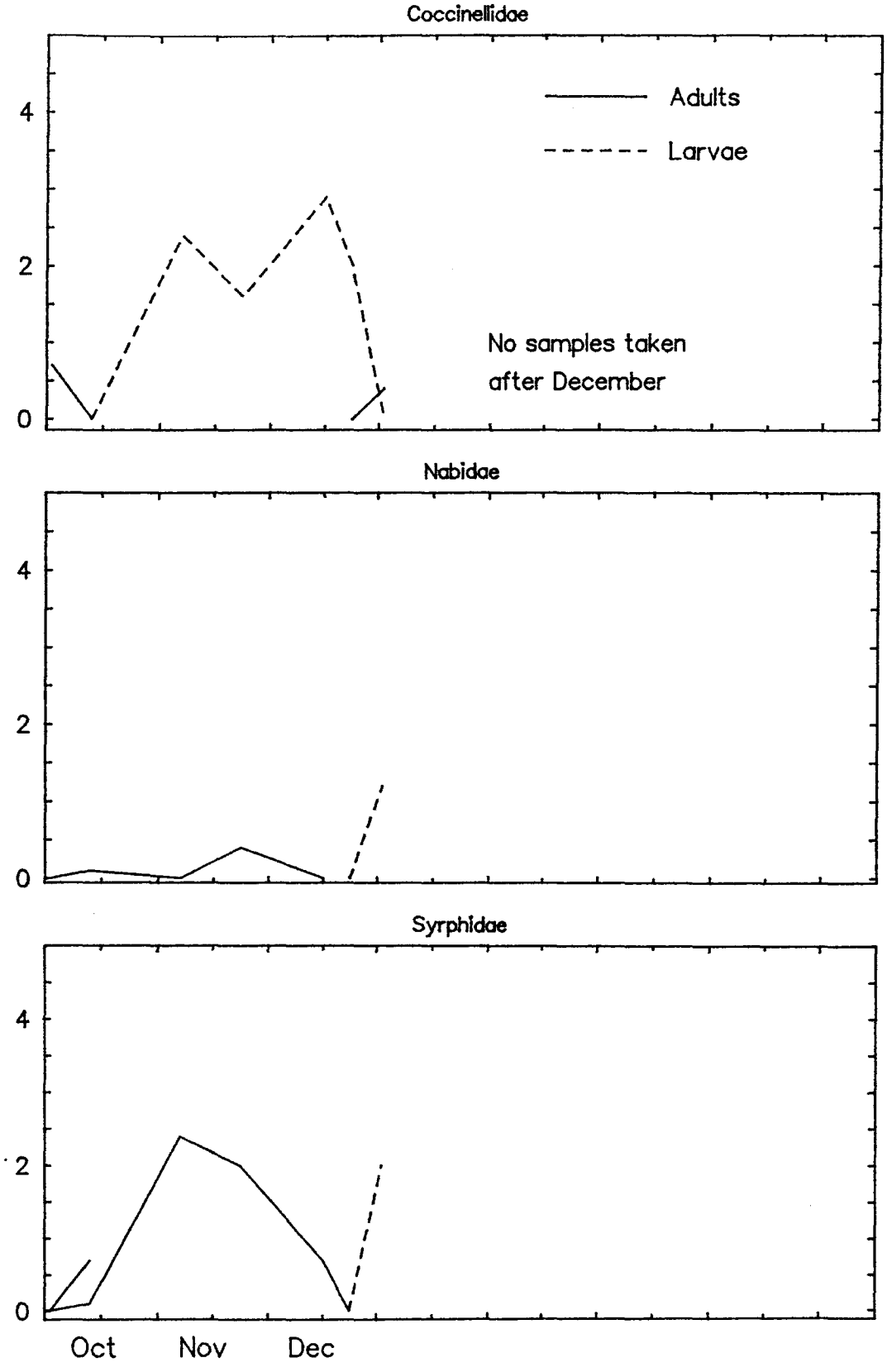
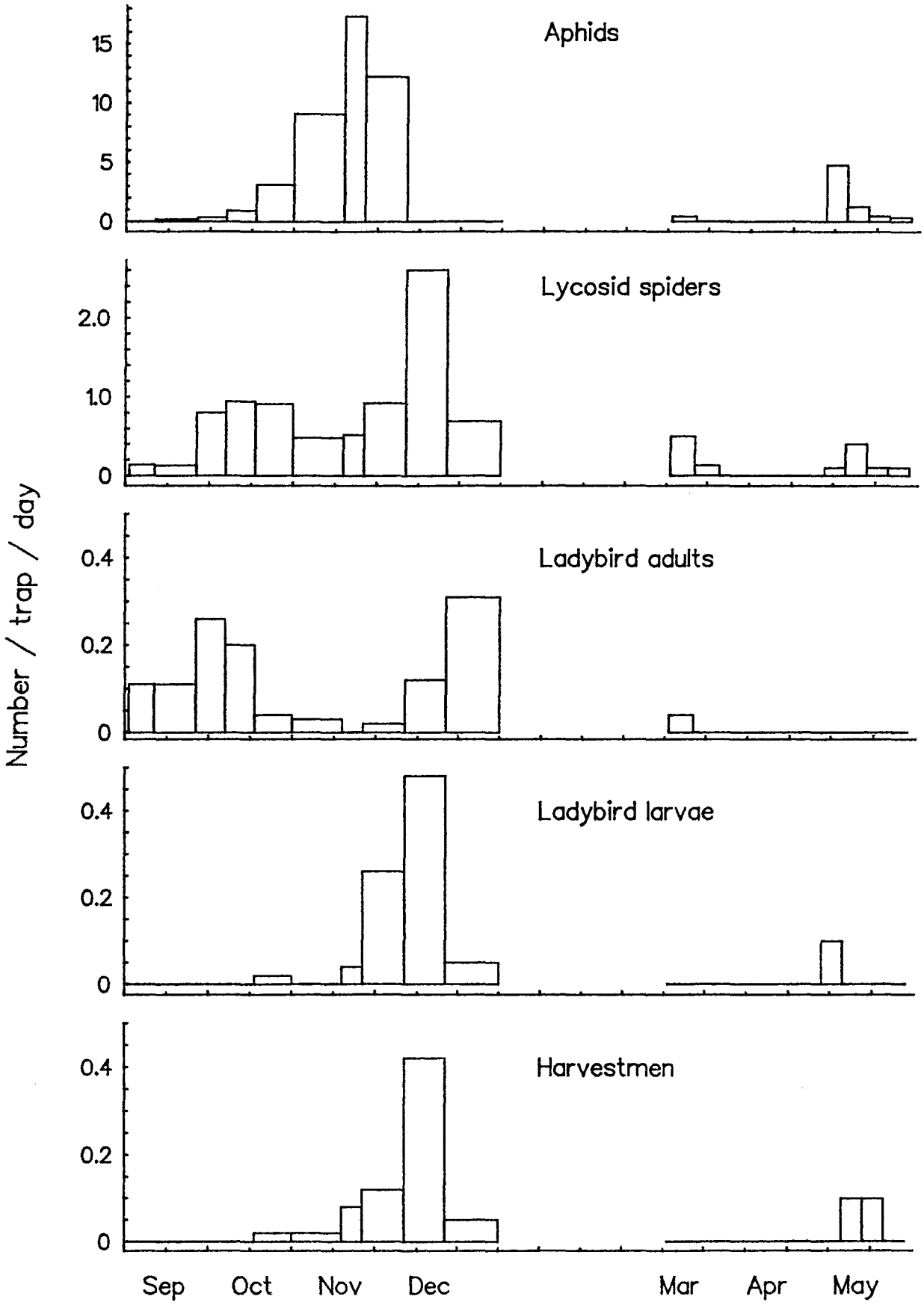

Coccinellidae
Adults
Larvae
No samples taken
after December
4
2
0
Nabidae
4
2
0
Syrphidae
4
2
0
Oct
Nov
Dec

Fig. 2-8: Pitfall trap catches from site R.21 during the spring and autumn of 1985-86. No samples were collected between December and March



Aphid Parasites

Comparing the density of mummies recorded from stem samples with the aphid density measured by the D-vac gives a crude estimate of the intensity of parasitism in the aphid population. This method is biased, because it falsely assumes that aphid mummies and live aphids are present in the field, and therefore available to be sampled, for the same length of time (Hodek *et al.*, 1972). However, given that mummified aphids seldom exceeded 1.5% of the aphids present, and then only after the aphid population had crashed, it is unlikely that parasites were contributing significantly to aphid mortality.

DISCUSSION

The data on predator abundance presented here may differ from those collected by other New Zealand workers purely on the basis of the sampling technique used. Cameron *et al.* (1979) and Bates and Miln (1982) recorded the ladybird *C. undecimpuntata* as the most abundant predator in their sweep net samples. Leathwick and Winterbourn (1984) also recorded this ladybird as the most abundant predator in sweep net samples taken during the day, but in samples taken at night it was less numerous than both lacewings and harvestmen. Moreover, they found that the number of sampled predators of all species was four times higher at night than during the day, suggesting that sweeping during the day could result in an underestimation of the role of predators in the regulation of aphid populations.

Vickerman and Sunderland (1975) compared both the D-vac and sweep net sampling methods at different times of the day in cereal crops and also found variation in sweep net catches. Variations in sweep catches have occurred with wind speed and rainfall (Hughes, 1955; Cherry *et al.*, 1977), temperature and the type of net used (Saugstad *et al.*, 1967), and the efficiency of the operator (Southwood 1978). However, perhaps the most important variable affecting sweep net sampling with regard to this work is that species differ in their availability to be caught by the net. Hence sweeping is not suitable for comparing the abundance of different species or for evaluating the effectiveness of various groups of aphidophagus insects (Hodek *et al.*, 1972). Sweeping samples only the upper portion of the foliage (Heathcote, 1972; Siddique, 1985) which is the area where BGLA congregate (Rohitha and Penman, 1981), and where coccinellids predominantly hunt for aphids (Frazer and Gilbert, 1976), and can be seen apparently sunning themselves on warm days. It is probably their preference for the upper regions of the plant which is responsible for these species being dominant in sweep samples.

Sweeping, at least during the day, thus appears to be a poor indicator of lacewing abundance and is likely to overestimate the importance of coccinellids as aphid predators. Harris (1980) was sampling lupins with a sweep net for a considerable time before adding a D-vac to his sampling routine. He immediately discovered that the crop contained a large population of lacewings, whose presence had not been indicated by sweeping.

The data presented here differ from those of other New Zealand workers in that lacewings were present in vastly greater numbers than any other species of aphid natural enemy. As discussed above, much of this difference may be a result of the sampling techniques used. The only published work from New Zealand lucerne fields where a D-vac was used is that of Rohitha *et al.* (1985) who in the Waikato district recorded adult and larval lacewing densities of 15 m^{-2} and coccinellids at four m^{-2}. The most abundant predator was, however, the syrphid *Melanostoma fasciatum.*

In this work coccinellids were frequently present, but generally only in low numbers. *Nabis* spp. can be common after January and are sometimes abundant (Henderson, 1979; Cameron *et al.*, 1983; Siddique, 1985) but seldom occurred in any numbers in these samples. The presence of syrphid larvae in the stem samples when they were scarce in the D-vac samples suggests the D-vac is unable to suck them off the foliage. Rohitha *et al.* (1985) came to a similar conclusion which implies that the present data on abundance of syrphid larvae are unreliable.

D-vac sampling also failed to indicate the presence of large numbers of lycosid spiders in the lucerne. These large hunting spiders were recorded in lucerne by Henderson (1979), in sugar-beet by Wratten and Pearson (1982), and shown to be feeding on aphids by Leathwick and Winterbourn (1984). The presence of aphids in the pitfall traps implies that they were moving around on the soil surface, as has been shown to occur in cereals in Britain (S.D. Wratten, pers. comm.). Pea and spotted alfalfa aphids, for example, readily drop from plants when disturbed (Evans, 1976a; Frazer and Gilbert, 1976; Bishop *et al.*, 1980), which must expose them to ground-dwelling predators. The importance of surface dwelling predators such as the carabid *Agonum dorsale,* in the suppression of British cereal aphid populations (Griffiths, 1982), indicates that in New Zealand these lycosid spiders, should be considered in future evaluations of natural enemies of lucerne aphids.

The efficiency of suction samplers is affected primarily by nozzle wind speed (for heavy and/or tenacious species) and speed of enclosure (for active flying species). The D-vac is excellent on the latter count, but the nozzle wind speed is, with several types of collecting head, on the

borderline of efficient extraction (Southwood, 1978). This low wind speed almost certainly explains the D-vac's inability to collect Lycosid spiders, which are heavy, and syrphid larvae, which cling to the vegetation. However, for many species the D-vac gives good estimates of the numbers present (Dietrick *et al.*, 1959; Pruess *et al.*, 1977; Butcher, 1986) and is capable of effectively sampling aphids and most of their natural enemies from lucerne (Rohitha *et al.*, 1985). D-vac efficiency is also much less affected by environmental factors (Dietrick *et al.*, 1959) and diel patterns of behaviour (Vickerman and Sunderland, 1975), than is the sweep net.

Adult lacewings are light and delicate and are not strong fliers. When disturbed they immediately feign death and drop from the plant, which would make sampling them by the taking of stem samples difficult. Adult lacewings seldom occurred in the stem samples taken here. However, the fact that they are light and delicate should make lacewing adults susceptible to sampling by suction machine. By contrast lacewing larvae are reclusive, preferring the parts of the plant which provide the most shelter (Hilson, 1964), and as wind speed is likely to be reduced in such places the larvae may be difficult to extract with the D-vac (see Chapter 5). The D-vac is not, for example, efficient at extracting mites where they are associated with webbing (Butcher, 1986).

The overall occurrence of predators was erratic and was probably influenced by a variety of factors. The lack of synchrony between predators and the aphid populations, particularly in the spring, is likely to be a major factor limiting their ability to suppress aphid numbers (Cameron *et al.*, 1979). In keeping with other findings (Kain *et al.*, 1979; Rohitha *et al.*, 1985) the peak aphid populations occurred in spring, usually before the predators had established. This probably reflects the low developmental threshold temperature for the BGLA (2.63^{o}C) which is the major component of these early populations (Syrett and Penman, 1981; Rohitha and Penman, 1983). Predators may be better synchronized with the slower developing PA and SAA (Rohitha *et al.*, 1985).

The restriction of significant numbers of the lacewing parasite to the latter part of the season implies that parasitism is only likely to influence the growth of lacewing populations in the autumn (see Chapter 5). However, if this relationship is temperature regulated (i.e., due to differing thermal requirements) then this may not be true in warmer climates (e.g., northern New Zealand or Australia).

In summary, the present data suggest that previous workers may have underestimated the number of lacewings present in lucerne crops, and overestimated the number of coccinellids, because of sampling bias. There is an abundance of literature testifying to the unreliability of

sweep sampling, and although the D-vac is not infallible it appears to be a far superior alternative, at least for the comparative evaluation of natural enemies of aphids in lucerne. Highlighted by these results is the need to use a number of sampling techniques in a comparative way in order to get a representative picture (Hodek *et al.*, 1972).

Lacewings occurred more often and in far greater numbers than any other predator. Coccinellids occurred often but usually in low numbers. Two of the expected aphidophagous species (syrphids and nabids) did not occur in significant numbers in these samples, although it is likely that the absence of syrphid larvae is to some extent an artifact of the sampling technique. Two arachnid predators (the harvestman *P. opilio* and the lycosid spider *Lycosa* spp.) were present in sufficient numbers to warrant considering them as potentially useful aphid predators.

CHAPTER 3: Aspects of the predator-prey relationship.

INTRODUCTION

Functional and numerical responses are basic to any investigation of predator prey relationships (Holling, 1966). The functional response (Solomon, 1949) relates the number of prey consumed by a predator to changes in prey density. Invertebrate predators typically eat more prey at higher prey densities, but do so at a decelerating rate (Holling, 1959; Murdoch, 1973). Such a relationship can be described mathematically by the 'disc' equation (Holling, 1966), and a predator exhibiting such a response (Type II - Holling, 1966) is considered to have only limited ability to regulate an increasing prey population (Hassell *et al.*, 1976).

The numerical response relates changes in the number of predators to prey density and has two fundamentally different types (Readshaw, 1973). An aggregative response occurs where predators congregate in areas of high prey density, while a reproductive response is where the number of predators recruited into the next generation increases with prey number. The reproductive response is directly related to the rate at which the predator can catch and consume suitable prey which will in part be determined by the functional response (Beddington *et al.*, 1976). It should therefore be instructive to study both the functional and reproductive numerical responses at the same time.

The objectives of this experiment were;

1. To define the shape and magnitude of the functional response curve and hence to establish the ability of *Micromus tasmaniae* to respond to increases in prey density by eating more prey.

2. To determine the ability of *M. tasmaniae* to respond to increases in prey density by producing more offspring.

3. To relate these basic components of the predator-prey relationship to the occurrence of *M. tasmaniae* in the field.

METHODS

Traditionally, functional response experiments describe a 'short term behavioural phenomenon' with experiments lasting only a matter of hours (Murdoch, 1973). In order to counter natural variability in feeding rate, some authors have 'standardized' hunger by starving their predators prior to feeding experiments (e.g., Hull *et al.*, 1977; Propp, 1982; Siddique and Chapman, 1987b). This, however, raises the possibility of biasing the feeding or attack rate by starting with hungry predators. Hungry predators are more active, and more effective at prey capture, than satiated ones (Sandness and McMurtry, 1972; Glen, 1975). An alternative approach is to conduct longer duration experiments that will account for day to day variation in prey consumption (e.g., Santos, 1975). The functional response (number of aphids killed) and numerical response (number of eggs laid) for *M. tasmaniae* were investigated using a longer duration experiment.

Only first generation laboratory reared lacewings were used, to ensure that inbreeding within the laboratory colony did not influence fecundity. Newly emerged male and female lacewings were paired and kept in 60 x 25mm P.V.C. tubes, with an excess of pea aphids, for 7-14 days to allow for reproductive development and mating. Only pairs of lacewings which had produced eggs were used in the experiment. Pea aphids were reared on beans (*Vicia faba*) in a glasshouse colony. Adult *M. tasmaniae* show a strong feeding preference for small aphids (Chapter 6), but as first instar aphids have a relatively high handling mortality, second instar aphids were used as the standardized prey stage.

The experimental arena was a plastic petri dish 110mm in diameter and 20mm deep. Moisture was supplied by a piece of dampened filter paper on the floor of the dish. For female lacewings a piece of nylon gauze mesh, approximately 50 X 15 mm, was folded under the lid such that it protruded into the dish. This presented a substrate for egg laying, although in many cases eggs were laid onto the roof, sides and floor of the petri dish.

Individual adult lacewings of both sexes were presented with one of six prey densities (2, 5, 10, 20, 30 or 40 aphids/dish) for a ten day period at a constant 15^{o}C. Each day the lacewings were transferred to new dishes containing the appropriate density of fresh aphids. The number of aphids eaten, and the number of eggs laid, was recorded for each 24 hour period. The remains of all partially eaten aphids were weighed each day, and lacewings were weighed before and after the experiment, using a CAHN G-2 electrobalance. Each day five aphids selected at random were weighed to give a mean wet weight per aphid, and to ensure continuity in size of aphids presented.

After the completion of five replicates preliminary analysis showed that the data on female lacewings were highly variable. Three more replicates were initiated, with the lowest density being dropped and a higher one (50 aphids/dish) added.

RESULTS

The functional response as measured by the number of aphids killed over a range of prey densities is presented in Fig.3-1. The data, which indicate a Type II functional response, were fitted to Holling's disc equation by nonlinear regression. Female lacewings ate more aphids than did the males, which is not unexpected given the females' larger size and the metabolic demands of egg laying.

The number of eggs laid is directly related to the biomass of prey consumed (Fig.3-2), and is probably responsible for the greater variation in the functional response data for females. Inclusion of initial body weights into the regression analysis of eggs laid against aphids killed, improved the goodness of fit from $r^2 = 0.77$ to $r^2 = 0.82$. This small increase in r^2 value indicates that size has only a minor influence on the number of eggs laid by a female lacewing, at least within the size range for adult females used in this experiment. A similar result was obtained by Mills (1981) for *Adalia bipunctata*, where inclusion of adult weight in the regression made no improvement to the r^2 value. Therefore, after some allowance is made for maintenance metabolism, reproductive rate is directly related to the number, and hence biomass, of prey consumed. The slope of the regression line gives an estimate of the conversion efficiency of aphid biomass into eggs, and the x-intercept a measure of the basal metabolic requirement (Beddington *et al.*, 1976; Ives, 1981; Mills, 1981).

In this case (Fig.3-2) the regression line crosses the x-axis at a negative value, which indicates eggs laid in the absence of food. This anomalous result can best be explained by examining the weight changes of the female lacewings over the duration of the experiment (Fig.3-3). At low prey densities the lacewings are obtaining insufficient nourishment to maintain normal metabolism and reproductive output. Even so, these adults continue to lay eggs at the expense of their own body-weight. Undoubtedly this cannot continue indefinitely, and in fact by the end of the ten day experiment four of the five females, at the lowest prey density, had stopped laying eggs. However, this phenomenon adds an interesting twist to the expectation (Beddington *et al.*, 1976) that reproduction will cease once food intake drops below the basic maintenance level, and suggests a strong commitment to reproduction by this species.

Fig. 3-1: Functional response of Micromus tasmaniae. Curves fitted to Holling's disc equation using non-linear least squares regression. Error bars are 95% confidence intervals for the means.

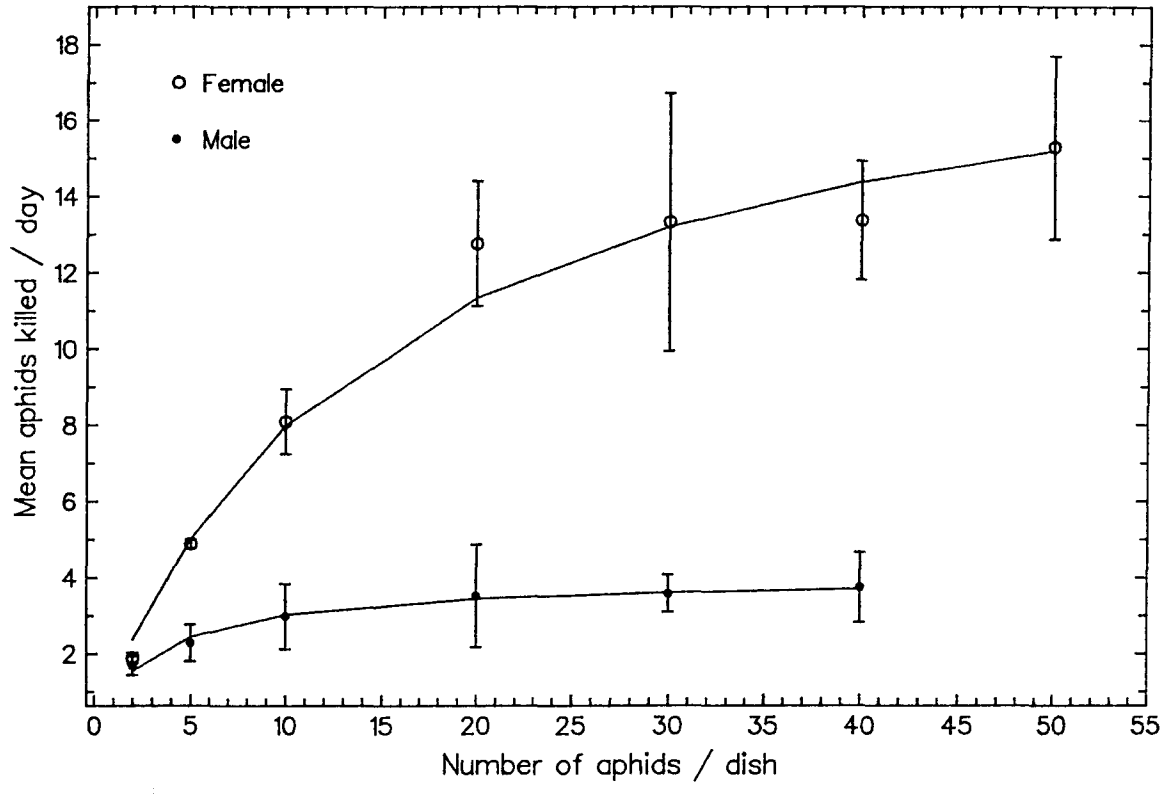
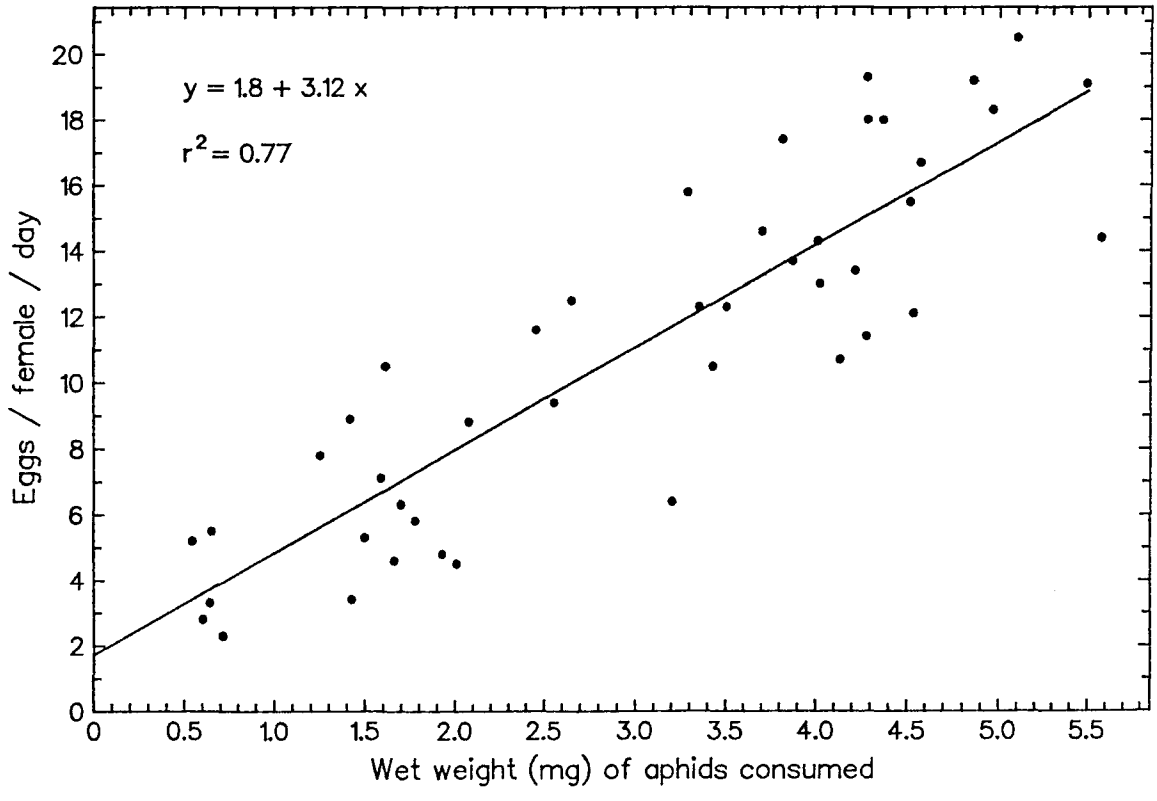


Fig. 3-2: Number of eggs laid by Micromus tasmaniae at different levels of food intake



As would be expected given a linear relationship between fecundity and the number of aphids consumed, the fecundity-prey density relationship (Fig.3-4) approximates the shape of the functional response curve. The lacewing's ability to respond to increases in prey density by increasing oviposition rate, will therefore be limited by the magnitude of its functional response. This relationship will be affected although probably not significantly (Beddington *et al.*, 1976), by the fact that the proportion of each prey killed which is actually eaten, decreases with increasing prey density. A significant regression ($F = 7.86$, $P < 0.01$) between the mean weight of aphid remains and aphid density indicates that where more prey were available less of each aphid killed was utilized.

Both Ives (1981) and Mills (1981) studied egg production in coccinellids feeding on pea aphids, so their data is comparable with the present data on *M. tasmaniae* (Table 3-1). However, a comparable figure for the maintenance food requirement is not available because *M. tasmaniae* does not follow the expectation that egg laying will stop once the basal requirement is reached.

TABLE 3-1: Estimates of basal metabolic requirements (mg wet weight of aphids/day) and conversion rate (eggs/mg wet weight of aphids) for predators fed on pea aphids (*Acyrthosiphon pisum*)

Species	Temperature	Maintenance Requirements	Conversion Rate	Source
Coccinella californica	15	3.48	0.656	Ives (1981)
	21.5	5.25	1.08	Ives (1981)
Coccinella trifasciata	15	1.95	0.438	Ives (1981)
Adalia bipunctata	20	6.0	1.6	Mills (1981)
Micromus tasmaniae	15	3.34 **	3.12	This study

** Food intake level at which weight loss = 0; mean egg production at this feeding level was 12 eggs/day.

Fig. 3-3: Change in body-weight of adult female Micromus tasmaniae at different levels of food intake.

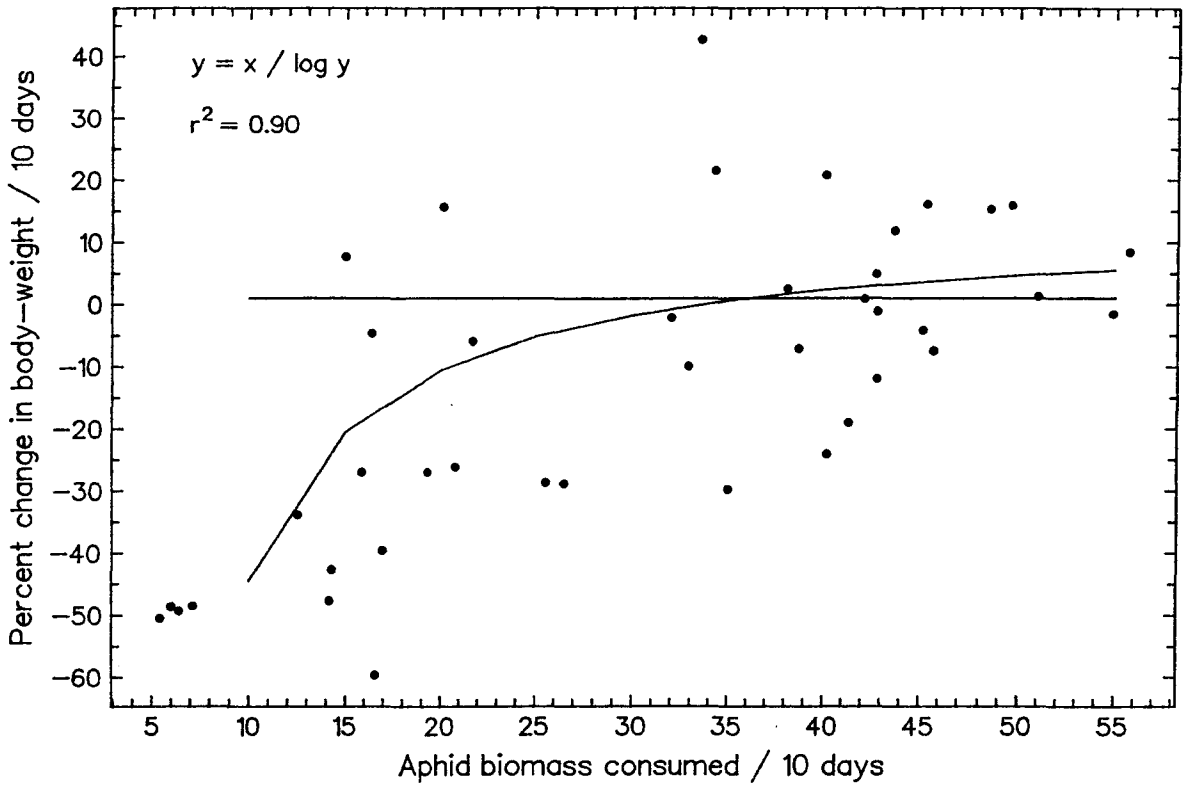
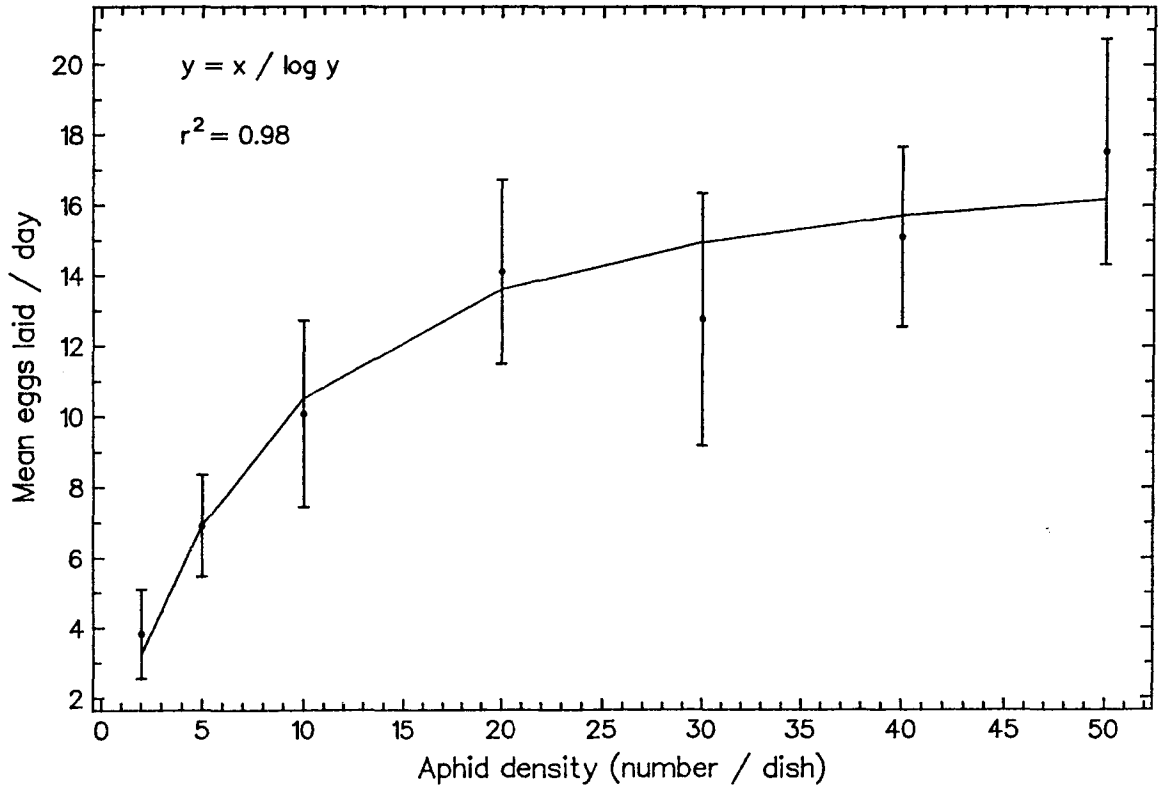


Fig. 3-4: Numerical response of Micromus tasmaniae. Error bars are 95% confidence intervals for the means.



However, a daily food intake of 3.34 mg wet weight of aphids is sufficient to maintain body weight (from Fig.3-3) and produce 12 eggs/day (from Fig.3-2). This indicates that the actual metabolic maintenance requirement for *M. tasmaniae* must be very low.

DISCUSSION

Various authors have suggested modifications and/or alternatives to the use of Holling's disc equation for the analysis of functional response experiments (Rogers, 1972; Royama, 1971; Mills, 1982; Livdahl and Stiven, 1983). However, recent reviews and evaluations of the various methods (Houck and Strauss, 1985; Williams and Juliano, 1985) recommend the use of Holling's equation, but with alternatives to the use of linear transformations to estimate the coefficients of the model (i.e., attack rate (**a**) and handling time (**Th**)).

A significant problem is that these parameters (**a** and **Th**), which define the shape of the type II functional response curve, are seldom measured experimentally, but rather, are estimated as constants, from the functional response model (Mills, 1982). However, not only may these parameters not be constants (Fox and Murdoch, 1978; Eveleigh and Chant, 1981) but also the majority of methods used to estimate them may be highly inaccurate (Houck and Strauss, 1985).

In this experiment, because of the dual objectives of the experimental design, prey were not continually replenished as they were eaten. Therefore, the number of available prey decreased during each 24 hour period. At high prey densities this would have had minimal effect because there was always ample prey available. However, at low prey densities lacewings were fed at below maintenance food requirements, and virtually all available prey were eaten. Although this should result in increased hunger and hence a higher attack rate, restricted prey number kept the attack rate artifically low. Therefore, in the present experiment, any attempt to estimate attack rate (a) as a constant must be in error. Despite this, the data are adequately described by Holling's equation, which implies that the estimated parameters serve in an adequate predictive capacity even if they are not what they reputedly stand for. This reinforces the concept that the parameters estimated from the 'disc' equation have limited biological reality as estimates of the attack rate and handling time (Livdahl and Stiven, 1983).

However, the asymptote of the functional response will be accurately estimated in the present experiment, because with the excess of prey supplied those eaten by the lacewings will not significantly reduce the availability of prey. Although comparison of feeding rates is often difficult because of the effects of temperature, aphid species and size (Hodek, 1970), the upper

level of prey consumption by *M. tasmaniae* is low compared with many aphid predators, particularly the coccinellids (Hodek, 1973; Ting *et al.*, 1978). It follows then that the lacewings ability to respond to increases in aphid density will be limited.

In the field, *M. tasmaniae* appears to aggregate in areas of higher prey density (Leathwick, unpublished data), while in the laboratory, higher prey densities lead to an increase in oviposition rate through the direct effect of food intake on egg production. A two factor numerical response to increasing prey density is therefore indicated, but, the two factors may not be additive. Mutual interference at higher predator densities may result in reduced oviposition and/or an increased tendency to emigrate (Holling, 1961; Evans, 1976b).

Holling (1961) raises the concept of the number of predator species present being related to prey density. Such a relationship would function primarily through the effects of differences in the functional response of each species. Each would have a minimum prey density (threshold) necessary to maintain it in the field, and a maximum rate of prey consumption and recruitment to the next generation, all dependent on the functional response. For example, *Coccinella californica* has a higher basal requirement for food than *Coccinella trifasciata* and therefore needs a higher prey density to keep it in the field (Ives, 1981). *M. tasmaniae* has a low basal metabolic requirement, but the effect of its predisposition to laying eggs may influence the prey threshold necessary to keep it in the field. Unfortunately the maintenance requirement value for the dominant coccinellid predator found in New Zealand lucerne crops (*Coccinella undecimpunctata*) is unknown. However, prey threshold should reflect predator size (see Ives, 1981) so *C. undecimpunctata* would be expected to have a higher prey threshold than *M. tasmaniae*. In other aspects of this study (Chapter 2), *M. tasmaniae* occurred more consistently than the coccinellid, being present in nearly all samples taken throughout the season. *C. undecimpunctata* was more sporadic in its occurrence (see also Henderson, 1979; Rohitha *et al.*, 1985) as would be expected for a predator with a higher prey threshold.

M. tasmaniae has a much higher conversion efficiency of aphids to eggs than the coccinellids. However, at high prey densities this advantage may be negated by the coccinellids higher voracity (i.e., a predator which is only half as efficient at converting food into eggs can produce as many eggs by eating twice as much). *M. tasmaniae's* ability to respond numerically to increasing prey numbers will be restricted to lower prey densities. Once the prey density is sufficient for lacewings to feed at their maximum rate, they will be unable to respond to further increases in prey number.

In summary, the presence of *M. tasmaniae* and *C. undecimpunctata* may be determined to some extent by their functional/numerical responses. *M. tasmaniae* is capable of arriving early in the aphid population buildup and of reproducing at a high rate at moderate aphid densities by virtue of its low functional response curve and high efficiency at converting aphids to eggs. Its ability to suppress aphid populations is limited, however, by the same functional response curve. The coccinellids should arrive later because of higher maintenance food requirements, but be able to take heavy toll of the aphid population by virtue of a greater appetite.

CHAPTER 4: Estimating thermal coefficients for lacewing development.

INTRODUCTION

The relationship between developmental rate and temperature is approximately sigmoidal in shape (Campbell *et al.*, 1974; Bernhardt and Shepard, 1978), and over the mid-portion of an insect's temperature range, this curve approximates a straight line. This has led to the concept of heat units and the mathematically simple linear (day-degree) model for insect development. This model assumes a linear relationship between development and temperature, above some theoretical threshold temperature below which development ceases. The linear model has been widely used and generally provides a good first order estimate of insect development(Eubank *et al.*, 1973).

Some authors have cast doubts on the ability of day-degrees produced under constant temperature regimes in the laboratory to accurately predict insect development under naturally fluctuating field temperatures. In particular, Hagstrum and Hagstrum (1970) list examples where fluctuating temperatures apparently result in a faster rate of development than constant temperatures. Others have found that at low temperatures development is faster under fluctuating temperatures, while at high temperatures it is slower, and in the mid-range it is the same (Messenger and Flitters, 1959; Siddiqui *et al.*, 1973; Eubank *et al.*, 1973). These discrepencies are the result of trying to fit a straight line to what is in fact a curvilinear relationship (Taylor, 1982). However, in at least one case fluctuating temperatures appear to cause an increase in development rate which cannot be explained in this way (Gregg, 1982).

Within certain temperature constraints, the linear model can therefore be used to give good estimates of insect development in the field (Taylor, 1982; Hilbert and Logan, 1983). As long as the temperatures experienced by the insect in the field are within that portion of the development rate curve which is approximately linear, then day-degrees will give a reasonable estimate of development. Samson and Blood (1979) and Syrett and Penman (1981) both investigated the development of *Micromus tasmaniae* under constant temperature regimes in the laboratory and produced markedly different estimates for the developmental threshold temperatures. As the ultimate objective of the present work was to model lacewing development in the field using the concept of day-degrees, it was important to have a thorough understanding of lacewing development under different temperature regimes.

Lacewings in the field are presented with a variety of potential prey, principally three species of lucerne aphid, which raises the possibility of different prey species affecting rate of development (Campbell *et al.*, 1974; Bernhardt and Shepard, 1978).

The aims of the present work were to;

1. Clarify the relationship between temperature and lacewing development, particularly with respect to the influence of fluctuating temperatures. Also, to determine developmental threshold temperatures and thermal requirements (duration of each stage in day-degrees) which could be used in a developmental rate model.

2. Establish whether aphid prey species is likely to influence lacewing development in the field.

METHODS

Temperature

Eggs were collected by presenting strips of nylon mesh material to female *M. tasmaniae* for four to six hours. The age of any eggs laid on this mesh was therefore known with an accuracy of plus or minus two to three hours. Eggs were separated, by cutting the material into small segments, and placed individually into numbered plastic petri dishes. Development was monitored for each individual and the time of change from one stadium to the next was recorded as the midpoint of the time interval during which a change occurred. Each individual was checked twice a day, and more frequently when convenient. With experience it was possible to anticipate when an egg was about to hatch, or a larva moult, and at these times the frequency of inspection was increased.

Lacewings were reared under constant temperatures of 10,15,19 and 23^{o}C ($\pm$1^{o}C) in Contherm^{R} controlled environment chambers, or under naturally fluctuating temperatures in a roofed, wire mesh insectary. The insectary experiment was replicated seven times, throughout the year, in order to cover a range of temperature profiles. Temperatures were recorded using a thermohygrograph which was repeatedly checked for accuracy against 2 bulb thermometers. Larvae were fed daily with an excess of pea aphids cultured on lucerne plants in a glasshouse.

For the seven replicates carried out in the insectary hourly temperatures were read from the thermohygrograph sheets and stored in computer files. A Fortran computer program was written

to facilitate rapid computation from these large data sets. When given the day and hour corresponding to each recorded change in life-history stage, program DEV calculates development rate (1/hours) and mean hourly temperature, for each life-history stage, for each individual lacewing. The theoretical developmental threshold temperature (**To**) was estimated by plotting developmental rate against mean temperature and extrapolating by least squares linear regression back to the x-intercept. The reciprocal of the slope of the line estimates the duration of each stage (**K**), in day-degrees above the threshold temperature. The estimates of **K** were checked by calculating the duration of each life-history stage, in day-degrees above **To**, using a version of program DEV. This calculated day-degrees directly, using hourly temperature summations above **To**, and produced estimates of **K** almost identical to the reciprocals of the slopes of the regression lines.

Error estimates for **To** and **K** were calculated using the formulae from Campbell *et al.* (1974), i.e.,

$$Se(\mathbf{To}) = \frac{y}{b}\sqrt{\frac{s^2}{Ny^2} + \left[\frac{\text{S.e. of } b}{b}\right]^2}$$

$$Se(\mathbf{K}) = \frac{(\text{Se of } b)}{b^2}$$

$$\text{where } Se(b) = \sqrt{\frac{r^2}{SS(x)}}$$

S^2 = residual mean square of y

y = sample mean

r^2 = variance for y :- approximately = to S^2

b = slope of the regression

N = number of observations

Prey Species

Lacewing eggs were kept at 10°C and checked daily for hatching. Only larvae emerging between 900h and 1500h (recorded as 1200 midday) were used in the experiment and these were reared individually in 100 x 25 mm plastic tubes at 10°C. A low temperature was used to maximise the chances of detecting differences in development rate. Individual rearing prevented any possibility of cannibalism, allowed accurate determination of development, and prevented condensation build up in the tubes.

All larvae were inspected daily, dead aphids and aphid remains were removed and fresh aphids supplied. To avoid the possibility of aphid size influencing the results (i.e., larvae finding large aphids difficult to catch might eat less) only juvenile aphids were used. Development was monitored through the pupal stage and newly emerged adults were anaesthetized with CO_2 and weighed using a Cahn electrobalance.

Larvae were reared on one of 5 aphid diets.

1. pea aphid (PA) reared on lucerne.
2. bluegreen lucerne aphid (BGLA) reared on lucerne.
3. spotted alfalfa aphid (SAA) reared on lucerne.
4. equal numbers of pea aphid, blue green lucerne aphid, and spotted alfalfa aphid, all reared on lucerne.
5. pea aphid reared on beans.

The criteria for estimating food value of aphid prey were similar to those of Anderson (1962), i.e., larval and pupal duration, weight of unfed adults, and mortality. An index of growth rate was calculated as:

$$\text{Growth rate} = \frac{\text{weight of unfed adults}}{\text{larval duration}}$$

Larval duration was used as the denominator, (rather than larval + pupal duration) because this is the period where food is eaten, and the length of time spent feeding plus the quantity and quality of food should determine adult weight. All larvae were fed to excess so food quantity should not be a factor.

RESULTS

Temperature

The duration of life-history stages under constant temperatures are given in Table 4-1 and under fluctuating temperatures in Table 4-2. As with other Neuroptera (Dunn, 1954; Miermont and Canard, 1975) the three larval instars are approximately equal in duration with the first instar being the longest and the second instar the shortest.

Lacewing survival, from egg to adult, under the four constant temperature regimes ranged from 88%-100% (N=78), and under fluctuating temperatures it was 83% (N=158). These values contrast markedly with the survival figures (2%-25%) obtained by Syrett and Penman (1981), who attributed most mortality to condensation brought about by rearing many indivivuals in a single container. Similarly, Neuenschwander (1975) rearing *Hemerobius pacificus* averaged 30% survival with losses due primarily to cannibalism. Therefore, the extra effort involved in rearing the lacewings separately, was justified, in that not only did it allow for more accurate determination of developmental periods (Anderson, 1962), but also resulted in more realistic estimates of background mortality (i.e., that proportion of the population whose deaths could not be attributed to any external factors).

The linear equations fitted to the data, along with their correlation coefficients, estimates of the threshold temperatures (**To**), and the thermal requirements (**K**) are given in Table 4-3. The regressions of development rate against temperature under both constant and fluctuating temperatures show differences in slope (Fig.4-1). For both eggs and larvae, development at low mean temperatures is faster under fluctuating temperatures than at a constant temperature with the same mean, while at higher temperatures the reverse is true. This kind of relationship is common (Messenger and Flitters, 1959; Eubank *et al.* ,1973; Siddiqui *et al.*, 1973), and is a result of the non-linearity of the development rate curve. At temperatures approaching **To** the linear model inaccurately predicts that development will decrease to zero. In reality the development rate curve is curvilinear and development is not only faster than predicted by the linear model, but continues below **To** (Neuenschwander, 1975). Similarly, at the upper end of the temperature range, although the mean temperature may be in the linear part of the curve, fluctuations reach into the nonlinear region where the slope of the development rate curve is decreasing. Development is therefore slower than predicted by a constant temperature linear model.

A closer inspection of the insectary temperature data showed that all replicates experienced temperatures above 25^{o}C, a temperature which has been shown to be outside the linear region of

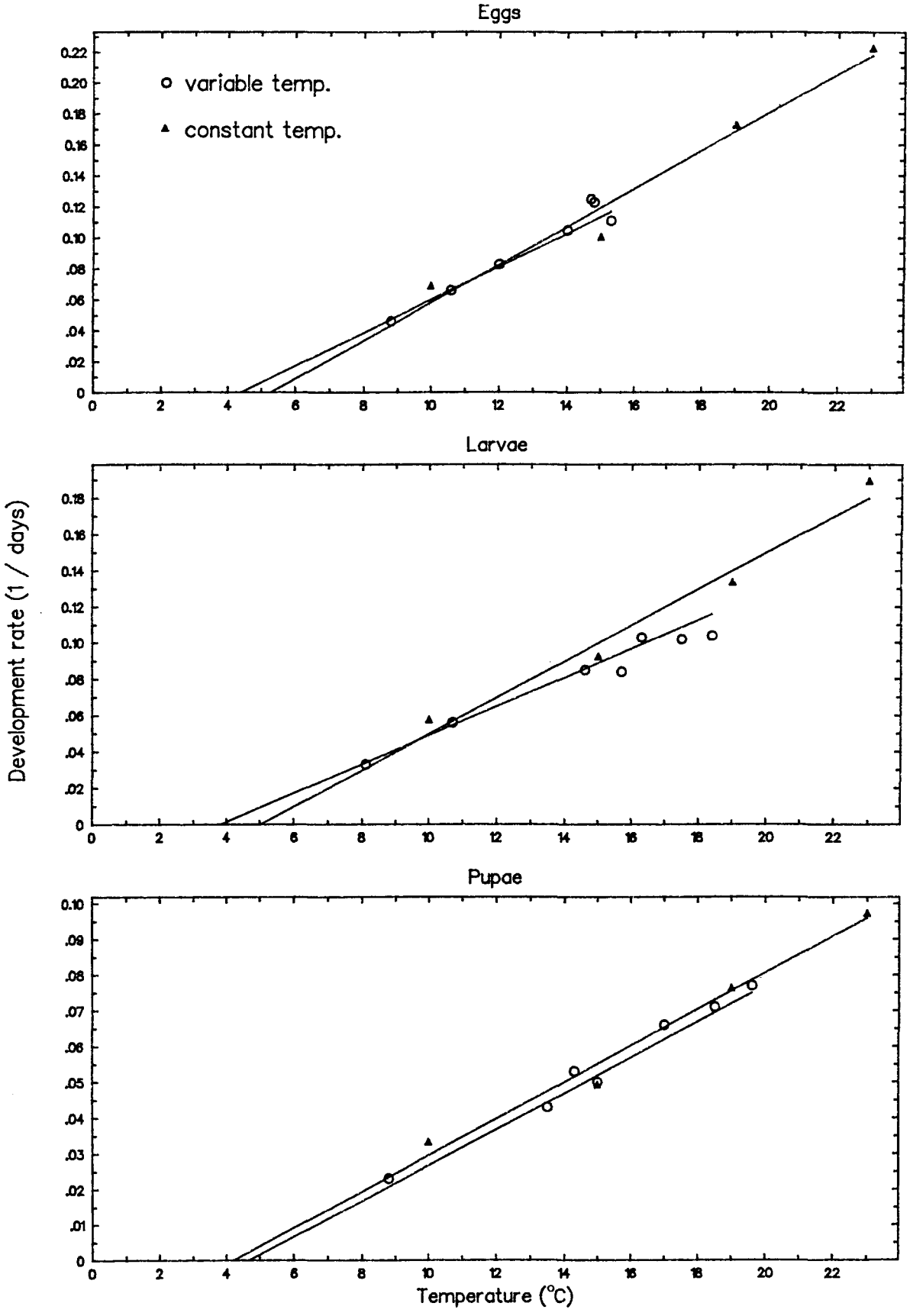
TABLE 4-1: Mean duration (days ± Se) of development of *Micromus tasmaniae* at different constant temperatures.

Temp.	N	Egg		Larvae		Pupae		Egg-adult	
10	17	14.6	(0.14)	17.4	(0.14)	30.6	(0.40)	62.6	(0.14)
15	17	10.0	(0.10)	10.9	(0.11)	20.5	(0.14)	41.4	(0.22)
19	21	5.8	(0.10)	7.5	(0.11)	13.1	(0.11)	26.4	(0.13)
23	18	4.5	(0.0)	5.3	(0.09)	10.3	(0.11)	20.1	(0.12)

TABLE 4-2: Mean duration of development of *Micromus tasmaniae* under naturally fluctuating temperatures in an insectary.

	Egg		Larval		Pupal	
Months	Mean temp. (range)	days	Mean temp. (range)	days	Mean temp. (range)	days
Sep. - Oct.	10.6 (4.0-25.5)	15.2	10.7 (2.0-22.0)	17.9	14.3 (3.0-28.0)	18.9
Nov. - Dec.	14.0 (6.5-30.0)	9.5	17.5 (9.5-29.5)	9.8	17.0 (9.0-28.0)	15.2
Nov. - Jan.	14.7 (10.0-28.0)	8.0	16.3 (9.0-25.0)	9.7	19.6 (11.0-29.5)	13.0
Jan. - Mar.	14.8 (11.-29.5)	8.1	18.4 (9.0-29.0)	9.6	18.5 (11.0-24.5)	14.1
Jun. - Sep.	8.8 (1.5-23.5)	21.8	8.1 (0-26.0)	30.1	8.8 (-0.5-24.0)	43.8
Oct. - Nov.	12.0 (3.0-25.0)	12.1	15.7 (3.0-25.5)	11.9	15.0 (6.0-31.0)	20.0
Apr. - May	15.3 (9.0-29.0)	9.0	14.6 (2.0-30.0)	11.7	13.5 (3.0-23.5)	23.2

Fig. 4-1: Development rates for Micromus tasmaniae under constant and variable temperatures. Lines were fitted to estimate threshold temperatures for development. For details see Table 4-3



the development rate curve (Syrett and Penman, 1981). Although only 3% of the total time was spent above 25°C, temperatures sometimes exceeded 30°C which is lethal to lacewings kept at that temperature for long periods (Syrett and Penman, 1981).

During four of the seven replicates temperatures passed below **To**. In three of these the time spent below **To** was small (less than 2%), but in replicate five, which was during the winter months, up to 16% of the total time was spent below **To**. Removing replicate five from the analysis had little effect on the slopes of the regression lines or the predicted **To** values, indicating that this replicate is not having a disproportionate effect on the results. The effect of the fluctuations into the upper temperature region is, therefore, equally important in determining the slope of the regression lines. The fact that the regression lines for pupae do not show this phenomenon may simply reflect insufficient range of temperatures to induce the effect and/or a wider linear-temperature range for pupae.

TABLE 4-3: Thermal requirements for development of *Micromus tasmaniae* under constant and variable temperatures under the linear (day-degree) model. To = Developmental threshold temperature; K = Thermal requirement in day-degrees above To.

Stage	Regression equation	r^2	To (± Se)	K (± Se)
constant temperature (N = 73)				
Egg	y = -0.0649 + 0.0123 x	95%	5.28 (1.06)	81.3 (9.0)
Larvae	y = -0.0502 + 0.0100 x	95%	5.02 (1.12)	100.0 (11.4)
Pupae	y = -0.0215 + 0.00509 x	97%	4.22 (1.01)	196.0 (18.4)
Variable temperatures (N = 127)				
Egg	y = -0.0471 + 0.0107 x	93%	4.40 (0.23)	93.5 (2.4)
Larvae	y = -0.0304 + 0.00795 x	95%	3.82 (0.39)	125.8 (2.5)
Pupae	y = -0.0236 + 0.00504 x	97%	4.68 (0.32)	198.4 (3.2)

Because **To** is estimated by extrapolation, the estimate of **To** is sensitive to small differences in the slope of the regression line. However, because **To** and **K** are strongly negatively correlated, small differences in **To** are automatically compensated for by changes in **K** (Campbell *et al.*, 1974). Confidence intervals (95%) for **To** and **K** were calculated and are presented in Fig.4-2 along with confidence intervals for **K** based on data presented by Syrett and Penman (1981). The confidence intervals for development under variable temperatures are considerably smaller than those from under constant temperatures. This reflects the higher number of individuals (N = 127 vs. N = 73), and the more frequent checking of developing individuals, which resulted in smaller residual mean squares for the regressions, and hence standard errors. The standard errors presented by Syrett and Penman (1981) are calculated by a different method and are therefore not strictly comparable.

Also in Fig.4-2 is the least squares regression line fitted to the three estimates of **To** and **K**. In two cases the r^2 values indicate a reasonable negative linear relationship, and hence support the concept of a negative correlation between **To** and **K**. It is difficult, however, to conclude much from the low r^2 value for larvae given only three points to plot, and the inaccuracy of the method for estimating **To**. Given this negative correlation and the broad overlap in confidence intervals, there appears to be no real difference between the **To** and **K** values obtained. Once a lacewing development model had been written it was possible to test the significance of these different values by using each set of coefficients in the model and comparing the outputs (A full description of the model and its uses is presented in Chapter 5).

Outputs from the model based on three sets of thermal coefficients (constant and variable temperature estimates from Table 4-3, and those of Syrett and Penman, 1981) are presented in Fig. 4-3. The model outputs are quite similar, particularly those based on the thermal coefficients estimated in these experiments, and what differences there are, are minor compared to the differences between model output and the field data (Chapter 5). There is little, if any, effect on the model predictions due to estimating development rate under fluctuating temperature regimes.

Prey species

The effect of the aphid diets on lacewing development differed between the sexes and so male and female data were analysed separately. Male lacewings showed significant ($P > 0.05$) differences in newly emerged adult weight, but no significant differences in development times (Table 4-4). Females, on the other hand, developed significantly faster on some aphid diets, but all

Fig. 4-2: 95% confidence intervals for the threshold temperature (To) and thermal requirement (K) for development of Micromus tasmaniae; -- estimated under constant and variable temperatures.

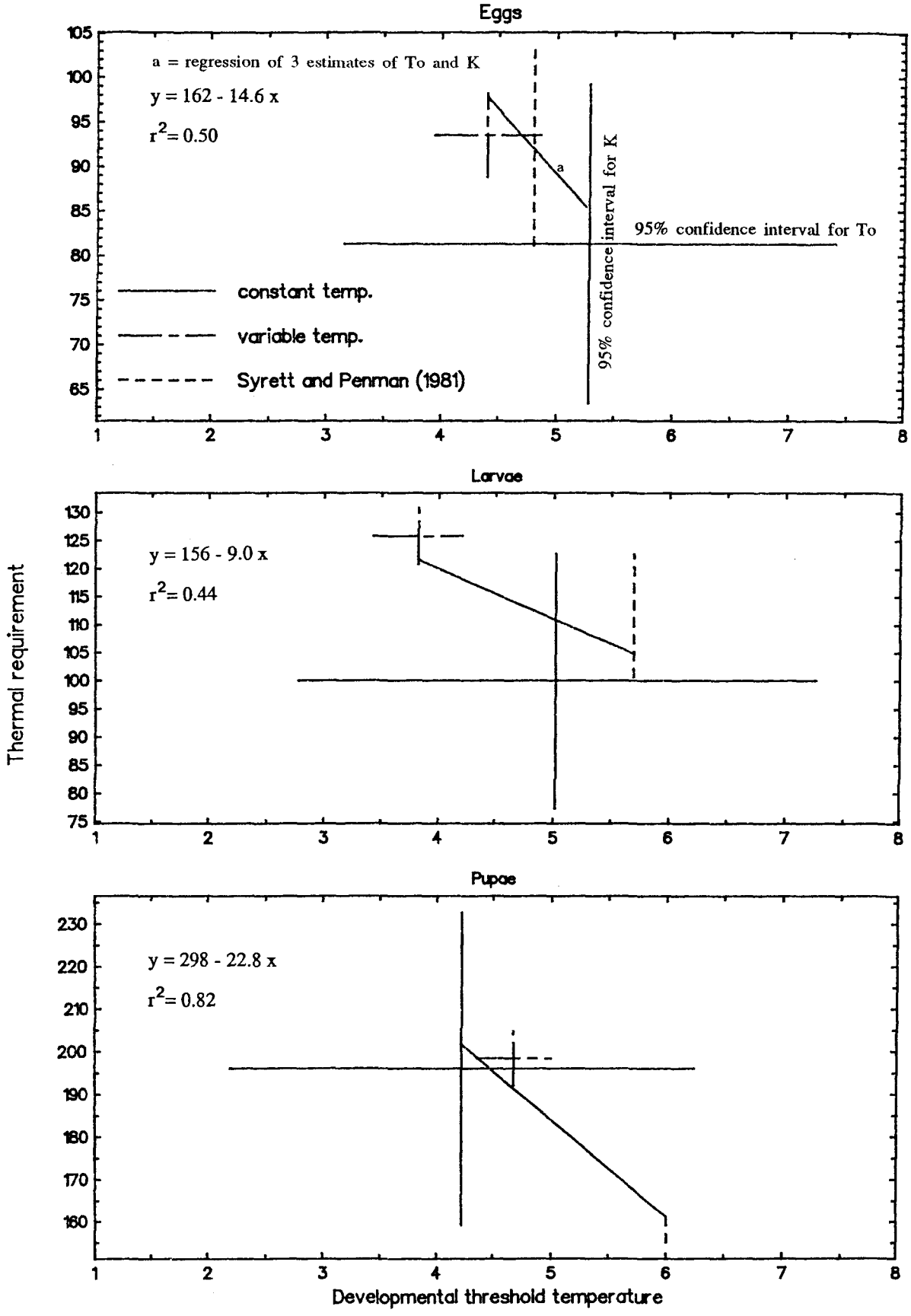
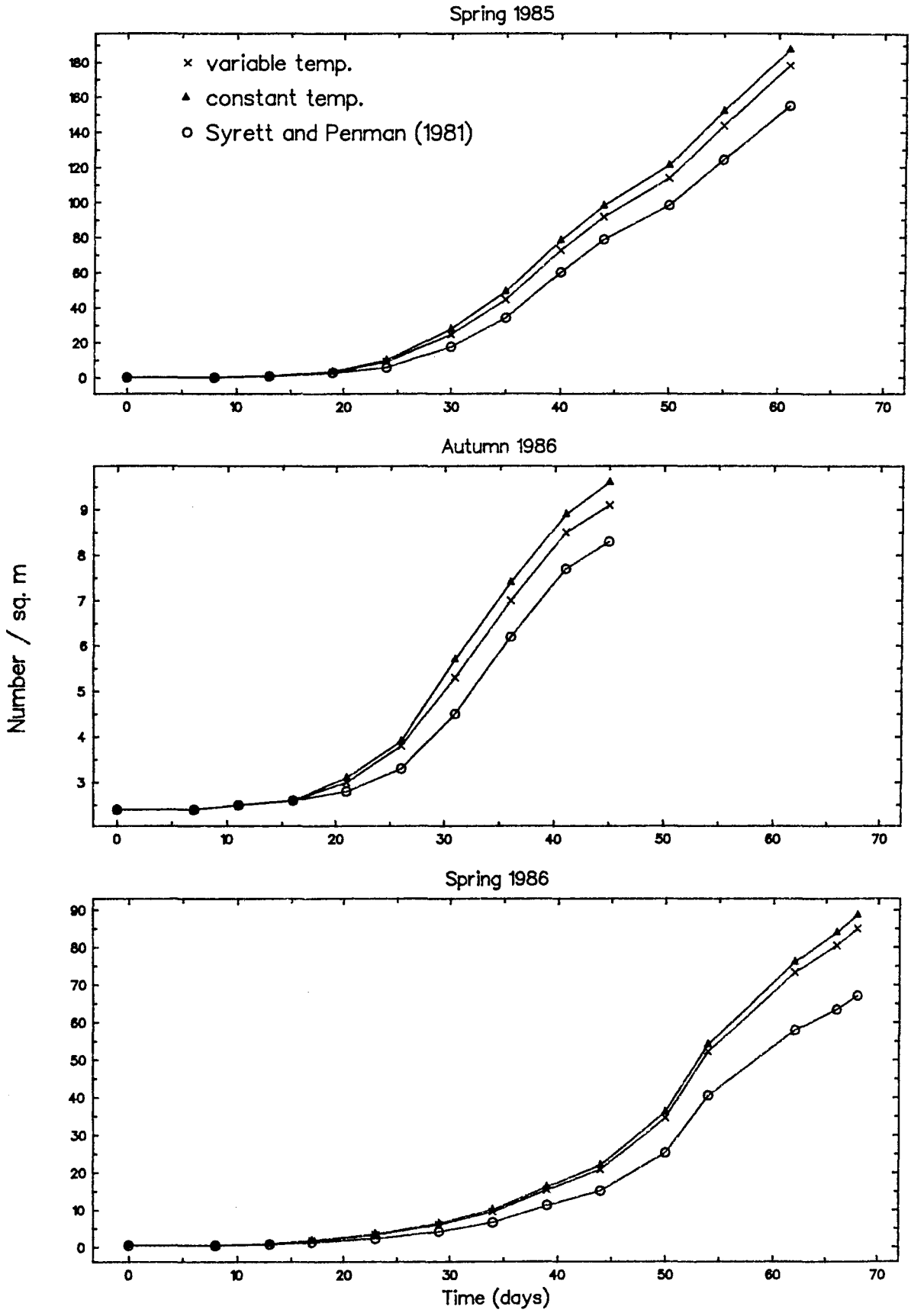


Fig. 4-3: Outputs from lacewing development rate model based on three estimates of the thermal coefficients. (see text for details)



adults produced were approximately equal in size. Thus, both males and females showed significant differences in growth rate.

Although the differences between diets were not always significant, there was a clear trend for pea aphids to be the least suitable diet. Lacewings reared on pea aphids were consistently amongst the slowest developers, produced the smallest adults, and had the lowest growth rates. There was also some evidence for a host plant effect with pea aphids. Female larvae reared on pea aphids off beans took significantly longer to develop than those fed pea aphids off lucerne, and the number of lacewings surviving to the adult stage was also reduced (Table 4-5). Lacewings reared on a mixture of the three aphid species were consistently the fastest developers, and in the females had the highest growth rate, although again many of the differences were not significant.

DISCUSSION

Samson and Blood (1979) estimated developmental threshold temperatures for *M. tasmaniae* of -0.1^{o}C for egg, 2.6^{o}C for larval and 1.4^{o}C for pupal development, all of which are considerably lower than the values predicted here (Table 4-3) and by Syrett and Penman (1981). Although Samson and Blood fed their lacewings on a different aphid species and therefore their results are not strictly comparable, it is more likely that the difference is a result of their having only two points from which to plot their regression lines, whereas three or four temperatures are recommended (Campbell *et al.*, 1974). Samson and Blood dropped the third temperature (a constant 28^{o}C) from the analysis because they felt it was above optimum for this species and therefore resulted in unrealistically low thresholds.

There is, however, the possibility that Samson and Blood were sampling a different biotype of *M. tasmaniae*, since different geographic populations of a species can differ in their thermal characteristics (Neuenschwander, 1975; Hutchison and Hogg, 1984).

When the data on development of *M. tasmaniae* at a constant 25^{o}C on a diet of SAA presented by Ting *et al.* (1978) are converted to growth rates, they fall below those predicted by both sets of equations in Table 4-3. This supports Syrett and Penman's (1981) assertion that 25^{o}C is outside the linear region of the development rate curve for *M. tasmaniae* . It is well known that insects reared at temperatures above their upper threshold develop at a slower rate than those reared under more favourable conditions (Nowierski *et al.*, 1983). However, the determination of upper temperature thresholds under conditions of constant temperature must be treated with caution (Hogg, 1985) because insects can often tolerate much higher temperatures, for short

TABLE 4-4: Development of *Micromus tasmaniae* on different aphid diets at 10°C. Letters indicate statistical differences (P > 0.05) based on 'Duncans new multiple range test'. Letters in common indicate a homogenous grouping of means. * Growth rate = Adult weight/larval duration.

Diet	Larval duration (days)	Pupal duration (days)	Adult weight (mg)	Growth rate * (mg/day)
Male				
PA (lucerne)	21.5 NS	36.8 NS	2.15 b	0.101 b
BGLA	20.7	36.3	2.42 a	0.117 a
SAA	21.4	35.8	2.31 ab	0.108 ab
PA/BGLA/SAA	20.5	35.6	2.18 b	0.107 ab
PA (beans)	21.7	37.2	2.21 b	0.102 b
Female				
PA (lucerne)	21.1 b	35.4 b	2.89 NS	0.137 b
BGLA	20.9 b	36.7 a	3.16	0.152 a
SAA	21.6 ab	34.8 b	3.10	0.145 ab
PA/BGLA/SAA	20.4 b	34.4 b	3.14	0.155 a
PA (beans)	22.4 a	35.8 ab	2.97	0.134 b

TABLE 4-5: Survival of juvenile lacewings reared on different aphid diets. Figures bracketed together are not significantly different (5%): Test for difference between proportions (Walpole, 1974: p. 221).

Diet	N	% surviving to pupae	% surviving to adult
PA (lucerne)	35	91	89
BGLA	32	94	88
SAA	31	97	94
PA/BGLA/SAA	22	95	91
PA (beans)	42	90	67

periods, with no ill effects (Campbell *et al.*, 1974; Neuenschwander, 1975). Upper temperature thresholds should be considered a balance between temperature and time exposed to that temperature. The higher the temperature the less time an insect would be expected to tolerate it. Temperatures in the 25-30^{o}C range may be outside the linear region of the lacewing's development rate curve, but it is apparent, from the high survival obtained in these experiments, that temperatures in this range are not lethal unless maintained for long periods.

Comparison of the field model outputs using different sets of thermal coefficients shows only minor differences in predicted development. It is possible that these differences are simply artifacts of experimental error, given that the method of estimating thermal coefficients is not very accurate (Campbell *et al.*, 1974). Syrett and Penman (1981) fitted a straight line to three points, and extrapolated to estimate **To**. The scope for variation inherent in fitting a line to just three points could account for the differences in model output. By comparison the estimates produced in the present study are the product of plotting each individual separately, giving N values of 73 and 127. The thermal coefficients estimated in this way give very similar model outputs.

Where temperatures fluctuate near to or below **To** the actual value of **To** becomes important (Campbell *et al.*, 1974). The higher the estimated **To**, the more often temperatures will pass below it, and under the linear model, development will cease when in reality it does not. Therefore, the higher the **To** value the greater the discrepancy between predicted and observed development. Thermal coefficients estimated under fluctuating temperatures similar to field conditions should give a better result than constant temperature estimates, because they give lower **To** estimates due to the incorporation of the effects of low/high temperatures.

However, in this case at least, this is not so. Although the field temperatures on which the model is run pass below **To** for up to 5% of the time, and below 8^{o}C (into the non-linear region of the development rate curve) for up to 20% of the time, there is very little difference due to the different **To** values. In fact, the higher **To** values give the fastest development, which is the reverse of the expected. Presumably, because the predicted development at these temperatures is very low, it would be necessary for temperatures to be between **To** values for a very long time, for any difference in predicted development to become apparent. Therefore, contrary to the prediction of Campbell *et al.* (1974), the effect on predicted development of different values of **To**, even in situations where temperatures fluctuate close to and below **To**, is minimal.

The effect of different prey species on development is to alter **K** while **To** remains the same (Campbell *et al.*, 1974). The differences shown here are relatively insignificant (Anderson, 1962;

Smith, 1965; Blackman, 1967; Hukusima and Kamei, 1970) and probably reflect subtle differences between suitable host species. Lacewings in the field will be presented with two, often all three, species of lucerne aphid, and would therefore be expected to develop faster than lacewings reared in the laboratory on a diet of pea aphids only. In this case, the increase in developmental rate is only 3-4%, but it demonstrates clearly that unless care is taken to ensure that the diet of laboratory reared insects is equivalent to that in the field, the temperature coefficients produced may not be suitable for predicting development in the field (Hughes, 1963; Campbell *et al.*, 1974).

A potentially confounding factor which is not considered here, and is generally disregarded in the literature, is the effect of prey number on development. At low prey densities, the length of time spent in each larval instar may increase (Beddington *et al.*, 1976), effectively increasing **K**. When development is predicted under conditions of abundant food the result is a maximum rate of development, strictly applicable only to situations where prey is plentiful.

In summary, development of *M. tasmaniae* is approximately linear in the temperature range $8^{o}C$-$25^{o}C$. When temperatures fluctuate below $8^{o}C$ development will be faster under fluctuating temperatures than under constant temperatures with the same mean. When temperatures fluctuate above $25^{o}C$ development will be slower than under constant temperatures with the same mean. Therefore, the observed relationship between lacewing development and temperature is as predicted in the literature. Except under unusual temperature regimes, there is no evidence to support the concept (Hagstrum and Hagstrum, 1970) of a linear model based on fluctuating temperatures being superior at predicting development in the field than a constant temperature model. Estimating thermal coefficients under fluctuating temperatures will generally result in lower estimates of **To**, but the effect on predicted development is minimal because of the negative relationship between **To** and **K**.

Diet has the potential to alter thermal coefficients, and in this case the field diet would be expected to shorten lacewing development by 3-4% compared with the laboratory experiments. The major difficulty in using the linear model for insect development is undoubtedly its inability to accurately predict development once temperatures fluctuate outside the linear range. Development predicted by a linearly based model will be faster than reality at high temperatures and slower than reality at low temperatures.

CHAPTER 5: Lacewing population dynamics

INTRODUCTION

Lucerne forage crops present a very short-term environment, with virtually the entire above ground biomass being removed at regular intervals by the farmer. Lucerne aphids and their natural enemies are therefore obliged to go through a continual process of establishment, population growth and then an abrupt decline. The study of lacewing population dynamics, therefore, presents a challenging problem for not only does this species have complete overlap in generations which makes census data difficult to interpret (Varley *et al.*, 1973), but the lucerne environment allows virtually no opportunity for a stable population structure to develop. Life-tables are the basic tool for population studies, but classical forms require that the species being studied has either discrete generations or a stable age structure (Southwood, 1978). The variable life-table of Gilbert *et al.* (1976) offers one solution to this problem.

The variable life-table is one in which the birth and survival rates change with time in a realistic way (Gilbert *et al.*, 1976), and is in effect a simulation model. This approach to modelling stresses realism, and model construction requires extensive laboratory and field data on the biology and population dynamics of the species (Gutierrez *et al.*, 1984). The goals and methods of this approach are reviewed by Gilbert *et al.* (1976) and Getz and Gutierrez (1982).

Because little was known of the biology of *M. tasmaniae* the objective of this study was to gain a better understanding of the factors influencing lacewing bionomics. Sampling a population gives the number of individuals present at a series of instants in time, but fails to explain the number of individuals passing through the different life-history stages or the mechanisms causing population change. By constructing a realistic model it was hoped to;

1. Convert the numbers of lacewings observed in the field into the actual number passing through each juvenile stage to the adult stage.

2. Establish major causes of lacewing mortality.

3. Quantify the importance of migration on the observed changes in lacewing numbers.

METHODS

Field studies

The trial site was situated in a 2.5 hectare lucerne (cultivar Wairau) field on the Lincoln College research farm. One end of the field was fenced off to enclose an area of just over one half of a hectare. A border strip was mown six metres in from the fence line on three sides and 12 metres in from the fourth (southern) boundary. This border, which was kept short with regular mowing, functioned as an 'insect free' zone between the trial site and the surrounding fields. This left an experimental plot of approximately 3000 m^2, an area sufficiently large to allow regular removal sampling without seriously depleting the resident insect population.

The fields to the north, east and west were ryegrass pasture and to the south was the remainder of the lucerne field. As the prevailing winds in this area are from the north the trial area was normally upwind from the only potential source of immigrant insects. In this way it was hoped to have an isolated population which could be studied in detail. The movement of lacewings to and from the trial area was monitored using sticky traps around the perimeter of the field. Traps (see Fig.5-1) 300 x 210 mm in size, were made of 'Clarex^r' acrylic perspex sheet mounted on short pieces of aluminium tube (12 mm diameter). Sheets of clear acetate were stuck to each side with a comercial sticky trap product ('Tack-Trap^r') and a further coating of 'Tack-Trap' to the outside of the acetate supplied the insect catching surface. Although partially opaque these traps were primarily colourless to avoid any possibility of insects being attracted to them (i.e., they were intended to be purely interception traps).

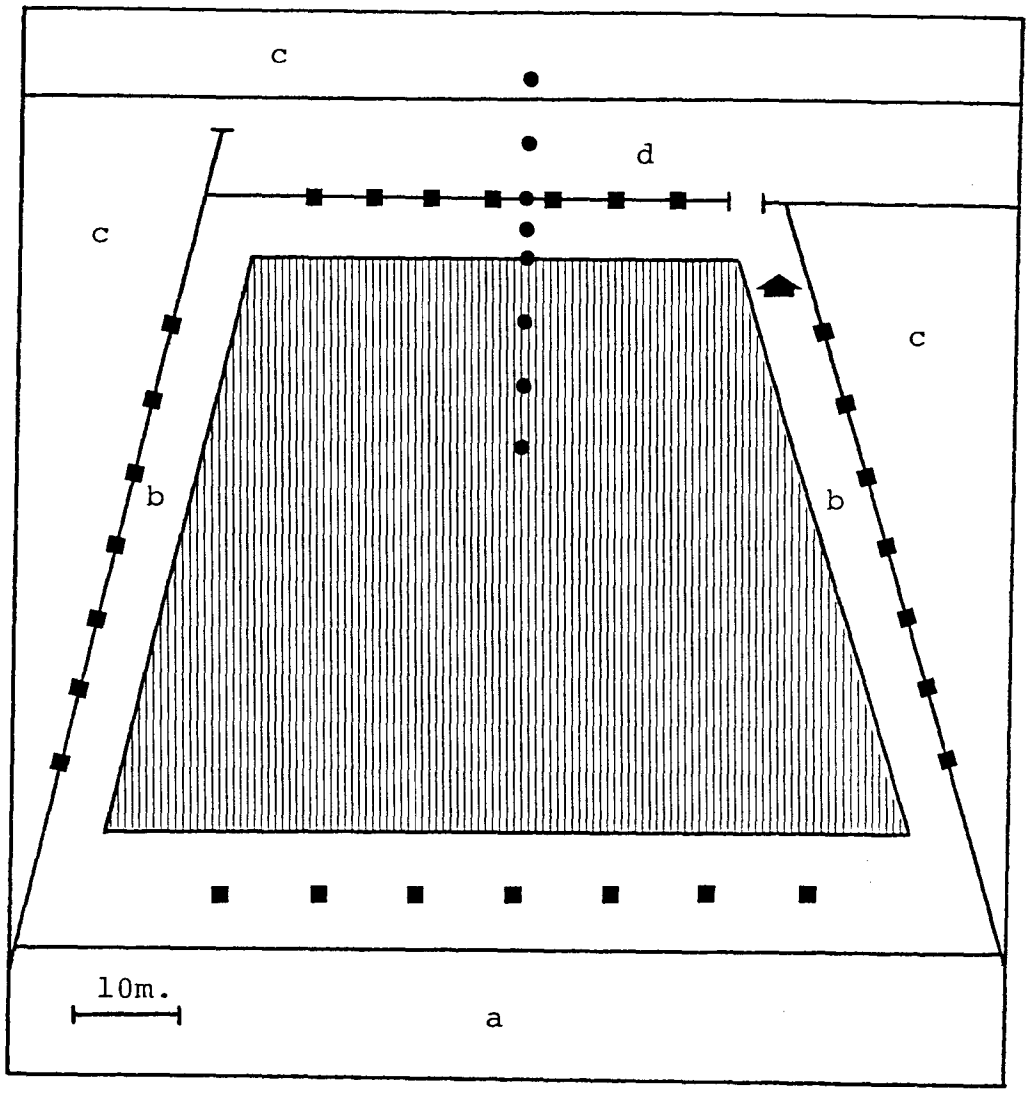
Seven of these traps were spaced evenly along each side of the plot, either mounted on the fence posts (as in Fig.5-1) or, as at the southern end, mounted on poles six metres out from the plot and six metres in from the adjacent lucerne field (Fig.5-2). The bottom edge of all traps was 1.5 metres above the ground. The trial area was therefore ringed with flight traps at a distance of six metres (Fig.5-3). Traps were changed approximately weekly by peeling off the acetate sheets and laying them on pieces of white hardboard which had a simple grid drawn on them. The hardboard sleeves were placed in a grooved box (Fig.5-4) which kept them separate and allowed easy transport around the field and back to the laboratory. Once the insects on each acetate had been counted the acetates were discarded.

The direction in which a lacewing was travelling when caught on a trap was inferred from the side of the trap on which it was caught. All lacewings caught on the sides of traps facing the

Fig.5-1: Directional flight trap used to measure movement of Micromus tasmaniae into and out of the experimental plot.

Fig.5-2: At the southern end of the plot flight traps were mounted on poles in the middle of a 12 m border separating the experimental plot from the remainder of the lucerne field.

Fig.5-3: Layout of experimental plot at site R.21 during 1984-86.



Key

- Stevenson screen
- transect flight traps
- Directional flight traps
- experimental plot

a - lucerne
b - mown border
c - grass pasture
d - stock race

experimental plot were taken to have been flying out of the field and all those caught on the outer sides were taken to have been flying in. Thus, although only a relative sampling method, these traps gave not only an estimate of flight activity over time but also a measure of the direction of flight. The ratio of lacewings caught flying in to those caught flying out gives an indication of net gain or net loss to the resident population.

Before inferences could be made regarding lacewing immigration and emigration from the flight trap data it was necessary to know how far lacewings fly within the crop. A transect of sticky traps was set up in the spring of 1985, with traps at six metre intervals from 18 metres inside the plot to 18 metres outside (see Fig.5-3). Circular sticky traps made from 1.25 litre clear plastic drink bottles (Fig.5-5) were mounted on poles at 0.75 metres and 1.5 metres above ground. The number of lacewings caught on each trap was recorded, and the traps replaced at regular intervals.

Most components of the lucerne fauna were sampled, but because the main objective was to construct a variable life table for lacewing development, lacewings were sampled more intensively and extensively than other species. Lucerne aphids, lacewing larvae and adults, and other predator species (see Chapter 2) were sampled with a 'D-vac' motorized suction sampler. One sampling unit consisted of the cone of the 'D-vac' being lowered vertically into the lucerne until hard on the ground and held there for approximately 30 seconds, before being lifted vertically off. Each such sub-sample covered an area of 850 cm^2. A clear indication of age structure requires a minimum of 100 individuals to be sampled (Gilbert *et al.*, 1976), and so whenever feasible sample size was adjusted to ensure at least this many lacewing larvae were collected. The standard sampling routine for lacewings consisted of ten samples each of ten sampling units (a total area sampled of $8.5m^2$). Less samples were required when lacewing numbers were high. A subsample of this, usually five samples of five sampling units, was used to estimate the other components of the lucerne fauna. Such a sampling routine allowed the flexibility necessary to sample a range of species with varying population densities and still maintain the accuracy required for the lacewing data.

Samples were collected in a haphazard manner which involved walking through the crop taking samples in an 'apparently random' manner (i.e., without conscious bias). They were stored in plastic bags at 10^oC until sorted. Initially half of the samples were sorted by hand and half were extracted in 'Berlese' heat extraction funnels. The results obtained by these two extraction techniques over five sampling occasions were compared using two-way ANOVA. For adult, second and third instar lacewings there was no significant difference in number counted, but for first instar larvae heat extraction yielded significantly ($P < 0.01$) lower numbers than hand sorting.

Fig.5-4: Grooved box and boards used to transport acetates from the flight traps back to the laboratory.

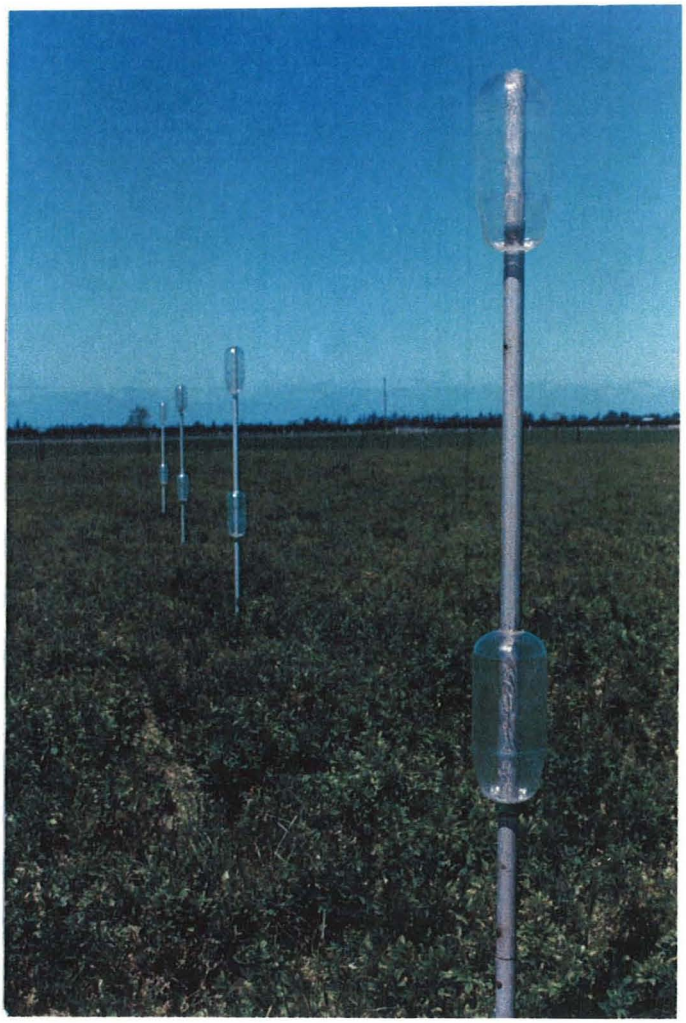


Fig.5-5: Transect flight traps used to measure non-migratory flight activity of Micromus tasmaniae.

First and second instar larvae were not used in the final comparisons (see below), and so for the autumn and spring 1986 sampling all samples were heat extracted, in order to save time.

From each sample collected, lacewing larvae were removed alive, sorted into instar, and reared through to the adult stage to estimate levels of parasitism. Determining instar size by measuring head width would have been very time consuming considering the large number of larvae being dealt with and so instars were separated on the basis of size. To produce a size reference collection for each instar, larvae were reared individually from eggs and each day several individuals were transferred to tubes of 70% alcohol. Changes of instar were determined by the presence of the moult skin.

Lacewing egg density was estimated by collecting vegetation and searching for lacewing eggs. A 625 cm^2 quadrat was thrown into the lucerne to select a sample site without conscious bias. All the lucerne stems and any weeds within the quadrat were cut at ground level with a pair of scissors, and placed carefully into a plastic bag. Ten such samples were taken each sampling day and kept at 10^oC until they could be sorted. Neither of these techniques sampled lacewing pupae (see Chapter 2).

Field temperatures were recorded using a thermo-hygrograph in a Stevenson's screen, raised 100 mm off the ground, and sited adjacent to the lucerne.

The Model

The model developed in this study used the relationship between lacewing development and temperature, studied in an insectary (Chapter 4), to estimate development in the field. To avoid the difficulty of predicting oviposition in the field, samples were taken to estimate the number of eggs present. If these two components are estimated correctly then the model should accurately predict the age distribution and density (before mortality) of lacewings in the field. Discrepancies between predicted and observed densities would be caused by various mortalities acting on the field population which the model did not incorporate, or by the migration of adults.

The procedure followed was that recommended by Gilbert *et al.* (1976) of first producing a model, and then progressively tuning it, based on additional biological information. This approach not only allows the modeller to follow the gradual improvement in his model but can also suggest where to look for new pieces of important information. A simple transitional model was constructed which moves individuals from one stadium to the next based on the physiological time

for each step of the model, relative to the physiological time required for full development of each stadium. For example;

IF

first instar larval duration is 40 day-degrees; and

the time between samples taken at T_1 and T_2 is 20 day-degrees

THEN

the number of first instar larvae passing to second instar is the number at T_1 * 20/40

AND

the number of first instar larvae at T_2 is

number at T_1 * (1 - 20/40) plus the number of eggs hatching

which is calculated in a similar manner

Effectively the model is a Leslie matrix (Leslie, 1945) with varying stage durations. Age-specific mortalities were added to tune the model to the field data. A flow chart and the Fortran 77 listing of the model are given in the Appendix.

RESULTS

Flights

A first attempt at collecting field data in the summer of 1984-85 was abandoned because of severe drought conditions. However, although sampling indicated very low populations of aphids and predators in the plot, flight trap catches suggested that insects (including lacewings) were moving in and out of the area in approximately equal numbers (Fig.5-6). These results were encouraging in that they showed not only that the flight traps would catch lacewings but also that the flight orientation of the lacewings caught, relative to the experimental plot, was as expected, That is, with no aphids to hold them in the field all lacewings flying in would be expected to fly out again almost immediately, resulting in equal numbers flying both ways.

Of course, this result could also occur due to the traps not functioning in a directional manner. However, at later stages when resident populations were declining rapidly, many more lacewings were caught leaving than entering the plot (see Fig.5-11b). There is every indication, therefore, that the flight traps were capable of detecting directionality of flights, and that they should supply an assessment of gain or loss of lacewings independent of the model.

The data from the transect traps (Fig.5-7) suggest that lacewings fly quite close to the ground and that the 1.5 metre perimeter traps may have been better at a lower height. However, reducing trap height would have caused problems where the traps were susceptible to interference by sheep. Fewer lacewings were caught at the edge of the plot and the number declined with distance out from the lucerne (Fig.5-7). This suggests that 'trivial' flights account for many of the lacewings caught within the plot and that the falloff in numbers with distance out from the plot reflects the decline in 'trivial' flights over the mown border. Therefore flight traps sited six metres out from the edge of the lucerne should be well placed to detect migratory flights. This is supported by Hilson's (1964) observation that *M. tasmaniae* seldom flew more than three or four metres unless migrating.

Field data

In all three seasons considerable numbers of lacewing eggs and larvae were sampled and in the spring of both years high densities of adults occurred (up to 100 m^{-2}). However, the majority of these adults appeared after the decline in the aphid populations (Fig.5-8). Flight trap catches and a high proportion of alate aphids prior to the decline indicated that emigration was a major cause of the decline in aphid numbers. So, although very high densities of adult lacewings were recorded many of these would have occurredtoo lateto have had any significant impact on the size of the aphid populations.

The general precision of sampling for lacewing adults and larvae was high. Except for occassions when population densities were very low, standard errors were usually less than 20%, and on a number of occasions were less than 10%, the value of the mean. Although not entirely within the 10% guideline recommended by Southwood (1978), these errors are more than adequate to measure the many-fold changes in lacewing numbers.

The level of agreement between model predictions for larval density and the field data increases with larval instar size (Fig.5-9). In general the model predictions for third instar larval density approximate those observed in the field (Fig.5-10). Given that the model works by shifting individuals from one stadium to the next, and that survival is high throughout, it follows that if the model accurately predicts third instar larval densities, it should also accurately predict the number of first and second instars. The lower field values recorded for first and second instars therefore indicate a bias in the sampling method.

Fig. 5-6: Number of Micromus tasmaniae caught on flight traps during the abortive 1984-85 season.

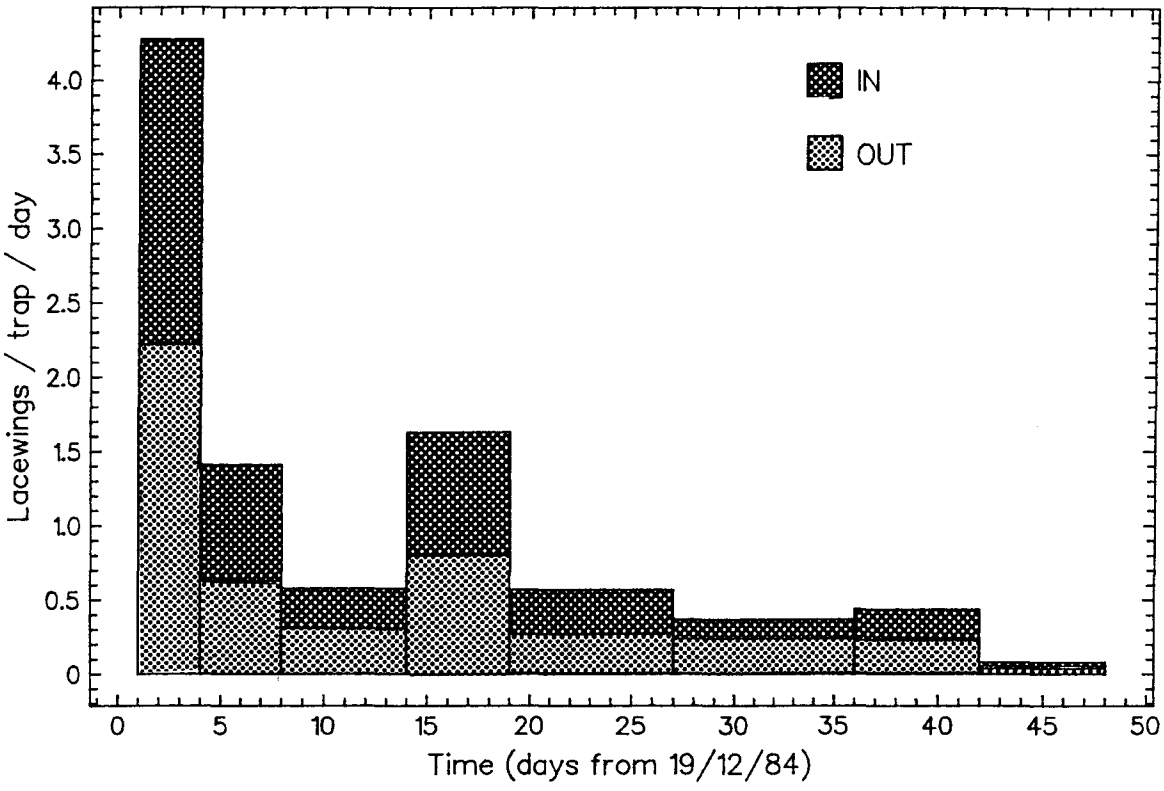


Fig. 5-7: Number of Micromus tasmaniae caught on transect traps (spring 1985).

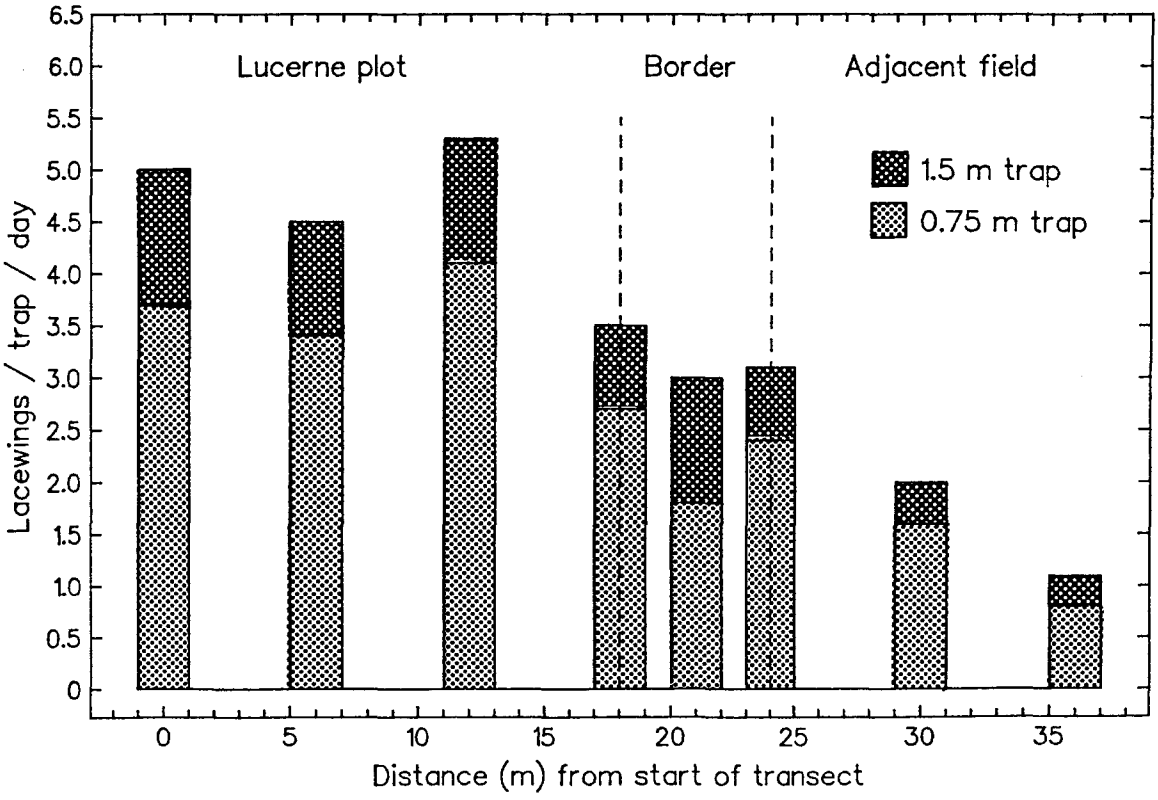


Fig. 5-8: Mean number of aphids and Micromus tasmaniae adults and juveniles sampled from site R.21 during the spring of 1985 and 1986

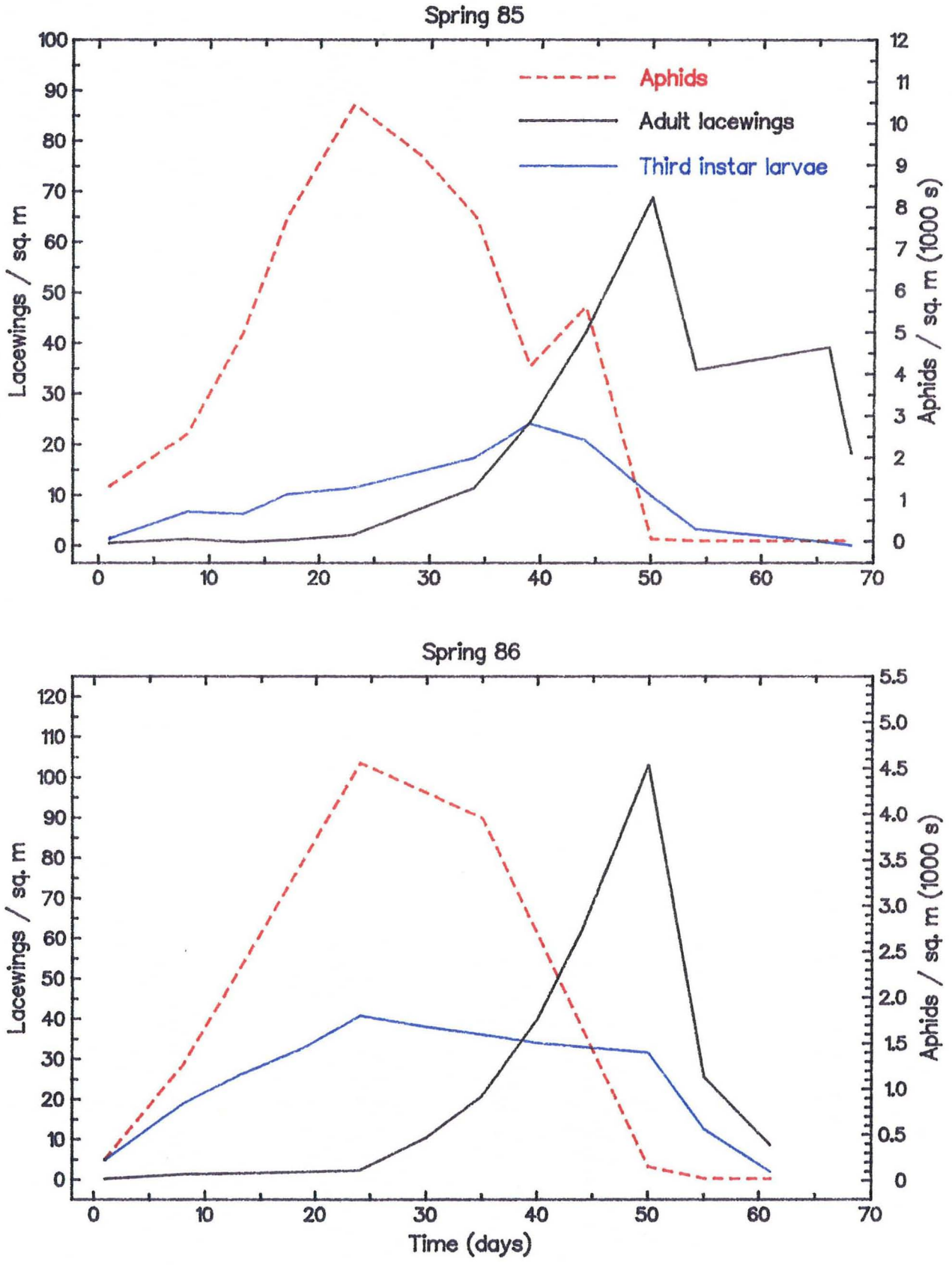
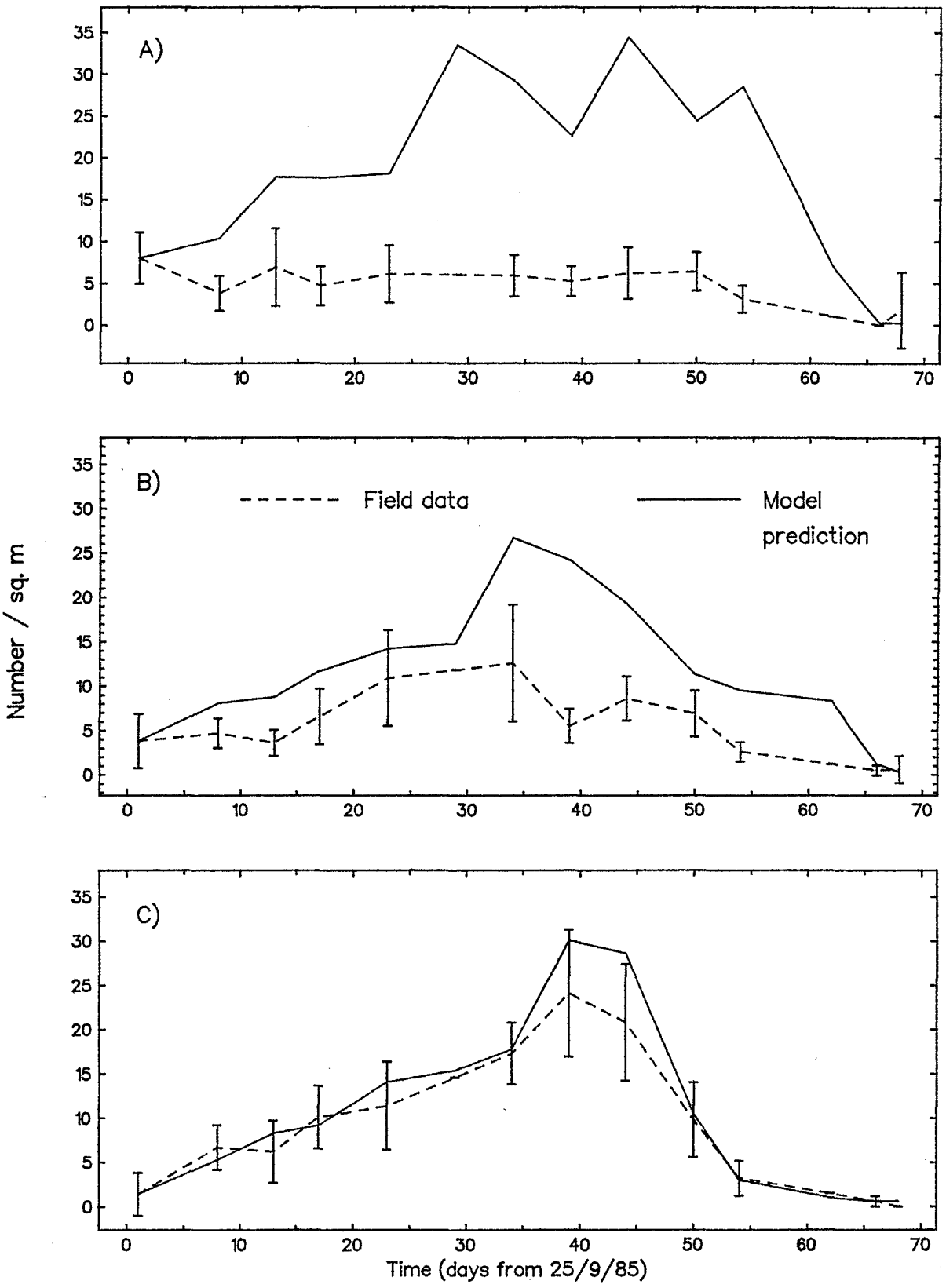


Fig. 5-9: Comparison of predicted and observed densities of Micromus tasmaniae larvae at site R.21 in the Spring 1985. Error bars are 95% confidence intervals for the means.

A) First instar larvae.
B) Second instar larvae.
C) Third instar larvae.



First instar lacewing larvae are small (0.05-0.25 mg) and very difficult to sort from samples due to their habit of hiding in small spaces/crevices. This reclusive habit may well make the smaller larvae difficult to sample by suction sampling (Chapter 2). Whatever the cause, field sampling underestimates population densities for first and second instar larvae. All comparisons between the model and field data were therefore restricted to third instar larvae and adults.

Frazer and Gilbert (1976) state that for sampling coccinellids in lucerne, standard forms of suction machines are 'hopelessly inadequate'. If the D-vac sampler used here was significantly undersampling the number of third instar and adult lacewings present, then the model, when compared with the field data, should overestimate the numbers present. Alternatively, of course, the egg density measurements could be similarly biased, in which case there is a constant sampling bias and the true lacewing densities were much higher than observed. However, it is probably more reasonable, in the absence of any evidence to the contrary, to assume that although the sampling techniques are open, as always, to error, they do in fact go a long way toward estimating true population densities.

Modelling

Prey Availability

Initially the model incorporated only background mortality (i.e., unexplained mortality not associated with any external factors) which was estimated from lacewings reared individually in an insectary development rate experiment (Chapter 4). Survivorship was high, with values of 88.6% for eggs, 98.3% for larvae, and 98.5% for pupae. However, after the first run of the model it was apparent that considerable lacewing larval mortality coincided with the rapid decline in aphid number. In order to account for this a mortality (SURVIVE) was incorporated into the model, which linked larval survival to the ratio of aphids to lacewing larvae.

The relationship between survival and the availability of food is likely to be complex and to differ for each instar. Because little was known about this relationship it was necessary to assume parameter values intuitively and then to observe the influence that changing their values had on the model output. SURVIVE was initially calculated as the number of aphids, divided by ten times the number of lacewing larvae, with the constraints that SURVIVE could not be greater than 1.0 (survival cannot be greater than 100%) or less than 0.2. This formula assumes that for each step of the model 10 or more aphids for each lacewing larva is sufficient for 100% survival. While this is clearly an oversimplification (third instar larvae eat many more aphids than first instars) it serves

as an indicator of the availability of food. As the number of aphids available to each larva falls below ten, larvae begin to die due to lack of food, down to a minimum survival of 20%. This 20% minimum survival makes allowance for the presence of alternative food supplies and for cannibalism.

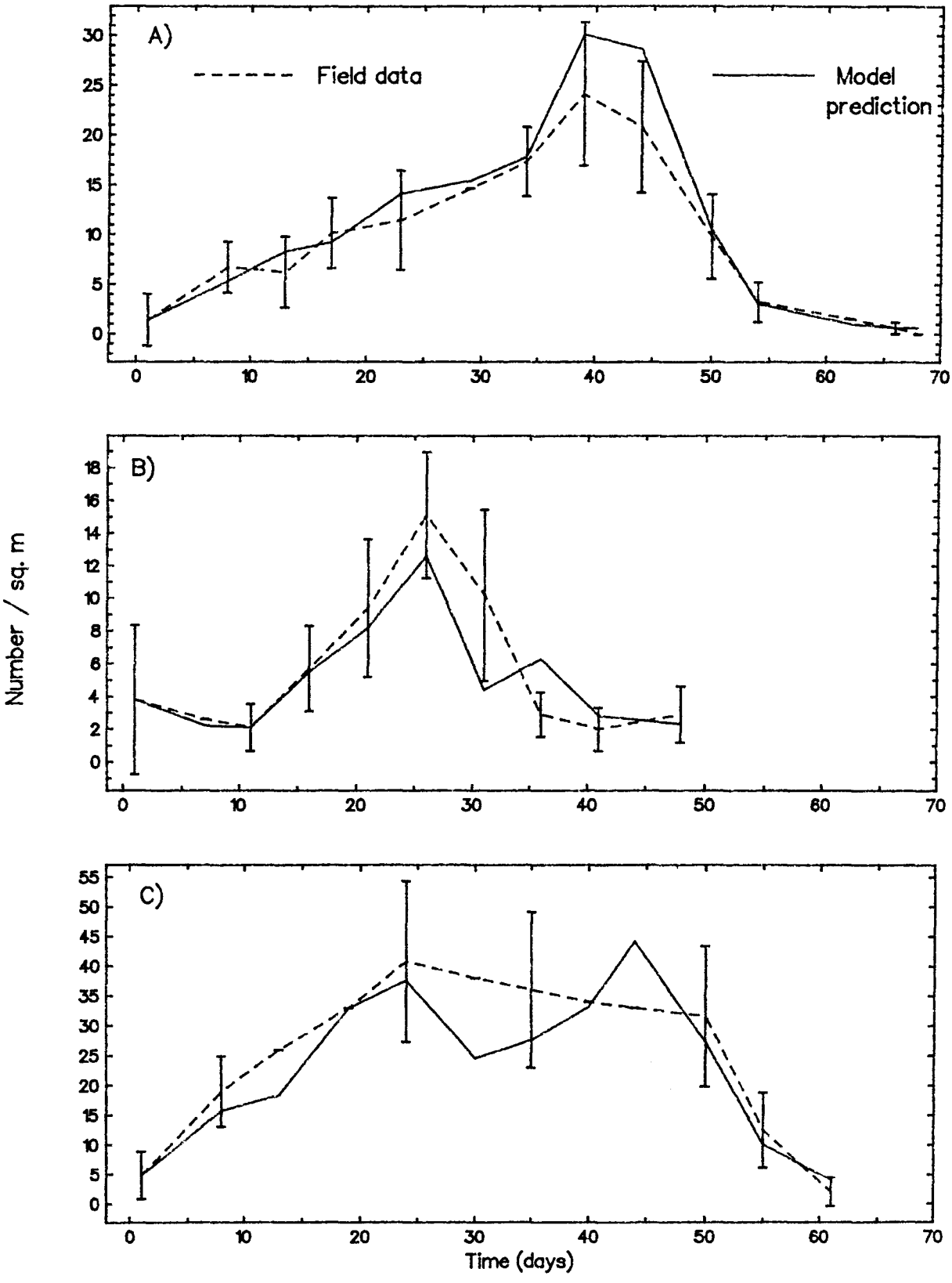
When the model was run with different values for these parameters it was found that model output was relatively insensitive to changes in the aphid:lacewing ratio but sensitive to changes in minimum survival. The insensitivity to predator:prey ratio reflects the rapid decline of the aphid population in the field from a situation of prey abundance for the predators, to one of prey scarcity. SURVIVE therefore changes rapidly from maximum to minimum survival values regardless of the predator:prey ratio used. The rate of decline of the lacewing larval population was therefore determined largely by the minimum survival value and hence the model's sensitivity to changes in its value. The best fit of the model to the field data was given by amending the model to incorporate a double step down to the minimum survival value. In the spring 1985 run an initial 40% survival, followed at the next step by a 10% minimum survival gave the best fit to the field data. In spring 1986 values of 70% followed by 40% were best, while in the autumn '86 run the aphid decline was too late to have any significant effect. This delayed decline to low survival is logical, as it must be expected to take some time to deplete all the available food sources. The difference in rate of decline between years may have been due to the presence, in the spring of 1985, of a considerable (25 m^{-2}) population of ladybird larvae. This would have produced more intense competition for food, and possibly deaths through predation, resulting in a more rapid decline in lacewing numbers.

Larval Density

With one exception, the model incorporating only background mortality and mortality linked to food supply, successfully predicted field population densities for third instar larvae (Fig.5-10). It was necessary to impose a 70% larval mortality at the second step (day 11) in the autumn 1986 run in order to make the model fit the field data. Although this mortality coincided with a period of adverse weather conditions (high winds and rainfall, low temperatures), other periods of bad weather which occurred had no noticeable effect on larval mortality. It is not clear why this very large mortality occurred. Lacewings are known to suffer from virus attack (Hilson, 1964; Leathwick, unpublished data) and it is possible that high humidity initiated an outbreak of virus disease. However, no diseased larvae were recorded in the field samples. Alternatively, the larvae may have been affected by some combination of climatic factors not immediately apparent from the meteorological data.

Fig. 5-10: Comparison of predicted and observed densities of third instar <u>Micromus tasmaniae</u> larvae at site R.21. Error bars are 95% confidence intervals for the means.

A) Spring 1985
B) Autumn 1986
C) Spring 1986



Because field sampling underestimated the number of first and second instar larvae, better estimates of the true larval densities are given by the model. Also, the model is able to convert these densities into the actual number of lacewings passing through each stadium over a given period of time (Table 5-1).

Adults

Predicting field densities of adult lacewings is more difficult, as the model predicts only the number of new generation adults passing through from the egg and larval stages.

TABLE 5-1: The highest observed densities of *Micromus tasmaniae* at site R.21 during 1985-86, along with the maximum predicted larval densities and the predicted number of individuals passing through the larval and adult stages prior to the lucerne being mown.

	highest density observed	highest density predicted	predicted number passing through
Larvae			
Spring 85	36	85	134
Autumn 86	28	26	49
Spring 86	58	118	296
Adults			
Spring 85	69	*	89
Autumn 86	3	*	6
Spring 86	103	*	163

* Predicted adult densities are unrealistic due to the non-inclusion of flights in the model.

The effect of the lacewing parasite, *Anacharis zealandica*, which oviposits in larvae and emerges from the pupae, needed to be considered when comparing observed and predicted adult densities. The percentage of field-collected larvae producing parasites was 2.8% in spring 1985, 86% in autumn 1986 and 11.8% in spring 1986. These values were incorporated into the model as the variable MORT, and at each step the number of pupae passing to the adult stage was adjusted accordingly.

The model output gives the total number of adults produced from larvae, up to the point when the lucerne was harvested (Table 5-1). At the time of harvest considerable numbers of pupae were present in the soil, but as the effect of crop harvest on microclimates within the lucerne field can be extreme (Pinter *et al.*, 1975), survival of these pupae is doubtful. Any adults which emerged after mowing, would in the absence of aphids for food, probably have emigrated.

A comparison of adult lacewing densities predicted by the model and sampled in the field is given in Fig.5-11a. Although the model is as yet unable to predict lacewing numbers with accuracy it is reasonable to suggest two things about lacewing bionomics. Firstly, in spring of both years large populations of adult lacewings occurred, and the model tells us that these can be accounted for as the product of recruitment, immigration is not required to explain the observed densities. Secondly, parasitism has a major effect on autumn adult numbers, preventing them from reaching spring levels (Fig.5-11). This also suggests a significant lack of autumn immigration.

Independent evidence for limited immigration is provided by the flight trap catches (Fig.5-11b). In both the spring runs catches of lacewings during the early stages were low, and although numbers built up during the later half (coinciding with the build up in number of adults) the flight orientation indicated a predominance of lacewings leaving the field. These lacewing flights coincided with the divergence of the model and field data shown in Fig.5-11, when the number of adults in the field declined. This occurred soon after the aphid populations had declined which suggests that food availability was probably the trigger for the lacewings to leave. A linear relationship between the number of lacewings caught on the flight traps and the $\log_e$ of aphid density within the plot (Fig.5-12) supports this view.

Interpretation of the autumn 1986 data is more difficult, largely because of the low number of adults present, which in turn is a result of the high level of parasitism. At first the trend appears similar to the two spring populations except that there is not the pronounced movement of lacewings out of the plot (fig.5-11b), nor is there any clear relationship between flights and aphid

Fig. 5-11a: Predicted and observed densities of adult Micromus tasmaniae at site R.21.

A) Spring 1985
B) Autumn 1986
C) Spring 1986

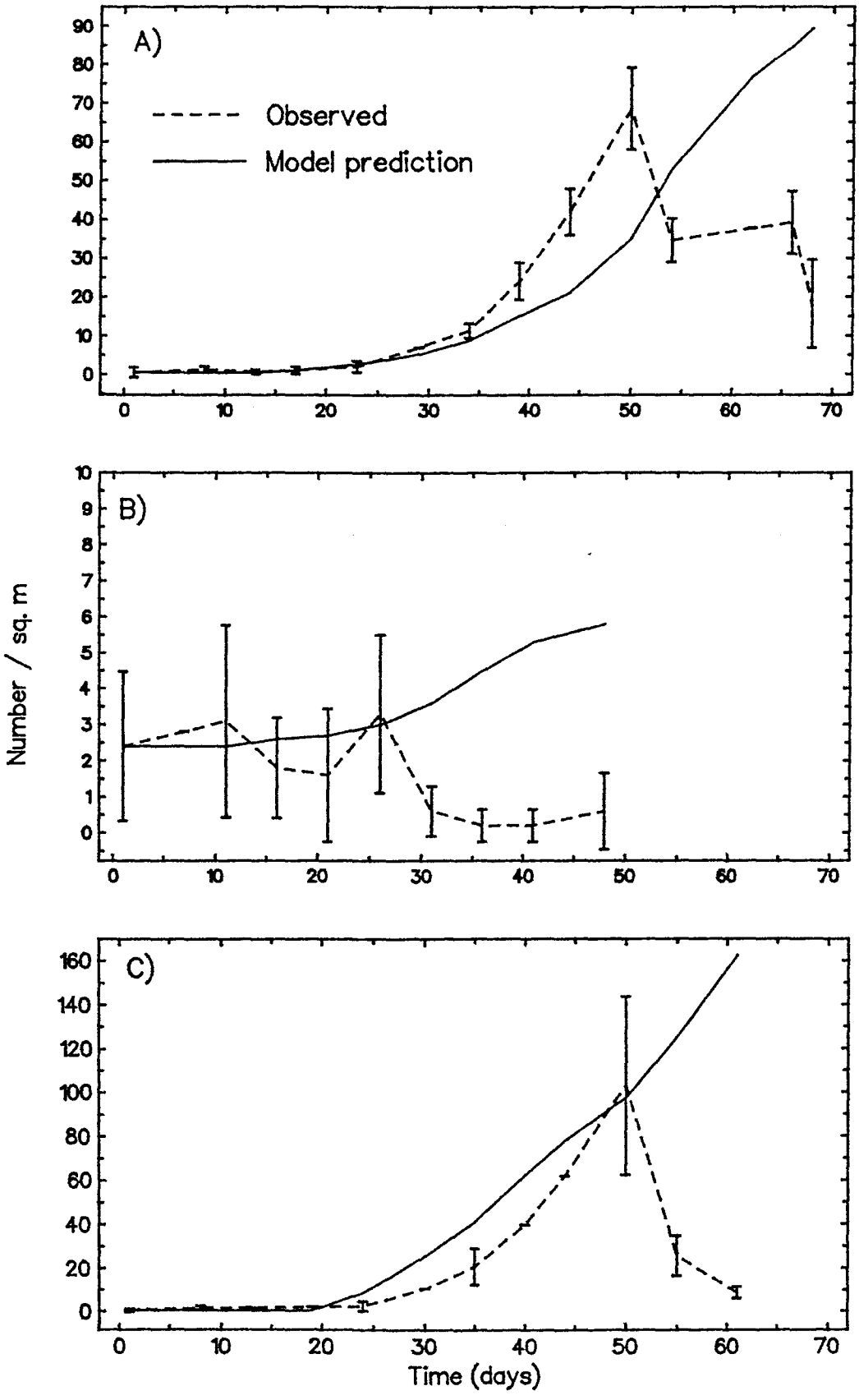


Fig. 5-11b: Number of adult Micromus tasmaniae sampled from within the lucerne, and caught on flight traps around the perimeter, at site R.21

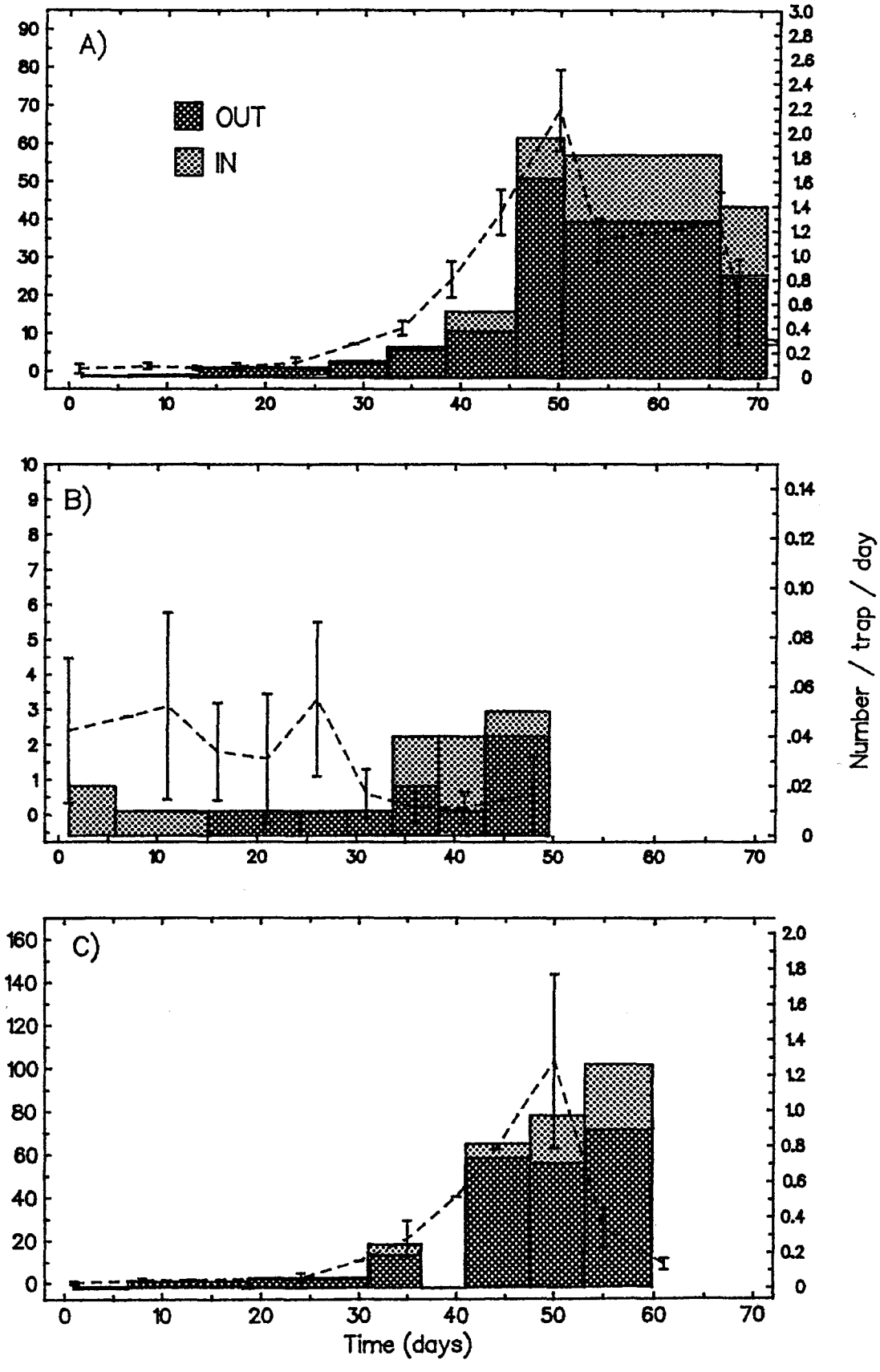
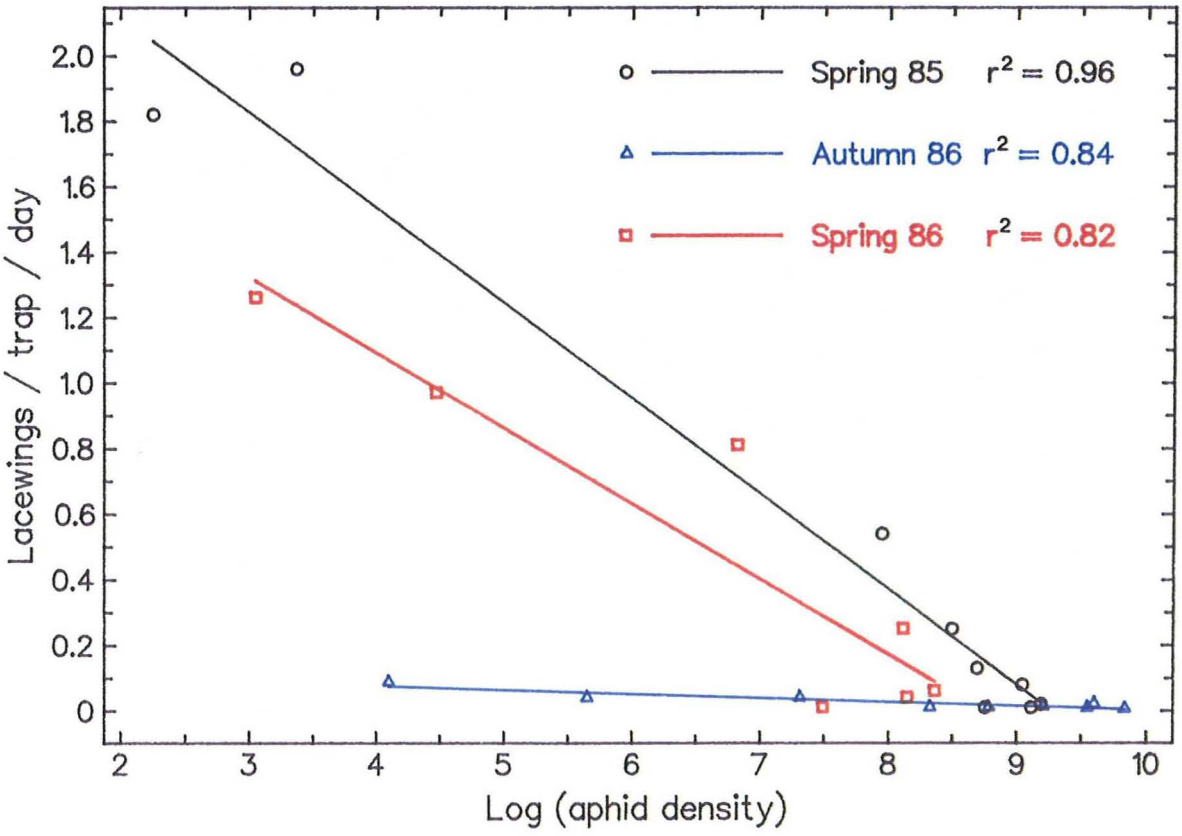


Fig. 5-12: Number of Micromus tasmaniae caught on flight traps plotted against log of aphid density in the plot, at site R.21



density (that is the slope of the regression line in Fig.5-12 is close to zero). This problem is discussed further below.

A picture emerges then of a small initial population of lacewing adults, producing large numbers of offspring, which in the absence of significant parasitism, gives rise to large numbers of new generation adults. In the absence of sufficient food these adults emigrate and are lost to the system. However, there is still a problem in predicting correct adult densities in the field.

Tuning the model

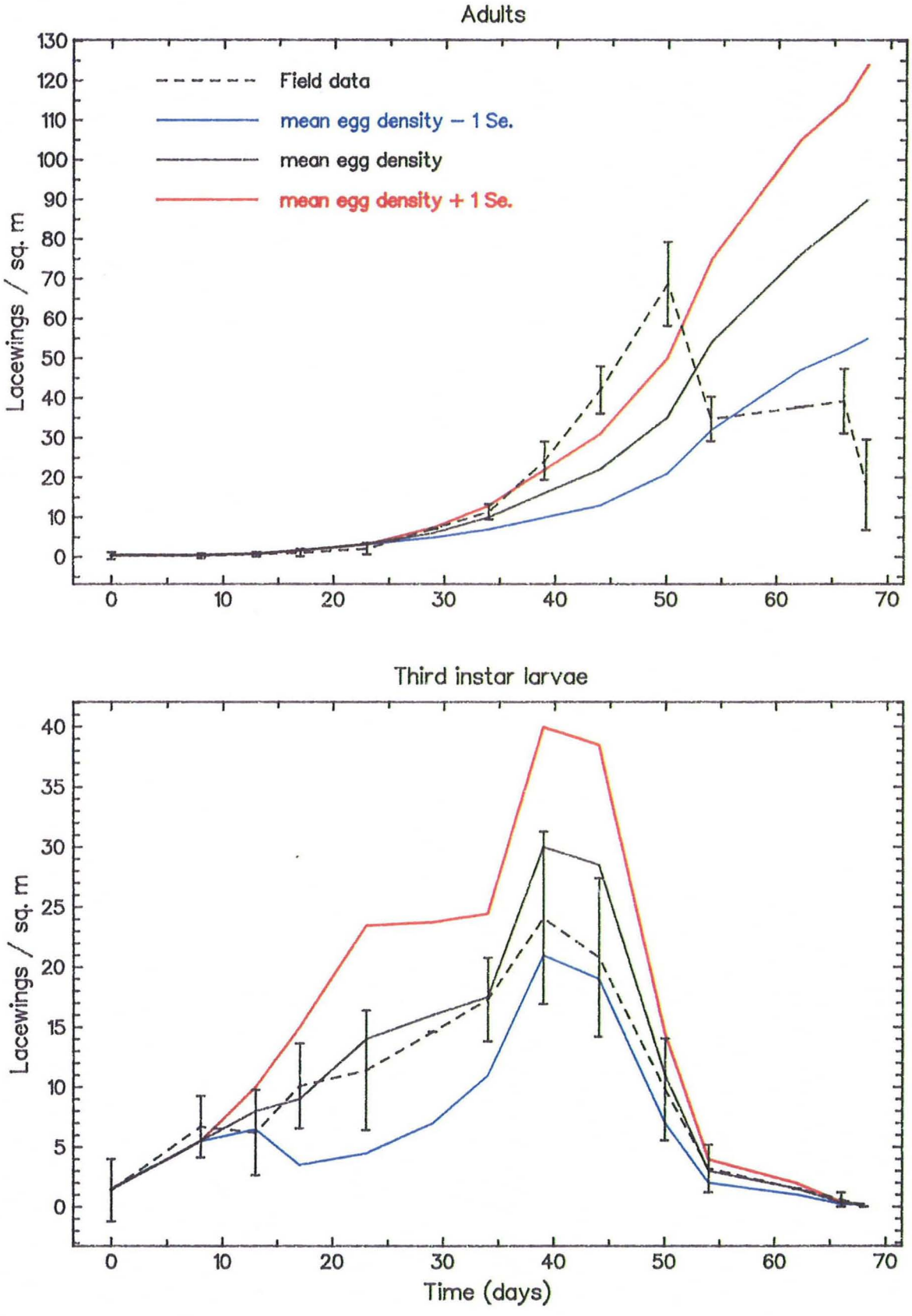
The correlation between lacewing emigration and aphid density (Fig.5-12) should enable the model to be modified to predict lacewing flights on the basis of aphid density. Attempts to do so using a predator:prey ratio similar to that used earlier to estimate larval survival, gave poor results for both the spring '85 and autumn '86 populations. A more detailed investigation of the factors affecting model output was therefore called for.

In the spring '85 run the timing of the decline was correct, the problem being rather that the model lagged behind the field data and hence the flights occurred before the model prediction had reached the peak numbers observed in the field. Three factors were identified as potentially contributing to this discrepancy in timing;

1. accuracy of egg density estimates
2. temperature
3. initial pupal population

Measuring egg density in the field was logistically difficult because of the large amounts of vegetation which had to be carefully searched. Sample size was therefore limited by the time necessary to search even a relatively small sample. Consequently, at low egg densities sample size was often smaller than desirable, resulting in large standard errors for the means (the average standard error was 51% the value of the mean). To test the sensitivity of model output to variation in egg density, the model was run on egg density values plus or minus one standard error from the mean. The resulting outputs (Fig.5-13) show that although a strong bias in egg density estimates was capable of improving the prediction for adult number, in doing so it overestimated the density of third instar larvae. It is unlikely, therefore, that any inaccuracy in estimating egg density was contributing significantly to the observed delay in predicted adult emergence.

Fig. 5-13: Sensitivity of model output to variation in egg density estimates. The model was run on values of plus or minus 1 Se. of the mean. Error bars are 95% confidence intervals for the means.



Because initial third instar larval densities were low (Fig.5-10) initial pupal densities were assumed to be zero; pupae were not sampled in the field (Chapter 2). A small number of pupae may have been present at the start of each run and, therefore, adult densities may have been underestimated. It is unlikely, however, given the low lacewing populations present at the beginning of each run, that significant numbers of pupae were present.

An analysis of the field temperature data (Fig.5-14) indicates that in the first two runs more time was spent at temperatures in the non linear part of the development rate curve (Chapter 4) than in the third run. In the spring '85 run there was twice as much time below $8^{o}C$, and three times as long below $4.5^{o}C$, than in the spring '86 run. It would be expected then (see Chapter 4) that the first run would predict a slower rate of development, relative to the field population, than would the third run, and this is what was observed (Fig.5-11).

The model was therefore run with reduced threshold temperatures, to compensate for the time spent at temperatures outside the linear range. The output for spring '85 was advanced and flight prediction on the basis of the aphid:lacewing ratio improved (Fig.5-15). However, prediction was not good and outputs for the other runs was also advanced. Therefore, although the model can predict the number of adults produced it cannot accurately predict the timing of emergence. This is probably due to the inability of day-degree models to accurately predict development at temperatures outside the linear portion of the development-rate curve (Chapter 4).

The problem with the autumn '86 run was different, in that the observed decline in the field data did not coincide with the depletion in available aphid food, nor was there any indication from the flight trap data that the decline was due to lacewings leaving the field. Interpretation of this data is made difficult by the low number of individuals involved, i.e., the observed decline in adult numbers from a mean of 3.3 m^{-2} to 0.6 m^{-2} might simply reflect a decrease in sampling efficiency with increasing crop height. However, this explanation would not account for the non-appearance of newly emerged adults which the model indicates should occur. The model could only be made to fit the field data by increasing the mortality due to parasitism (from 86% to 95%) and by incurring an 85% mortality on adults and pupae at day 31. No immediate explanation for this mortality is apparent.

A combination of background mortality, starvation, parasitism and emigration is sufficient to explain most of the observed changes in lacewing numbers. The model does not, however, predict with accuracy the timing of adult lacewing emergence in the field, and although it identifies several instances where high mortalities are apparent it cannot establish any likely cause.

Fig. 5-14: The proportions of total time which field temperatures spent below, within or above the linear region of the development-rate curve. (8-25°C approximates the linear region)

A) Spring 1985
B) Autumn 1986
C) Spring 1986

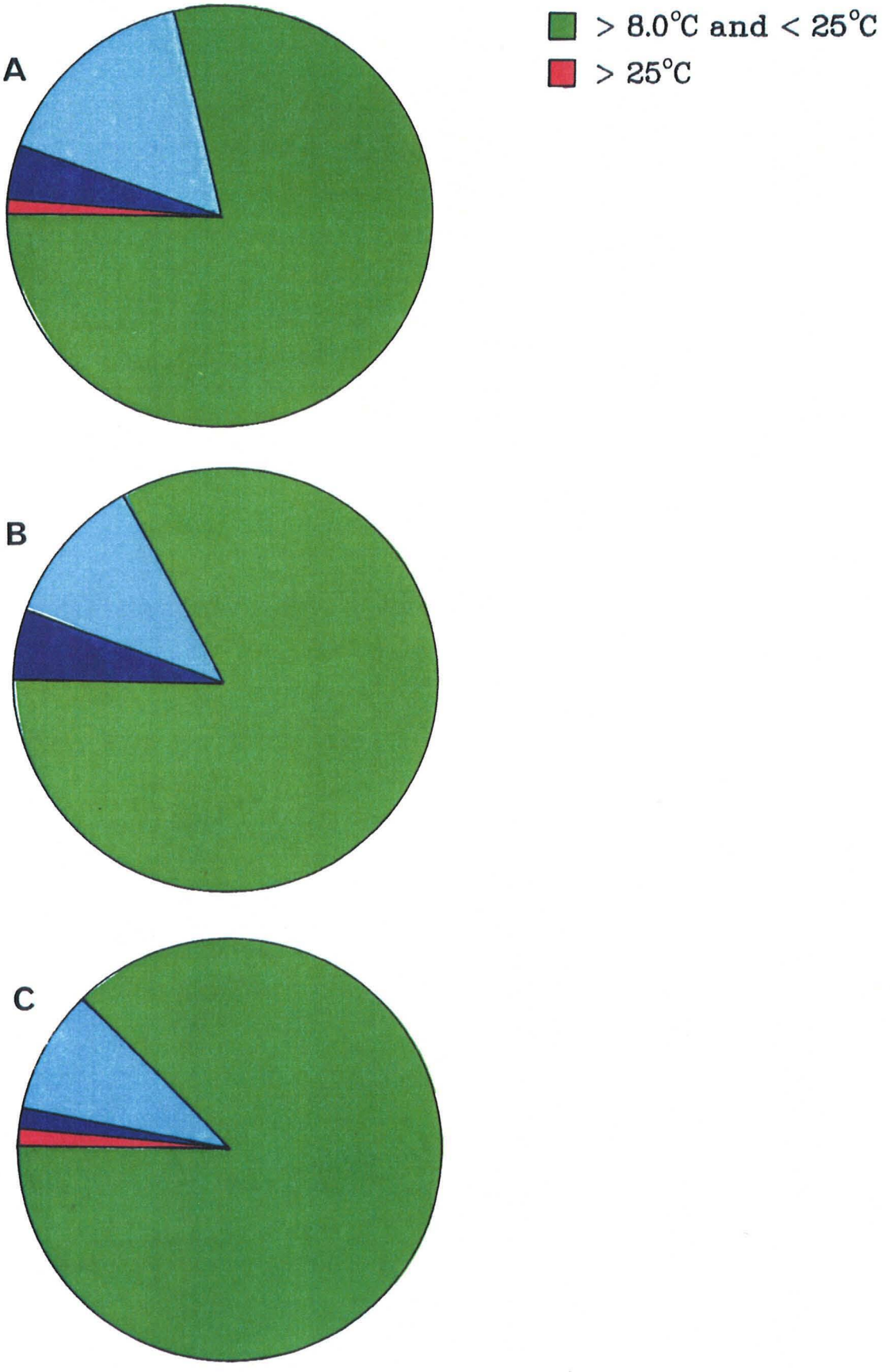
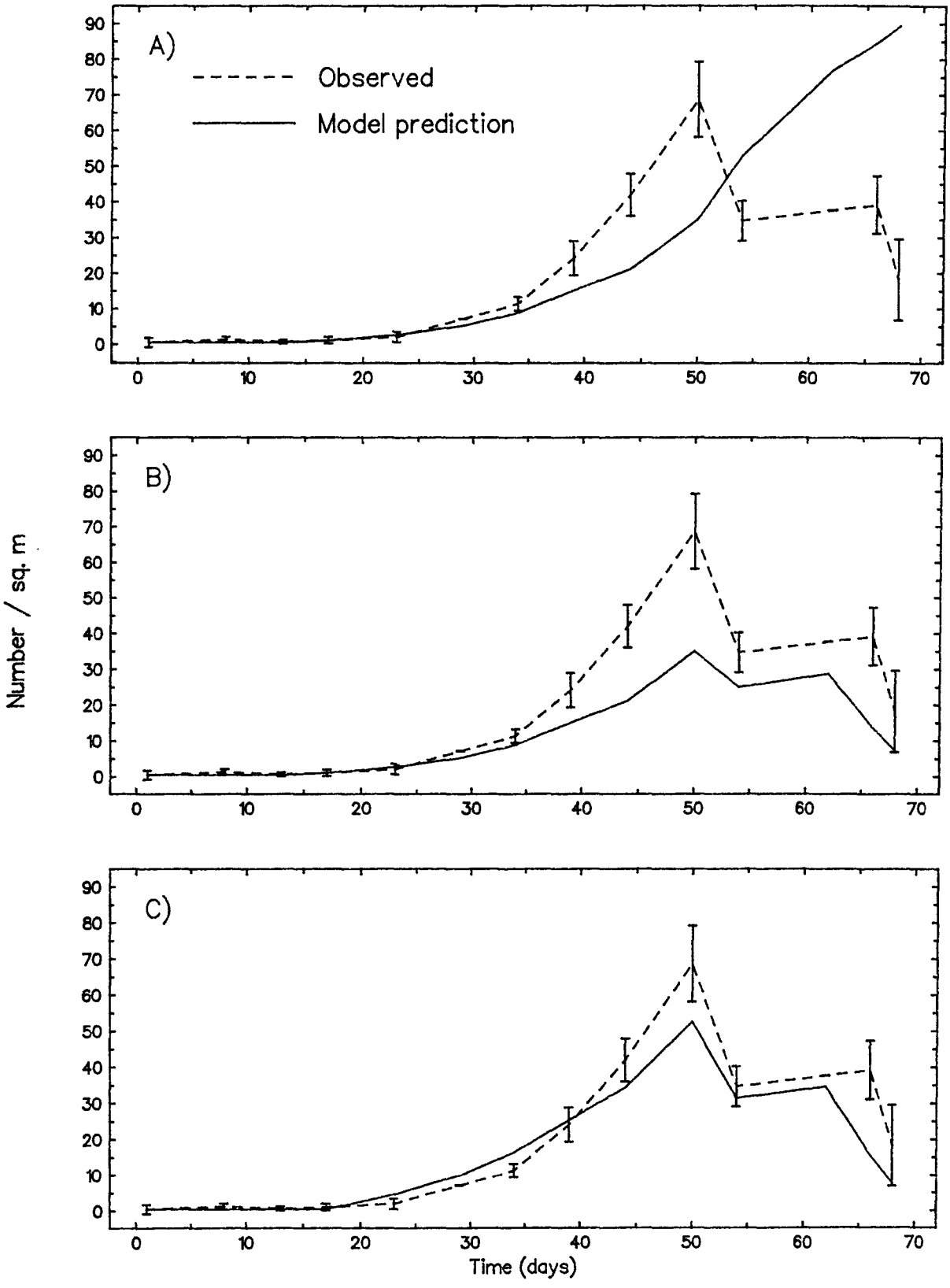


Fig. 5-15: Tuning the model

A) Observed and predicted densities for adult M. tasmaniae before flights were built into the model. spring 1985

B) Flights incorporated into the model. Discrepancies due to errors in timing.

C) Flights incorporated into the tuned model.



DISCUSSION

There are a number of different kinds of computer model (Barlow, 1983) and their functions are easily confused. Also, as with all modelling, there is the question of how to validate a model, and hence the conclusions drawn from it. The model used in this work falls into the category of a simulation, or time-varying life table (Gilbert *et al.*, 1976). Its function is not predictive, but rather is to enable a better understanding of the population dynamics of the species being studied (Getz and Gutierrez, 1982). By repeatedly sampling field populations, and then attempting to reproduce these populations in a model, where each component must be based on sound biological data, the modeller moves away from studying population statistics to an investigation of true population dynamics, and the underlying mechanisms of population change (Gilbert *et al.*, 1976).

The standard procedure for producing such a model, is to begin with a simple model and gradually modify it until it fulfills its function. The level of complexity a model must attain is determined by its objectives, and any extra detail beyond this point is unnecessary. The initial model should be biologically sound, and any changes to the structure of the model should be based on sound biological data (Berryman and Pienaar, 1974).

This lacewing model used a relationship between development and temperature, established independently under near field temperatures, to predict lacewing development in the field. The base line for both the real and simulated populations was the density of eggs present in the field, which makes each run of the model site specific. Although this nullifies the models predictive capability, it greatly increases its accuracy, by avoiding the problem of having to estimate oviposition rates in the field, which is often difficult (Gilbert *et al.*, 1976). The initial model then, is quite simple and robust.

Modifications to the model were made on the basis of independently obtained data (background mortality and parasitism), or logical deduction (availability of food). The logical deduction came about through the ability of the modelling approach to identify areas which are important to the population dynamics of the animal being studied. For example, it is obvious that a ready supply of food is vital to any growing population, but to study the relationship between food supply and population decline in the laboratory, or in the field, would be a complex task. The model indicated that the availability of aphids was a major cause of lacewing mortality in the larval stages, and initiated migratory flights by the adults.

The need to invoke additional mortalities in autumn 1986 highlights the inadequacies in our basic knowledge of lacewing biology. As Gilbert *et al.* (1976) point out, one of the most useful features of any modelling attempt is 'to discover why the model gives the wrong answer'. A model's inability to 'give the right answer' does not invalidate the model, but rather highlights the inadequacies in the knowledge about that species or relationship.

The present modelling exercise has identified a number of important factors pertaining to lacewing bionomics. The bias in the sampling method, so evident from a comparison of model output and field data, could not have been detected from the sampling data alone. Similarly, although sampling a population indicates population density it does not tell the observer how many individuals are actually produced. Previous work in New Zealand on lucerne aphids and their natural enemies has produced statistics of numbers over time, which considering the likely sampling bias and short larval development time, has probably considerably underestimated the true number of lacewings present.

The use in the model of the percentage parasitism figures collected in the field, gives a check on their validity. If the percentage parasitism figures were significantly out in estimating the parasite's impact on the lacewing population, then it should not be possible for the model to predict the field population. *A. zealandica* does not significantly inhibit lacewing population growth early in the season, but its effect in the autumn can be severe. This is contrary to the views of Hilson (1964) who claimed that this parasite was unlikely to be important in lacewing biology. Hilson also claimed that *A. zealandica* would only oviposit in third instar larvae, while in the present study parasites were reared from both first and second instar larvae, as well as thirds.

Similarly, the high egg survival used in the model supports the laboratory finding (Chapter 6) that egg cannibalism is unlikely to influence population size in this species. Although egg cannibalism is important in coccinellids (Dixon, 1959) and chrysopids (Canard and Duelli, 1984), if it occurred to any extent in *M. tasmaniae* the model should have consistently overestimated lacewing density.

The modelling approach has helped explain the observed changes in lacewing numbers and has focused attention on several important discrepancies. *i.e.*, the bias in sampling, the overriding influence of the availability of food, and the potential for the lacewing parasite to decimate the emerging population. Perhaps the most significant conclusion from the modelling exercise is that the large populations of lacewing adults which occurred, could be accounted for entirely by reproductive recruitment. High adult densities built up quickly and the casual observer may have

attributed them largely to immigration, due to the 'apparently low' larval densities preceding. The model, however, indicates that immigration need not be involved and this is supported by the flight trap data.

The lacewings appear to be exploiting the aphid population to produce a large second generation. Under the present lucerne management system these newly emerged adults leave the field in search of food and a potentially valuable resource is lost to the farmer. There appears to be scope for a change in lucerne management in order to retain some of this lacewing population (see Chapter 7).

CHAPTER 6: Feeding, Oviposition and Cannibalism

INTRODUCTION

This chapter describes a series of laboratory experiments carried out to establish basic parameters relating to the biology of *Micromus tasmaniae* and its role as an aphid predator.

METHODS AND RESULTS

Lacewing voracity

Patterns of growth and prey consumption

Preliminary feeding experiments involving lacewing larvae produced wide variation in the number of aphids consumed. Following the pattern of larval development from eclosion to pupation revealed that feeding rate, and larval weight gain, differed within each instar (Fig.6-1). Before passing to the next stadium larvae pass through a non-feeding phase, with an associated loss of body weight. A larva may thus feed voraciously one day and ignore all offers of food the next. Attempts to measure prey consumption by larvae can therefore be reliable only on the basis of the number consumed per instar.

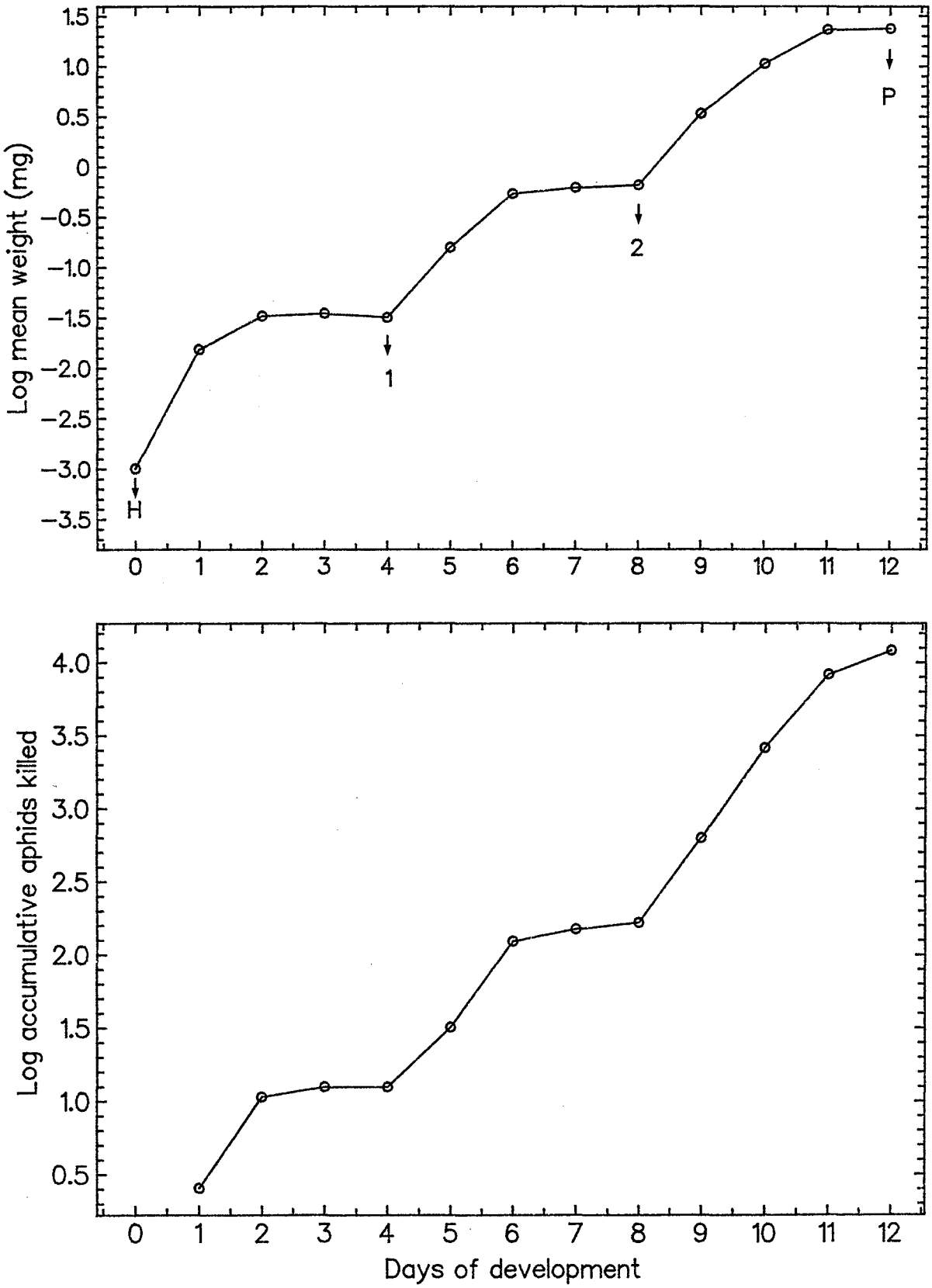
Experiment 1: prey size choice

The aim of this experiment was to determine whether *M. tasmaniae* shows preferences for feeding on different sizes of aphids.

Lacewings were reared individually in plastic petri dishes, at 15^{o}C ($\pm$1^{o}C), and presented with equal numbers of the four pea aphid (*Acyrthosiphon pisum*) instars. Fresh aphids were supplied daily and the number of aphids of each instar eaten was recorded. Larvae were reared from egg hatch to pupation and adults for a five day period.

The proportion which each aphid instar contributed to the total number of aphids eaten (Table 6-1) indicates a preference for small aphids by all lacewing stages. Such size preference generally reflects a predator's ability to capture different sizes of prey (Maelzer, 1978). Lacewing larvae are quick to recognize and attack their prey, probing and inserting the mouthparts to secure their victim, and anchoring themselves against a struggle with the tip of the abdomen. Larvae will

FIG. 6-1: Pattern of growth and number of prey killed for Micromus tasmaniae larvae at 15°C. Arrows indicate times of hatch, first and second moult, and pupation.



attack aphids many times their own weight. Adults, however, seldom attempt to hold their prey, simply walking up to an aphid and starting to eat, usually from the abdomen. Aphids frequently attempt to walk away, with the lacewing following behind, and in the laboratory it is not uncommon to find larger aphids (third instar pea aphids or larger) with wounds on the dorsal surface of the abdomen, presumably having escaped from adult lacewings.

This difference in method of prey capture is reflected in the prey size choice shown by adults and larvae. Even first instar larvae weighing less than 0.3 mg are better able to capture and subdue third instar pea aphids, than are adults, which can weigh up to 7.0 mg.

TABLE 6-1: Feeding preference shown by *Micromus tasmaniae* for different sizes of pea aphid. Data are percentage of aphids of each instar killed. All instars were present in equal numbers. If no size preference would expect 25% of each aphid instar to be eaten.

	Aphid instar			
	1	2	3	4
Mean aphid weight ± (sd) mg	0.12 (0.023)	0.27 (0.052)	0.51 (0.114)	1.14 (0.2733)
Lacewing Stadium	% of total aphids killed			
Adult				
Female	73.9	26.1	0	0
Male	90.5	9.5	0	0
Larvae				
First instar	81.6	10.5	7.9	0
Second instar	53.7	33.3	11.1	1.9
Third instar	35.8	35.5	22.3	6.4

Experiment 2: number of prey consumed

The aim of this experiment was to establish how many aphids of each aphid instar *M. tasmaniae* would eat.

Lacewings were reared individually in plastic petri dishes at 15°C (± 1°C) and fed one pea aphid instar only. First, second and third instar larvae were presented with aphids at densities of 5, 10 and 40 per dish respectively. Aphids were replaced daily for the full larval duration. Adults were fed 40 fresh aphids each day for 10 days. Only those aphid instars which were eaten in the prey size choice experiment were presented.

The number of aphids of each instar eaten by each lacewing stadium is given in Fig.6-2. Third instar larvae ate the most aphids consuming on average 85% of the total aphids eaten by the three larval instars (the first and second instars consumed 5% and 10% respectively). Female third instar larvae were significantly heavier than males prior to pupation (4.56 mg vs 3.46 mg; t-test, $P < 0.01$). When fed on first instar pea aphids female third instar larvae ate a significantly higher number than males (81.2 vs 64.8; t-test $P < 0.05$). However, when fed on second instar pea aphids the difference in the number of aphids eaten was not significant (38.9 vs 32.6; t-test, $P > 0.05$). This anomaly may be explained by the proportion consumed of each aphid attacked, because when the weight of aphid remains was taken into account, female third instar larvae had consumed a significantly greater wet weight of aphids than the males (13.3 mg vs 10.9 mg; t-test, $P < 0.05$).

Female lacewings are larger than males, which must reflect a greater biomass of food eaten and/or a greater efficiency at converting prey into lacewing biomass. These data suggest that females do acquire a greater biomass of prey through a tendency to attack more prey and also to utilize a greater proportion of each prey attacked. However, because the difference in number of prey consumed is not clear cut, the data for male and female larvae was pooled in Fig.6-2.

Adult females ate more aphids than adult males, which is to be expected considering their greater size, and the metabolic demands of egg laying.

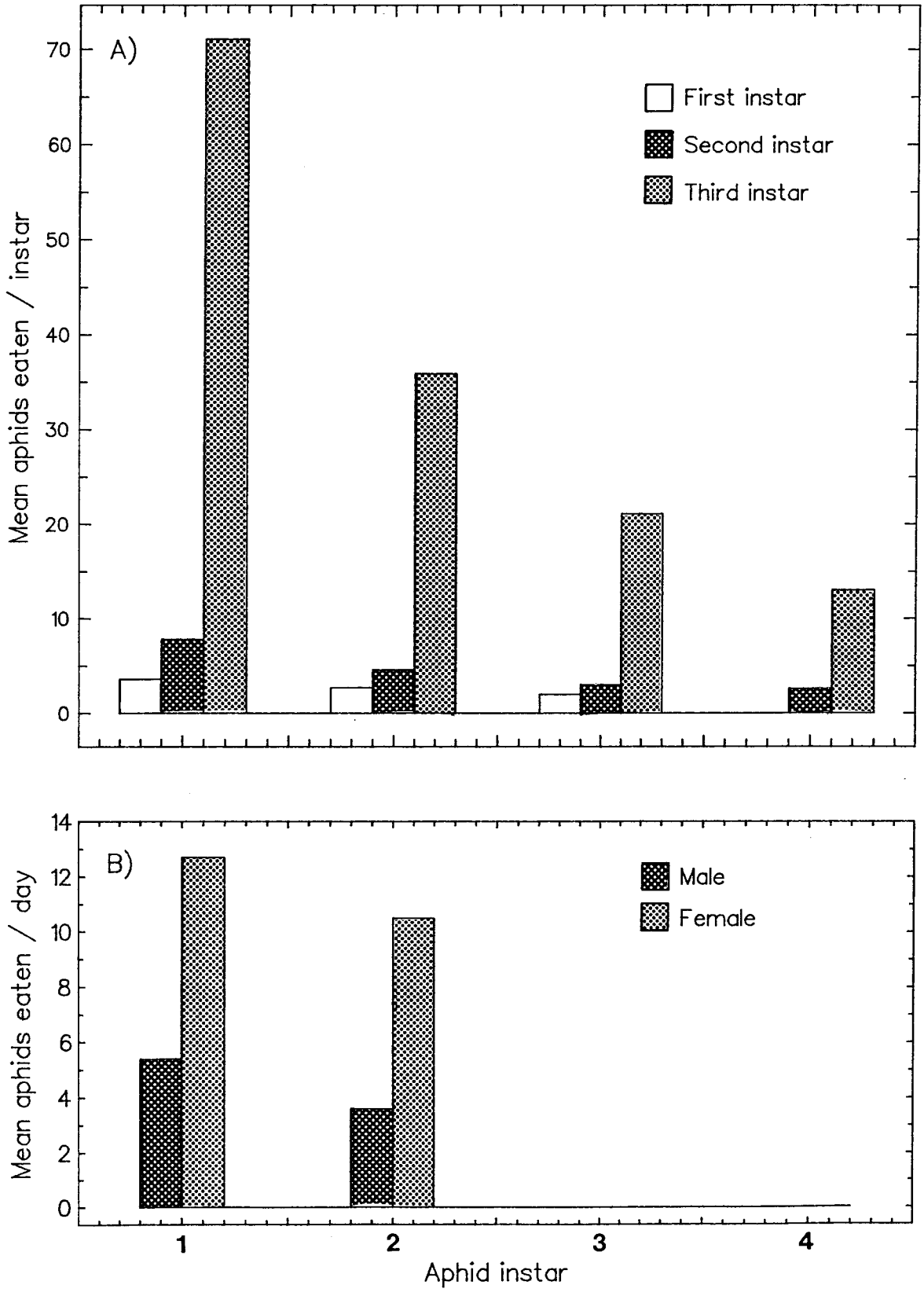
Adult longevity and oviposition

In order to establish the duration and pattern of egg laying, pairs of newly emerged male and female lacewings were reared in plastic petri dishes at 15°C until they died. An excess of pea

Fig. 6-2: Number of pea aphids of different instars eaten by <u>Micromus tasmaniae</u> at 15°C.

A) Larvae were presented with 5, 10, 40 aphids/day (instars 1–3) from hatch to pupation.

B) Adults were presented with 40 aphids/day for 10 days



aphids was supplied every two to three days and the number of eggs laid was recorded. Adults were weighed every two days initially, but less frequently after the onset of egg laying.

The mean length of the preoviposition period was 7.8 days and during this time female body weight doubled (Fig.6-3). The mean adult life span was 55 days for males (range 33-132) and 49 days for females (range 24-71) with total egg production averaging 474/female at an average of 11.5 eggs/day. The pattern of oviposition over the adult life span (Fig.6-3) shows a rapid rise to a rate of 12-16 eggs/day which declines only gradually until close to death.

Cannibalism

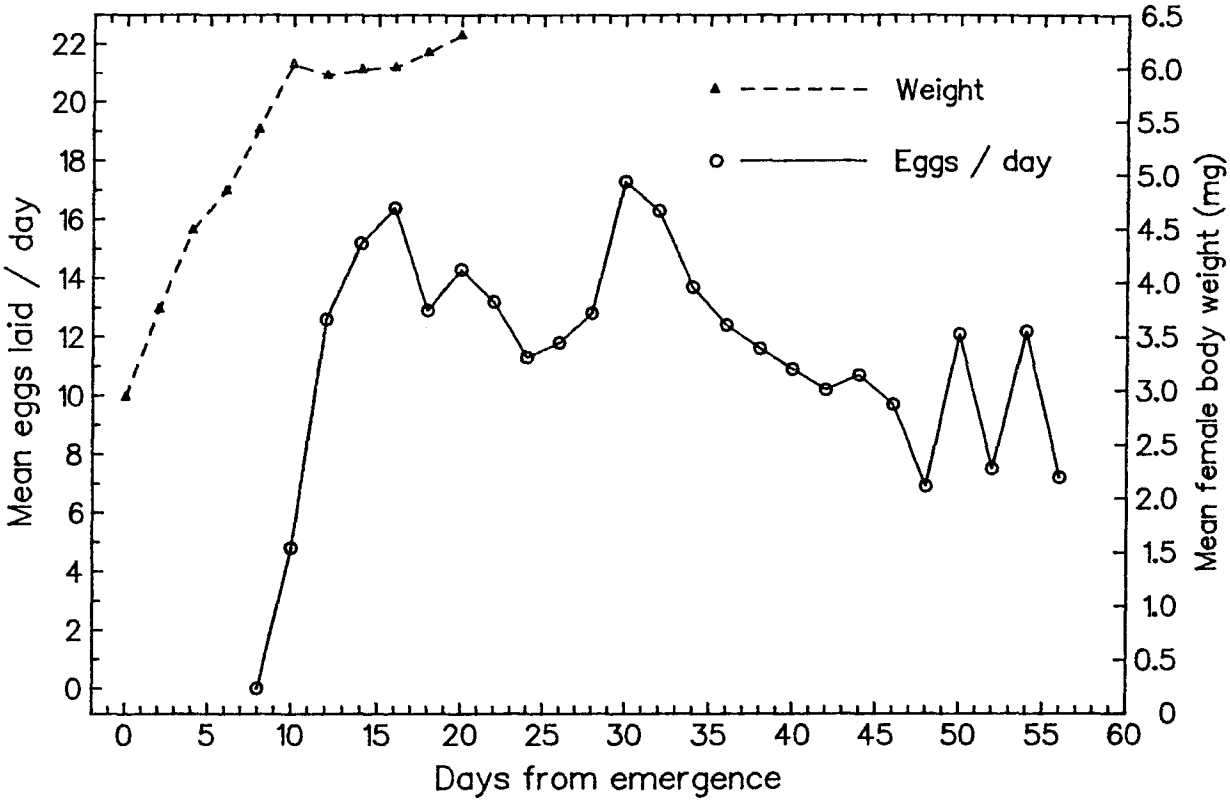
The aim of this experiment was to assess the importance of cannibalism both in laboratory rearing and in the field. Given no other source of food *M. tasmaniae* larvae will suck conspecific eggs and larvae. However, this fact does little to explain the importance of cannibalism in the field, where other food sources are available, albeit sometimes at low densities. This experiment was therefore undertaken to gain some indication of the lacewings 'innate tendency' to eat conspecifics.

Adult female lacewings were kept in 60 x 25 mm plastic tubes, with an excess of pea aphids, for two to three days. After the females had been removed the number of eggs laid in each tube was recorded. The tubes were then searched once a day and all emergent larvae were removed and recorded. The number of larvae emerging, relative to the number of eggs in the tube (after allowing for non-viable eggs) was then used as an indicator of the number of eggs sucked by the newly emerged larvae.

These larvae were confined for up to 24 hours after eclosion, with no alternative source of food or moisture, at densities far in excess of those normally occurring in the field. If newly emerged larvae show any tendency to suck other eggs, then the number of larvae produced should be considerably lower than that expected from the number of eggs present. Moreover, egg cannibalism would be expected to increase with egg density, by virtue of the greater number of eggs encountered by the newly emerged larvae.

A similar procedure was used to investigate larval cannibalism. Larvae were reared at different densities, with an abundance of pea aphids for food, on the assumption that if larval cannibalism is to occur it will be more evident at high densities. As with the egg experiment the densities of larvae used were far in excess of those ever likely to occur in the field.

Fig. 6-3: Mean female body weight over the preoviposition period, and distribution of egg laying over the female life span. Nine females were reared from emergence to death at 15°C on a diet of pea aphids.



Data on egg viability and larval survivorship from a developmental rate experiment where each lacewing was reared separately (Chapter 4) were used to predict the number of eggs hatching and larvae pupating for each egg/larval density. A significant deviation from this expected relationship would indicate a mortality associated with the presence of other lacewings. In the absence of any evidence of disease, cannibalism would be the likely cause.

When the regression lines fitted to the experimental data were tested against the expected relationships (Fig.6-4) there were no significant differences in slope between the lines. There is therefore no evidence of significant egg cannibalism by emerging first instar larvae, or of larval cannibalism under the conditions of these experiments.

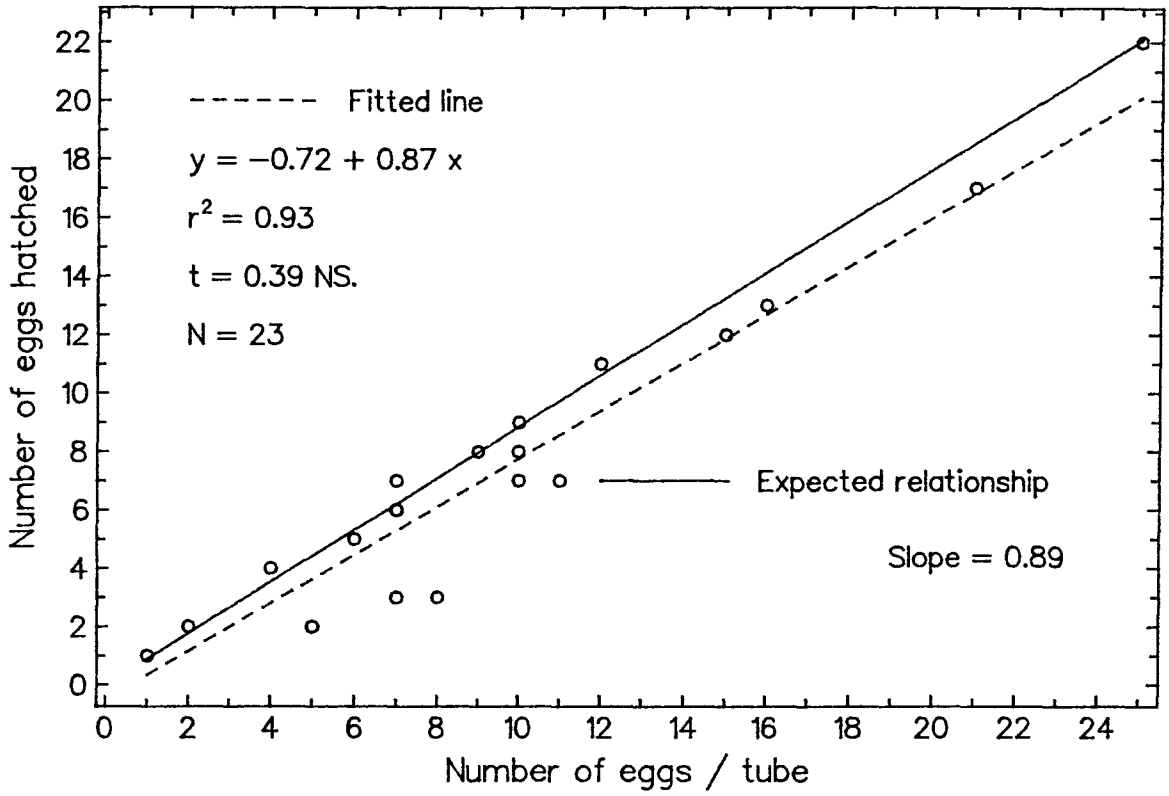
DISCUSSION

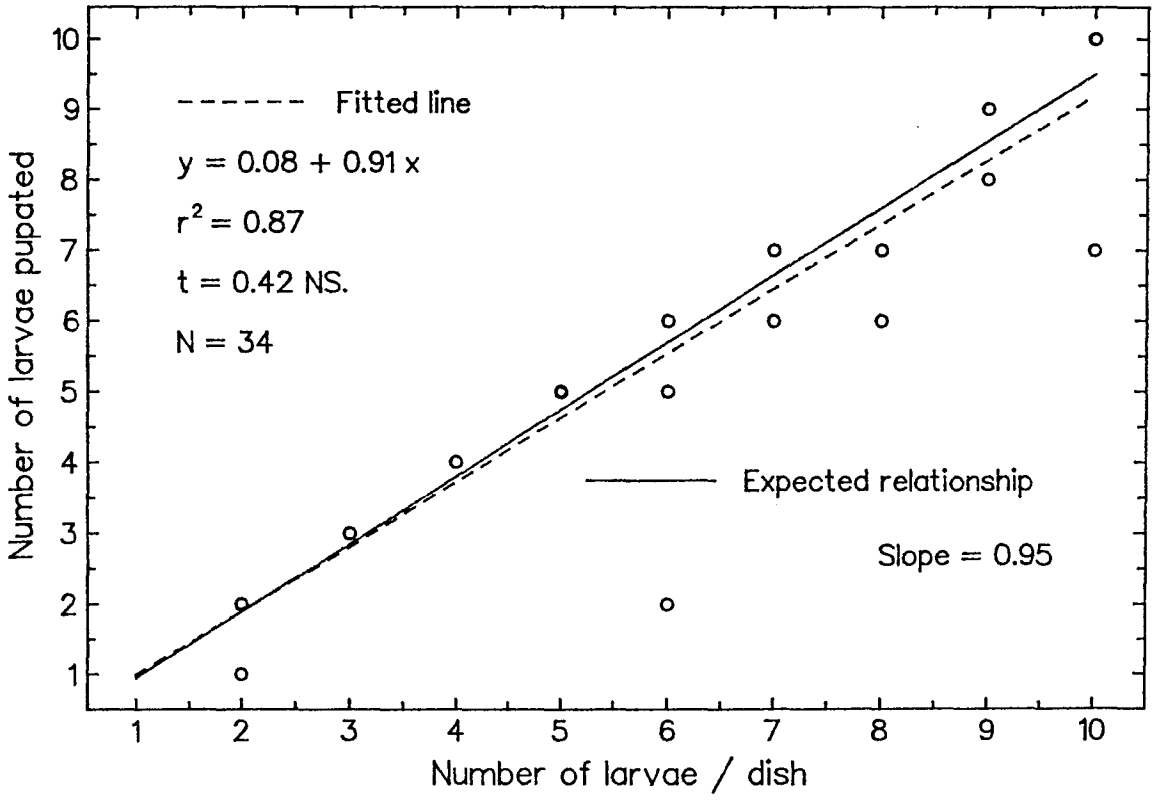
The implications of *M. tasmaniae's* preference for small prey are difficult to unravel. The best predator should be the one which removes the greatest number of aphids from the population and a strong preference for small aphids implies that more individuals will be eaten per gram of biomass consumed than if prey are chosen more at random. The prey size preference of different species should therefore be a useful parameter to consider when comparing predators.

For example, when the present prey size choice experiment was repeated with adult *Coccinella undecimpunctata*, they showed a smaller preference for small aphids than *M. tasmaniae* (aphids taken were 44% first instar, 24% second instar, 19% third instar, and 13% fourth instar, Leathwic publ.). Therefore, for each gram of aphids consumed *M. tasmaniae* adults would remove more aphids from the population than would the adult coccinellids. However, if a large proportion of small aphids will die anyway due to other causes, then eating them will have little influence on the size of the resulting aphid population. No real conclusions are possible without reference to the age-specific mortality schedule of the aphid population.

Dixon (1959, 1970) showed that survival of the coccinellids *Adalia bipunctata* and *Adalia decempunctata* was linked to the ability of the first instar larvae to catch aphids. Because they were able to catch only the smallest aphid nymphs, survival of the first instar larvae was linked to the density of first instar aphids, rather than that of the aphid population as a whole. A similar situation is reported for *Anthocoris nemorum* (Russel, 1970) where the first four instars are largely restricted to feeding on first instar aphids. Although first instar *M. tasmaniae* show a preference

Fig. 6-4: Regression of the number of eggs hatching against egg density, and the number of larvae pupating against larval density The expected relationship was calculated using data on egg viability and larval survival when M. tasmaniae were reared individually. t = test for differences in slope





for small aphids they are quite capable, in the laboratory at least, of capturing larger ones. This indicates an ability to survive at low prey densities by virtue of not being dependent on finding small aphids. M. tasmaniae adults also prefer smaller aphids, and yet when given no alternative, adults ate 4.7 late instar pea aphids per day (Leathwick and Winterbourn, 1984). Obviously there are difficulties associated with estimating field consumption rates from laboratory studies. Presenting different predator species with one prey size and type assumes that all species have the same prey preferences, which is most unlikely, and in the field the predator would have a choice of prey size and type.

Comparisons of feeding rate data from different workers must therefore be approached with caution. The rate at which a predator consumes prey may vary with prey size and species (Blackman, 1967), temperature (Hodek, 1957; Sundby, 1966), prey density (Holling, 1966), and the complexity of the experimental arena.

Data on consumption of lucerne aphids by predators in New Zealand are scarce, and give widely varying results. Feeding rates for adult *C. undecimpunctata* are estimated as 13-14 *Brevicoryne brassicae* per day at 29^{o}C and 6 per day at 16^{o}C (French, 1966); 30-32 *Acyrthosiphon kondoi* per day at an unstated temperature (Thomas, 1977); and 5.1 late instar pea aphids per day at 17-22^{o}C (Leathwick and Winterbourn, 1984). These differences in number of aphids consumed may reflect the different sizes of aphids used and the differing suitability of species as food for the beetles. *B. brassicae* has been shown to be less suitable than other aphid species as prey for many predators (Blackman, 1967; Leathwick, unpublished) which may result in reduced feeding rates (Blackman, 1967). Similarily the pea aphids used by Leathwick and Winterbourn (1984) were reared on beans (*Vicia faba*) which were not only larger than pea aphids reared on lucerne, but less suitable as food for *M. tasmaniae* (Chapter 4) and for *Nabis kinbergii* (Siddique and Chapman, 1987a). This may account for the low feeding rate for *N. kinbergii* (2.9 pea aphids per day) measured by Leathwick and Winterbourn (1984) compared to the figures of Siddique and Chapman (1987a) (9.0 pea aphids per day) for this nabid, and for *Nabis maoricus* (11 *A. kondoi* per day) by Henderson (1979).

The available New Zealand data suggests that *M. tasmaniae* has a relatively small appetite for aphids, certainly lower than the coccinellids, and possibly equal to the nabids only by virtue of its preference for small aphids. This is supported by overseas data (Simpson and Burkhardt, 1960; Sundby, 1966; Ting *et al.*, 1978; Principi and Canard, 1984) which shows many predators (especially the coccinellids) consuming much higher numbers of aphids than *M. tasmaniae* and other hemerobiids (Dunn, 1954; Neuencshwander *et al.*, 1975; Raychaudhuri *et al.*, 1981).

However, care is necessary when comparing consumption rates because all the Syrphidae and many Chrysopidae are predatory only in the larval stages. *M. tasmaniae*, as with all Hemerobiidae is predatory in both the larval and adult stages and the adult will consume more aphids than the larva by virtue of its longer feeding period. Therefore, although the larvae of many species are larger than the equivalent stage in *M. tasmaniae* and consume more aphids (Principi and Canard, 1984) the life time consumption of aphids by *M. tasmaniae* may in fact be greater (see Dunn, 1954).

As with feeding rates, oviposition and egg viability can be influenced by diet (Blackman, 1967; Siddique and Chapman, 1987a), making comparisons between authors difficult. However, the available data on *M. tasmaniae* (Hilson, 1964; Samson and Blood, 1979) and other hemerobiids (Miermont and Canard, 1975; Neuenschwander, 1975; Miller and Cave, 1987) all give similar results. Typically, a short preoviposition period (3-8 days) is followed by a long period of egg laying (2-5 months) with eggs of high fertility (85-95%) being laid at a rate of 10-20 per day. The short preoviposition period contributes to the overall short generation time of *M. tasmaniae*. At 15^{o}C the generation time (egg-egg) is 49 days (see Chapter 4), and at 23^{o}C is half that time. The short generation time and long period of egg laying account for the complete overlap in generations found in the field (Chapter 5), and in the absence of aestivation or hibernation ensures multiple generations each year (Hilson, (1964) estimated 6-7 generations per year in Canterbury).

In order to increase survival over the critical post eclosion period larvae of some species retain a remnant of the egg yolk sac (e.g., a few chrysopid species; New, 1975). Larvae of other species (e.g., coccinellids) spend a post eclosion period sitting on the egg batch where they frequently consume other eggs (Dixon, 1959; Maelzer, 1978). Although this is reputed to prolong the period available in which to find the first meal (Banks, 1956) there is some contrary evidence (Pienkowski, 1965). Few species of lacewing retain any egg yolk (New, 1975) but egg cannibalism is common amongst the chrysopids (Canard and Duelli, 1984). *M. tasmaniae* showed little tendency to suck eggs even at densities much higher than those in the field. Unlike many chrysopids which lay eggs in batches, *M. tasmaniae* lays its eggs singly, usually widely spaced over the vegetation. Newly emerged larvae therefore have neither the inclination, nor the opportunity, to suck conspecific eggs and so egg cannibalism is unlikely to be of any significance in this species.

New (1975) reported severe larval cannibalism in Australian species of Hemerobiidae, even when adequate food was available. Although *M. tasmaniae* is common in Australia, New's finding is contrary to the data presented here, and by Hilson (1964). Larvae of *M. tasmaniae* can be reared at above field densities with no losses due to cannibalism as long as food is supplied. It is hardly surprising that when starved they will resort to cannibalism.

Despite the difficulties of predicting field events from laboratory studies, a picture emerges of *M. tasmaniae* as a predator which is relatively small, both in size and in appetite, when compared with other aphidophagous groups. However, it may compensate for its lack of appetite by being predatory in both the larval and adult stages (cf. syrphids and some chrysopids), and by an ability to survive at low prey densities. The short generation time and multiple generations per year suggest a potential to respond numerically to changes in prey density.

CHAPTER 7: Discussion

This study on the ecology of *Micromus tasmaniae*, and its capability as an aphid predator, provides the opportunity to identify possible approaches to improving the biological control of aphids in lucerne crops. Determining the role of M. tasmaniae in the actual regulation of aphid populations was beyond the scope of this study (for reasons outlined below). However, given the present state of knowledge on predator-prey relationships it should be possible to make some value judgements on *M. tasmaniae's* potential as a biological control agent.

This chapter begins with a brief summary of the factors considered important in the regulation of population size, and worthy of consideration in the assessment of natural enemies. *M. tasmaniae* is then evaluated for its potential as an aphid predator, and factors limiting the biological suppression of lucerne aphid populations considered. Finally some possible strategies for enhancing aphid control are outlined.

The regulation of population density

Population density is the product of three variables: birth rate, death rate, and migration. Birth rate, although influenced by environmental factors (e.g., host plant physiology), is primarily a characteristic of the species, while the tendency to migrate is an interaction of environmental and species influences (Coppel and Mertins, 1977). Death rate, however, is primarily an environmental influence and it is by altering the death rate that natural enemies can influence the growth of their prey populations. Factors influencing death rate fall into one of three categories (Varley *et al.*, 1973; Coppel and Mertins, 1977).

1. Density dependent: i.e., agencies which destroy a larger proportion of the population as its abundance increases.
2. Density independent: i.e., catastrophic agencies such as weather, whose proportional effects are wholly independent of population size.
3. Inversely density dependent: i.e., agencies such as birds which destroy a fixed number of individuals regardless of their abundance so that as population size increases the proportion destroyed declines.

These three kinds of factors will interact, and all may play a role in population regulation.

On theoretical grounds a natural control mechanism must at some point include at least one element exhibiting density dependence (Murdoch, 1972; Hodek *et al.*, 1972; Readshaw, 1973; Coppel and Mertins, 1977). If a control agent does not destroy an increasing proportion of its prey as the prey population becomes larger, then the prey will escape the agent's ability to control it. A natural enemy acts in a truly density dependent manner only if it has a type III functional response (Murdoch, 1972; Hassell *et al.*, 1976) or exhibits an appropriate aggregative response (Beddington *et al.*, 1978). Most natural enemies, however, exhibit type II functional responses and so their ability to regulate populations is limited (Mills, 1981). In spite of this, there are numerous examples of natural enemies regulating prey populations (Hagen and van den Bosch, 1968; Huffaker and Kennett, 1969).

A density-dependent mechanism need not, however, be a single key factor (species). A collection of several factors (agencies or species) operating at different times may effect the same stabilisation of numbers (Huffaker *et al.*, 1971). A natural enemy complex may therefore be capable of suppressing a prey population by functioning in a density dependent manner, despite the fact that each species is limited in its ability to respond to increasing prey numbers. Such a mechanism may function through differences in the minimum prey threshold necessary to maintain a predator or parasite species in the field (Holling, 1961). At low prey densities only those species which require relatively few prey for survival and reproduction will be present. As prey density increases so the prey threshold necessary for the presence of other predator species is met and the number of predator species can increase. Consequently as prey density increases, natural enemy numbers increase and they exert increasing pressure on the prey population.

Such an interaction between natural enemies and their prey would account for the observed suppression of aphid populations by natural enemies (Wratten and Pearson, 1982; Chambers *et al.*, 1983; Milne and Bishop, 1987; Aalbersberg *et al.*, 1988), and also satisfy the theroretical need for density dependence. Although Murdoch (1972) has suggested other ways in which predators with type II functional responses may produce density dependent mortality in their prey, there is considerable evidence that the relationship discussed here does occur in the field (Holling, 1961; Gurney and Hussey, 1970; Tamaki and Weeks, 1972; Tamaki and Long, 1978; Ives, 1981). The evaluation of any single natural enemy species must therefore be considered in relation to the other parasite and predator species which occur in the same habitats.

Factors influencing the efficacy of natural enemies.

Although it is difficult to predict in advance which natural enemies will suppress pest populations, the factors considered important in natural enemy effectiveness fall under three broad headings (van Emden, 1966).

1. Voracity

Voracity, or number of prey eaten by a predator species, is a function of the appetite of the individual, the number of individuals present, the rate of multiplication of the species and its activity and searching behaviour (van Emden, 1966). The species which demonstrates the greatest individual appetite in the laboratory, is not necessarily the most voracious species in the field. The number of individuals present, which will be influenced by multiplication rate, largely determines the number of prey eaten. Other factors may also be important; for example when prey density is low, searching efficiency becomes of paramount importance (Huffaker and Kennett, 1969; Samson and Blood, 1980) while at certain temperatures some species become inactive (e.g., coccinellids below 15^{o}C (Frazer and Gilbert, 1976)) so that even when present they are consuming few or no prey.

2. Synchronisation

Natural enemy efficacy can be greatly reduced if there are areas in space or periods of time which permit the prey to escape attack (Coppel and Mertins, 1977). This is particularly so with aphids where the parthenogenetic phases give a numerical advantage over the sexually reproducing predator and parasite. Increasing numbers of predators and parasites produce an additive reduction in aphid numbers, whereas the aphids show a geometric rate of increase. However, one predator or parasite can eliminate a whole sequence of aphid generations with each aphid it destroys and so the early appearance of natural enemies in the aphid population will greatly increase their impact (van Emden, 1966; Tamaki and Weeks, 1972; Sunderland and Vickerman, 1980; Carter *et al.*, 1982).

A variety of factors influence the synchrony between a natural enemy and its prey. The seasonal occurrence of natural enemies often lags behind that of their prey, which reflects differences in their temperature thresholds for development (Syrett and Penman, 1981) or generation time (Campbell *et al.*, 1974). Where alternative foods are required by the adults for oviposition (e.g., Syrphidae, some Chrysopidae) the absence of these alternative foods can result in

delays in oviposition (Hodek *et al.*, 1972). In general, species where both adults and larvae (nymphs) are predatory are better synchronized with their prey and are more effective enemies (Hagen and van den Bosch, 1968) than those in which only adults or larvae are predatory. One of the aspects most worth studying for any aphidophagous species is the determination of the aphid density necessary not only to retain the natural enemy but also to induce ovigenesis and oviposition (Hodek *et al.*, 1972). The higher the aphid density required to support a predator in the field or to stimulate oviposition, the greater the lag between prey increase and predator appearance (Hagen and van den Bosch, 1968). Because predators with high feeding rates require high densities of prey (Kuenen, 1947), the lag may be considerable and the aphid's rate of increase too high to be offset by predation. The prey density may also exceed that causing economic damage, so the number of prey consumed may be less important *per se* than the relationship between the number of prey representing economic crop damage, and that necessary to keep the predator in the crop (Hodek *et al.*, 1970).

Ideally the natural enemies would be present in the crop before the pest arrives. Polyphagous predators may offer a distinct advantage over prey-specific species in that they can be present in a crop, feeding on alternative prey, before a pest arrives (Henderson, 1979; Potts and Vickerman, 1974). They are therefore in a position to begin feeding on the pest as soon as it arrives (i.e., show perfect synchrony).

3. Prey Reproductive Rate

The reproductive rate of the prey influences the effectiveness of a natural enemy removing a given number of prey from the population. The higher the prey's reproductive rate, the more voracious the natural enemy must be in order to have a significant influence on its numbers (van Emden, 1966). Reproductive rate is a product of fecundity, generation time and survival. Aphids, with their parthenogenesis, viviparity and rapid development, have an enormous reproductive potential which is why they have proved such difficult pests to 'control' using natural enemies (Hodek, 1970; Valentine, 1970). Reproductive rate is, however, influenced by certain environmental factors, including temperature and host plant physiology (van Emden, 1966). Natural enemy effectiveness is a balance between the potential of the predator or parasite to influence the prey (voracity) and the potential of the prey to 'escape' from the natural enemies' influence (reproductive rate), i.e., the death rate relative to the birth rate. The extent to which these potentials are realized is largely determined by synchronization (van Emden, 1966).

The interaction of all these factors is complex, with temperature perhaps the biggest confounding factor. For example the voracity of coccinellids and aphid reproductive rate both increase with temperature (within the acceptable limits for growth and development). However, coccinellid voracity increases faster than does aphid reproduction (Hagen and van den Bosch, 1968; Frazer and Gilbert, 1976) so that at low temperatures coccinellids are unable to suppress the aphid population but at high temperatures they can drive it to extinction.

Micromus tasmaniae as a predator of lucerne aphids.

The evaluation of any species as a potential biological control agent requires basic biological information on the species involved as well as on the prey. Data on hemerobiid lacewings are sparse, and although there is extensive information available on chrysopids, its relevance to hemerobiids is uncertain as there are numerous differences between the groups. However, with the information available, and the preceding outline of the attributes required of an efficient natural enemy, it should be possible to evaluate *M. tasmaniae* as a potential aphid 'control' agent.

Hemerobiids are generally smaller than other aphid predators. Larvae of *C. carnea* can weigh over 10 mg and other chrysopids as much as 40 mg (Principi and Canard, 1984), while *M. tasmaniae* seldom exceed 4 mg. Because of its small size *M. tasmaniae* is a predator with a small appetite for prey compared to many other species (Chapter 6). However, as many of the chrysopid species occurring in field crops are non-predatory as adults (New, 1975), care is necessary when comparing their prey consumption with the hemerobiids. For example, *M. tasmaniae* differs from *C. carnea* in that the most voracious predatory stage is the adult, not the larva, and although the larva of *C. carnea* is twice as large as the equivalent stage in *M. tasmaniae* and consumes many more aphids (Principi and Canard, 1984), the lifetime consumption of aphids by *M. tasmaniae* is almost certainly greater. A similar argument should apply to comparisons of prey consumption by syrphids, which are all non-predatory in the adult stage (see Dunn, 1954).

Perhaps the most significant finding of the present study was the size of lacewing populations which can occur in lucerne crops. The difficulty of sampling small larvae, and the fact that peak densities gave little indication of the true numbers produced over time (Chapter 5), suggests that the size of lacewing populations has previously been underestimated. So, despite each lacewing's relatively small appetite, as a group they may destroy more aphids than other predators, by virtue of their greater numbers. Between one lucerne harvest and the next up to 300 larvae m^{-2} may complete development, with each consuming 60-80 aphids during its development. The larvae alone can, therefore, account for a considerable number of aphids.

The high numbers of *M. tasmaniae* present in the field reflect certain attributes of the species;

1. A low individual appetite for prey generally reflects an ability to survive at low prey densities (Russel, 1970) because fewer prey are required to complete development. Like most lacewing species, larvae of *M. tasmaniae* are very mobile aggressive hunters which makes them efficient at locating prey (Fleschner, 1950; New, 1975) even at low prey densities, and as even the smallest are capable of capturing a range of prey sizes, the availability of suitably-sized prey is unlikely to be a problem, as it is with some coccinellids (Chapter 6). These factors combined mean that *M. tasmaniae* can survive and develop at low prey densities.

2. A low prey threshold for the onset of oviposition (Chapter 3) enables *M. tasmaniae* to begin reproduction at an early stage relative to the increase in aphid numbers. Here, again, *M. tasmaniae* differs from those chrysopids which are not predatory as adults. A requirement for honey-dew has been shown to significantly delay oviposition by *C. carnea* in Californian lucerne fields (Neuenschwander *et al.*, 1975).

3. The short generation time (Chapter 6), coupled with low developmental threshold temperatures (Chapter 4) and ample egg production, gives this lacewing a high reproductive potential (Samson and Blood, 1980).

This combination of factors enables *M. tasmaniae* to survive and begin reproducing early in the aphid population growth phase and therefore to produce a large second generation in the relatively short time available under the lucerne management regime (Chapter 5).

A low temperature threshold for development appears to be characteristic of the Hemerobiidae and, unlike the chrysopids, most species do not undergo any form of winter diapause (Cutright, 1923; Neuenschwander, 1976). Hemerobiids are cool-adapted species which occur earlier in the season than most other predator groups (Neuenschwander *et al.*, 1975). They are therefore the species most likely to influence spring aphid buildups (Neuenschwander, 1976; Syrett and Penman, 1981). In the present study larvae of *M. tasmaniae* were recorded as early as September, a month before the first coccinellid larvae appeared.

This ability to survive and reproduce at low prey densities, and hence the ability to attack aphids in the early stages of population buildup, is the key to *M. tasmaniae's* potential role as an aphid predator. As has been demonstrated by modelling (van Emden, 1966) and predator

exclusion trials in the field (Edwards *et al.*, 1979), there are considerable benefits for biological control from a natural enemy attacking its prey population as early as possible. The greater the lag between predator and prey the more voracious the predator must be in order to suppress the growth of the prey population. *M. tasmaniae* is therefore capable of removing aphids from the population at the time when it will produce the greatest benefit in terms of peak aphid number.

Some of the characteristics which enable *M. tasmaniae* to attack aphids at low prey densities, are also the factors limiting its ability to respond to increases in aphid numbers. Because of the low individual appetite, the asymptote of the functional response curve is low. Similarly, although *M. tasmaniae* is efficient at converting aphids to eggs (Chapter 3) the maximum numerical response is also limited by the functional response. This need not, however, exclude *M. tasmaniae* from a role in regulating aphid populations. In the presence of a natural enemy complex, working in a density dependent manner as outlined above, as the aphid numbers increase the larger, more voracious predators would move in, resulting in increased aphid mortality (Tamaki and Long, 1978). Evans (1976) demonstrated that although *Anthocoris confusus* was an efficient predator against prey with a slow rate of increase, against aphids it was only capable of regulating population growth if additional mortalities were applied to the aphids. *M. tasmaniae* need only play its part, that of attacking the aphids while their numbers are still relatively low, to play an important role in the overall regulation of aphid populations.

Any impact this lacewing is having on the aphid population is, however, likely to be subtle. Because its most important effect will be occurring early in the aphid population growth phase and will involve removing a relatively low number of aphids, it will be more difficult to observe in the field. By comparison, large influxes of adult coccinellids, which are very visible insects, have been reported causing spectacular reductions in aphid numbers from populations which had already built up to a high density (W.P. Thomas, pers. comm.).

M. tasmaniae has many of the characteristics deemed desirable in a natural enemy and should therefore be effective in some measure at suppressing aphid populations. To measure the impact lacewings were having on the lucerne aphid populations in this study would have been difficult for a number of reasons:

1. Predator species representing more than six arthropod orders were present in the lucerne fields and the importance of some of these species as aphid predators is unknown. Evaluating the lacewing's effect on the aphids using any kind of exclusion techniques in the presence of so many other potential mortality agents would have been difficult.

2. Artificial predator/prey environments can give useful information, but their applicability to the outside world is always in question (Hodek *et al.*, 1972).

3. A simulation approach offered possibilites, but the New Zealand lucerne aphid situation is made complex by the simultaneous presence of three species of aphid. An investigation of the age-specific mortalities of three different species of aphid was clearly outside the scope of the present study.

However, there is circumstantial evidence which suggests that natural enemies, primarily M. tasmaniae, were suppressing the aphid populations. Peak aphid populations normally occur in the spring (Kain *et al.*, 1979) but in the spring of 1985 and 1986 when predators were present in considerable numbers, aphid numbers were lower than in the autumn of 1986 when predators were less abundant. Such correlations are, however, of little real value without the demonstration of coincident changes in the age structure of the aphid population (Hagen and van den Bosch, 1968).

Also, it is not essential that natural enemies control aphids on their own. A level of control which might be considered inadequate in isolation may be entirely satisfactory if combined with other mortality or limiting factors (Waterhouse, 1979). Thus the effect of natural enemies can be assessed only in relation to the other factors determining the size of the prey population (Kiritani and Dempster, 1973).

Contrary to Hilson's (1964) assertion, the parasite *Anacharis zealandica* is capable of significantly influencing the population dynamics of *M. tasmaniae* . High levels of parasitism, such as those observed in the autumn of 1986 (Chapter 5), will considerably reduce the size of overwintering lacewing populations, which may in turn affect the size of spring populations. This parasite-induced mortality will not, however, eliminate entirely the lacewings' effect on autumn aphid populations. Parasitized larvae feed and develop normally to the pupal stage so the effect of their feeding should still influence the aphid population.

Chrysopids are host to a wide variety of hymenopteran parasites, with all life-history stages being attacked, and larval and pupal parasites important in regulating chrysopid populations (Alrouechdi *et al.*, 1984). Because New Zealand's hemerobiid species are attacked only by *A. zealandica*, which is not known to attack chrysopids, there appears to be an opportunity to establish chrysopid species in New Zealand free from all parasitism. However, care should be taken in selecting which chrysopid species to introduce. The most well-known chrysopid species

have attracted most attention because of their abundance, rather than because of any confirmed regulatory effect on pest populations (New, 1984). In Californian lucerne fields *C. carnea* was found to be a late arrival due to its high developmental threshold temperature and its requirement for honey-dew for oviposition (Neuenschwander *et al.*, 1975). Also, *C. carnea* is not predatory in the adult stage and therefore it will consume less aphids in its life-time than *M. tasmaniae*. Given the previous discussion on the importance of close synchrony between predator and prey on the suppression of aphid populations, it is unlikely that *C. carnea* would have any significant impact on the size of aphid populations; it would arrive too late to suppress the initial aphid population, and have insufficient appetite to stop an expanding aphid population unless present in very large numbers. Species which are predatory in the adult stage would therefore appear preferable as candidates for introduction.

Attempts to identify a relationship between the presence of different predator species and aphid density, similar to that discussed above, failed to show any consistent pattern. This implies that either no such relationship exists or that other factors were influencing predator occurrence. It is possible that there were insufficient species present to demonstrate such a relationship. Only two of the recognized aphidophagous groups occurred in any number (Chapter 2) and their occurrence was erratic, with no obvious relationship to aphid number. If lucerne aphids are not satisfactorily controlled by natural enemies it may be due to an incomplete natural enemy fauna rather than the inadequacy of those predators and parasites which are present. If there are insufficient species present to respond to increases in aphid number, then control will be inadequate. The number of natural enemy species associated with lucerne aphids in New Zealand is low compared to overseas (Neuenschwander *et al.*, 1975; Wheeler, 1977) so gaps in the natural enemy fauna are a possibility. However, the importance of relatively unknown polyphagous predators such as harvestmen and wolf spiders (Chapter 2) would need to be considered in identifying such a predator deficiency.

Also, under the lucerne management regimes currently in use in New Zealand the entire above ground biomass is removed after each mowing, resulting in a highly modified microenvironment and food source for pests and beneficials alike. After the crop is mown, the lacewings, and presumably the other natural enemies as well, are forced to leave the field or die. The continued presence of a species in the crop is therefore dependent on reestablishment of populations following each lucerne harvest. This need to repeatedly relocate and reestablish is probably responsible for the erratic occurrence of natural enemies in lucerne crops in this country and is likely to be a major limiting factor to the biological control of lucerne aphids in New Zealand (Cameron *et al.*, 1979). Natural enemies are capable of having significant effects on

lucerne aphid populations (Henderson, 1979; Bishop and Milne, 1986) and their influence could be much greater, and more consistent, if synchronization with the prey were improved.

The effectiveness of *M. tasmaniae*, and the other predator species, at regulating lucerne aphid populations is therefore significantly influenced by the lucerne management system. Despite this, the present study has shown that very large (100+ m^{-2}) populations of adult lacewings can be produced in the relatively short time between lucerne harvests. These lacewing populations, which must represent a potentially valuable resource to the farmer, are subquently forced out of the fields, and are effectively lost, following each harvest.

Management strategies.

As outlined above, the extent to which a predator or parasite is able to regulate a prey population is a balance between the ability of the natural enemy to kill prey (voracity), the capacity of the prey to produce new prey (reproductive rate), and the synchrony between the two in time and space. This section considers some of the methods by which this balance may be altered to the detriment of the prey species, and to the advantage of the lacewing population. This is by no means a comprehensive list of strategies, but rather considers those in which lacewings (chrysopids and hemerobiids) have been involved in the past.

1. Integrated control using selective chemicals.

Pesticides offer one of the most obvious and simple methods of coping with pest problems. However, single applications of chemicals produce only a temporary reduction of localized populations and do not contribute to permanent density regulation as may biological agencies. Repeated use of chemicals has in fact resulted in a variety of new problems such as insecticide resistance, outbreaks of secondary pests, rapid resurgence of the primary pest and accumulating pesticide residues (van den Bosch *et al.*, 1982). It has long been recognized that the integration of chemical and biological control strategies offers a viable and attractive alternative to solely chemical-based pest control (Stern et al., 1959).

Among the insects, lacewing larvae (*C. carnea*) have the highest known level of natural tolerance to pyrethroid insecticides (Ishaaya and Casida, 1981) and are also highly tolerant to a number of other pesticides (Bigler, 1984). This tolerance appears to stem largely from the lacewing's unusually active pyrethroid esterase enzymes (Ishaaya and Casida, 1981) which enable it to tolerate chemicals which are detoxified hydrolytically (Bigler, 1984). As is usual with

lacewings, most experiments have involved the ubiquitous *C. carnea*, but the available data suggest that this high natural tolerance to some insecticides is universal amongst the Chrysopidae (Lawrence et al., 1973; McDonald and Harper, 1978; Bigler, 1984). *M. tasmaniae* is also highly tolerant to some of the same chemicals (Syrett and Penman, 1980) which suggests that the mechanisms involved may be common to all lacewings.

Whatever the mechanisms, this high natural tolerance offers a very real opportunity for the integration of biological control using lacewings together with selective insecticides. Stern *et al.* (1959) developed an integrated control program for spotted alfalfa aphid in lucerne in California, and several authors have suggested the potential for using selective chemicals against lucerne aphids in New Zealand (Wightman and Whitford, 1982; Cameron *et al.*, 1983).

However, toxicity testing in the laboratory is only the first step to establishing a chemical's selectivity. Although *M. tasmaniae* has shown a high tolerance to some pesticides under topical laboratory tests (Syrett and Penman, 1980), other factors may be equally important in the field. Chemical applications resulted in prolonged development in *Chrysoperla rufilabris* (Lawrence, 1973) and although Syrett and Penman (1980) found no evidence of impaired fecundity or development in treated *M. tasmaniae*, Penman (unpublished data) found that this lacewing would not oviposit on surfaces freshly sprayed with fenvalerate. Despite such complexities, and the need to select doses that reduce but do not eliminate prey populations, the very high tolerances shown by lacewings to some chemicals, offers a unique opportunity for the development of integrated control.

In lucerne forage crops, in Canterbury at least, farmers seldom spray for aphid control, partly for economic reasons and partly because grazing management options are available (Penman *et al.*, 1979). Spraying against aphids may be necessary in spring when natural control is most inefficient (Cameron *et al.*, 1983) and insecticides may be used against *Sitona discoideus*. Integration with chemicals is therefore a possibility. Certainly, in crops with a higher cash value (e.g., cereals or lucerne seed) where aphids are a problem and lacewings occur, the use of selective insecticides may be advantageous.

2. Augmentation by release.

Chemical insecticides should ideally only be used when the natural control agencies prove inadequate (Stern *et al.*, 1959). An alternative to using chemicals is to bolster the naturally occurring mortality agents by releasing predators or parasites. Two options are available;

inundative release, where large numbers of natural enemies are released, all at once, to produce a rapid decline in prey numbers (i.e., as a kind of 'biotic insecticide'), and augmentative release where gaps in the seasonal occurrence of natural enemies are filled by releasing laboratory reared predators or parasites (Turner and Teakle, 1979). Halfhill and Featherston (1973) successfully used inundative releases of the parasite *Aphidius smithii* to control pea aphids in lucerne in the United States.

There have been many studies, some highly successful, involving field releases of chrysopid lacewings against a variety of pests (for a review see Ridgeway and Murphy, 1984). These releases have been possible largely because of the availability of methods for rearing large numbers of lacewings. Neuenschwander (1976) suggested that because of its low temperature threshold for development, the hemerobiid lacewing *Hemerobius pacificus* showed potential for aphid control in lucerne by periodic release early in the season when other predators were precluded from becoming active by the low temperatures. The same may be true of *M. tasmaniae* which also has low temperature thresholds (chapter 4). For example, Cameron *et al.* (1983) released *A. eadyii* in spring against PA but temperatures prevented sufficiently rapid development and dispersal to effect control. The high reproductive potential of *M. tasmaniae* suggests that releases of even relatively low numbers of adults could result in large populations of larvae. Also, the low prey threshold necessary to keep lacewings in the field means they could be released early in the aphid population buildup.

Lucerne in New Zealand is most susceptible to aphid damage in the autumn (Kain *et al.*, 1979), at the time when the lacewing populations suffer the greatest mortality from parasitism. Releases of lacewings at this time may offset the effect of parasitism on lacewing number resulting in increased aphid mortality. This approach would have a real practical advantage in that a ready supply of both lacewings and aphids would be available in the field at that time of year, and the lacewings would only need to be reared through one or two generations. However, the reaction of the lacewing parasite to such a mass release of hosts would need to be considered before such a scheme was initiated.

The ease with which *M. tasmaniae* can be reared in the laboratory along with its high reproductive potential make it an attractive candidate for mass rearing and release. However, a considerable amount of practical research would be necessary to set up such a scheme, and even then, as is the case with chrysopids (Ridgeway and Jones, 1984) and parasites (Halfhill and Featherston, 1973), the cost of rearing the large numbers of insects needed seems to restrict their practical use to a few high-value crops.

3. Augmentation by attractants and supplementary foods.

The application of artificial food sprays to increase predator numbers has been successful with coccinellids (Hodek *et al.*, 1972) and chrysopids (Hagen *et al.*, 1970; Hagen and Bishop, 1979). Weekly applications to lucerne of a yeast, sucrose and water mix resulted in a three-fold increase in the number of chrysopid eggs and a reduction in the population of spotted alfalfa aphid (Hagen *et al.*, 1970). Although the food sprays acted as attractants to *C. carnea* and to various syrphid species, the syrphids would not oviposit in the absence of aphids. Coccinellids were not attracted by the food supplements but they did remain in areas where food was supplied and the onset of oviposition was advanced. Premature oviposition by *C. carnea* and the coccinellids as a result of the food sprays improved aphid control by effectively lowering the prey threshold for oviposition. The result was a reduction in the lag in occurrence between aphids and predators (Hagen *et al.*, 1970).

As most of the lacewing work has involved *C. carnea* , the adult of which is a pollen and honeydew feeder, there is no guarantee that food sprays will attract or sustain hemerobiid adults which are all predatory. The fact that coccinellids responded to the food sprays (Hodek *et al.*, 1972) and that *M. tasmaniae* can be maintained in the laboratory on a honey and water diet (although they will not produce eggs without prey) suggests that such food sprays may at least hold hemerobiids in the field through times of prey scarcity. However, given the volumes of food supplement required, the inconsistency of the resulting pest control, and the costs involved (Ridgeway and Murphy, 1984) this approach to aphid control does not appear to be a practical option at present.

4. Creating refugia.

When whole lucerne fields are cut there is enormous destruction of the resident insect fauna (van den Bosch, 1982). The result is a short duration crop environment where colonising ability is a major determinant of which species are present. Invariably the phytophagous species establish first with a lag of varying duration before the establishment of the predator species (van den Bosch *et al.*, 1982). As outlined above the need for continual recolonization and establishment is the most likely cause of the erratic and unpredictable occurrence of natural enemies in lucerne in New Zealand.

In monocultures, including lucerne, strip-harvesting, where alternating strips of the crop are harvested at different times, has resulted in higher numbers of natural enemies, lower pest populations and increased yields compared to solid-harvested fields (Schlinger and Dietrick, 1960; van den Bosch *et al.*, 1982; Cameron *et al.*, 1983; Nentwig, 1988). Strip-harvesting lucerne, by providing continuous suitable habitat, results in greater stability and prevents emigration of many natural enemy species at harvest (van den Bosch and Stern, 1969; Summers, 1976). Strip-harvesting, however, poses certain operational problems because the farmer is required to harvest more frequently, resulting in less efficient utilization of manpower and machinery (Summers, 1976; van den Bosch *et al.*, 1982). Therefore, despite its proven effectiveness this practice has not been widely accepted by growers (Summers, 1976).

The border-harvesting strategy suggested by Summers (1976) appears to offer a viable alternative. This practice involves a normal solid-cut harvesting regime but with the leaving of narrow uncut borders widely spaced across the field. These narrow borders supply sufficient refugia to shelter natural enemies over the mowing period resulting in an early buildup in numbers in the next lucerne growth period. In Summers' (1976) experiments the result was up to three times as many predators in the border-cut field as in the solid-cut one. When the uncut borders were incorporated into the total crop at next mowing (new borders being left) its advanced physiological state had no significant effect on overall hay quality. In fact, the advanced age of the lucerne plants in the borders may be an advantage in that it should be less suitable for the aphids, resulting in slower population growth. When combined with the congregation of natural enemies in the borders this should result in low levels of reinfection of aphids from the borders into the crop.

This harvesting strategy appears to offer a practical solution to the problem of loss through emigration of the large lacewing populations which can occur in lucerne (Chapter 5). Given the large increases in lacewing numbers which can occur (e.g., 100+ adults m^{-2} from an initial population of less than one adult m^{-2} :- Chapter 5), if even 10% of the emergent adults could be prevented, through the provision of refugia, from leaving the field then the resulting lacewing populations could be very large indeed. The continuous presence of a lacewing population in the field must greatly improve synchrony with the aphids. *M. tasmaniae* appears ideally suited to such a scheme. It can survive at low prey densities and is therefore less likely to leave the field at times of low prey density. There is little point in retaining predators in refugia if they leave soon after due to insufficient food. M. tasmaniae's high reproductive capability, short generation time and low prey threshold for oviposition mean it can respond numerically to increasing aphid numbers. If as occurs overseas (Summers, 1976), the greater predator abundance and earlier attack on the

aphids reduces peak aphid numbers then the lacewing's low individual appetite should be less of a disadvantage.

At harvest there may be large numbers of lacewing pupae in the soil (Chapter 5). The survival of these once the lucerne canopy has been removed must be doubtful given the high soil surface temperatures possible (In Arizona lucerne fields, soil surface temperatures reached 63^{o}C after mowing, Pinter *et al.*, 1975). However, the shaded border environment may well allow some of these pupae to survive and the resulting emergence of adult lacewings would further supplement predator numbers.

Cameron *et al.* (1983) found that in New Zealand under the cooler spring temperatures, the presence of reservoirs worked to the advantage of the aphids because the beneficials were generally restricted by their higher temperature requirements. The low temperature thresholds of *M. tasmaniae* make it the most potentially useful natural enemy at this time of year. Spring aphid numbers can be reduced by winter grazing (Penman *et al.*, 1979), but if the problem persists the lacewing's high tolerance to a number of insecticides means the use of a selective insecticide could be a viable option.

Conclusion

The population dynamics of *M. tasmaniae* in lucerne forage crops is regulated primarily by initial establishment of adults, food availability and in the autumn, parasitism. If even low numbers of adults can establish while the aphid density is still low then large numbers of larvae, and in the absence of significant parasitism, large numbers of second generation adults can be produced before the lucerne is harvested. Under the present lucerne management practices these large numbers of potentially useful predators are lost. Although this lacewing's appetite for aphids is low and therefore its ability to respond to large aphid populations limited, this may be offset by its ability to attack aphid populations early in the population growth phase and by the large numbers of individuals which can occur.

The limited extent to which lucerne aphids are regulated by natural enemies appears to be due more to the rather low number of natural enemy species occurring and to the harsh effects of the standard lucerne management regime than to the inefficiency of existing natural enemies. *M. tasmaniae* shows considerable potential to influence aphid numbers if present in conjunction with other predator species and/or under more amiable management systems. In particular, the

border harvesting strategy of Summers (1976) appears to offer considerable scope for improving natural regulation of aphid populations by preventing the complete loss of natural enemies after mowing. *M. tasmaniae* may be an ideal predator under such a management system because of its ability to survive and reproduce at low prey densities.

BIBLIOGRAPHY

Aalbersberg, Y.K., Van der Westhuizen, M.C. and Hewitt, P.H. (1988). Natural enemies and their impact on *Diuraphis noxia* (Hemiptera : Aphididae) populations.
Bull. Ent. Res. 78: 111-120.

Alrouechdi, K., Semeria, Y. and New, T.R. (1984). Ecology of natural enemies.
pp. 187-193. In Canard, M., Semeria, Y. and New, T.R. 'Biology of Chrysopidae'. Dr W. Junk Publishers.

Anderson, N.H. (1962). Growth and fecundity of *Anthocaris* spp. reared on various prey.
Ent. Exp. and Appl. 5: 40-52.

Banks, C.J. (1956). Observation on the behaviour and mortality in Coccinellidae before dispersal from the egg shells.
Proc. R. Ent. Soc. Lond. A. 31: 56-60.

Barlow, N.D. (1983). The role of modelling in practical pest management.
pp. 41-51. In Cameron, P.J., Wearing, C.H. and Kain, W.M. (eds). Proc. of Australasian Workshop on Development and Implementation of IPM: Auckland, Government Printer.

Bates, L.H. and Miln, A.J. (1982). Parasites and predators of lucerne aphids at Flock House, Bulls.
Proc. 35th N.Z. Weed and Pest Control Conf.: 123-126.

Beddington, J.R., Free, C.A. and Lawton, J.H. (1976). Stability and resilience in predator-prey models.
J. Anim. Ecol. 45: 791-816.

Beddington, J.R., Free, C.A. and Lawton, J.H. (1978). Characteristics of successful natural enemies in models of biological control of insect pests.
Nature 273: 513-518.

Beddington, J.R., Hassell, M.P. and Lawton, J.H. (1976). The Components of Arthropod Predation II. The predator rate of increase.
J. Anim. Ecol. 45: 165-185.

Bernhardt, J.L. and Shepard, M. (1978). Validation of a physiological day equation : Development of the mexican bean beetle on snap beans and soybeans.
Environ. Entomol. 7 (1): 131-135.

Bigler, F. (1984). Biological control by chrysopids : integration with pesticides.
pp. 233-247. In Canard, M., Semeria, Y. and New, T.R. 'Biology of Chrysopidae'. Dr W. Junk Publishers.

Bishop, A.L. (1979). The role of native beneficial organisms.
Aust. Appl. Ent. Res. Conf.: 96-110.

Bishop, A.L., Greenup, L.R. and Holtkamp, R.H. (1980). Management of *Acyrthosiphon kondoi* Shinji, blue-green aphid, and *Therioaphis trifolii* Monell f. *maculata*, spotted alfalfa aphid, by grazing and cutting lucerne.
Aust. J. Exp. Agr. Anim. Husb. 20: 710-716.

Bishop, A.L. and Milne, W.M. (1986). The impact of predators on lucerne aphids and the seasonal production of lucerne in the Hunter Valley, New South Wales.
J. Aust. Ent. Soc. 25: 333-337.

Blackman, R.L. (1967). The effects of different aphid foods on *Adalia bipunctata* (L.) and *Coccinella 7-punctata* (L.).
Ann. Appl. Biol. 59: 207-219.

Butcher, M.R. (1986). Aspects of the ecology of a strawberry crop with special reference to twospotted spider mite (Tetranychidae : acari). Unpublished Ph.D. Thesis, University of Canterbury, New Zealand.

Cameron, P.J., Allan, D.J., Walker, G.P. and Wightman, J.A. (1983). Management experiments on aphids (*Acyrthosiphon* spp.) and beneficial insects in lucerne.
N.Z. J. Exp. Agr. 11: 343-349.

Cameron, P.M., Thomas, W.P. and Hill, R.L. (1979). Introduction of lucerne aphid parasites and a preliminary evaluation of the natural enemies of *Acyrthosiphon* spp. (Hemiptera : Aphididae) in New Zealand.
pp. 219-233 In Crosby, T.K., Pottinger, R.P. (eds). Proc. 2nd Australasian Conf. Grassl. Invert. Ecol. Wellington, Government Printer.

Cameron, P.J. and Walker, G.P. (1984). Phenology and host preference of spotted alfalfa aphid on lucerne and white clover.
Proc. 37th N.Z. Weed and Pest Control Conf.: 77-81.

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

Canard, M., Semeria, Y. and New, T.R. (1984) (eds.). Biology of Chrysopidae. Dr W. Junk Publishers.

Canard, M. and Duelli, P. (1984). Predatory behaviour of larvae and cannibalism.
In Canard, M., Semeria, Y. and New, T.R. (eds.). Biology of Chrysopidae. Dr W. Junk. Publishers.

Carter, N., Gardner, S., Fraser, A.M. and Adams, T.H.L. (1982). The role of natural enemies in cereal aphid population dynamics.
Ann. Appl. Biol. 101: 190-195.

Chambers, R.J., Sunderland, K.D., Wyatt, I.J. and Vickerman, G.P. (1983). The effects of predator exclusion and caging on cereal aphids in winter wheat.
J. Appl. Ecol. 20: 209-224.

Cherry, R.H., Wood, K.A. and Ruesink, W.G. (1977). Emergence trap and sweep net sampling for adults of the potato leafhopper from alfalfa.
J. Econ. Ent. 70: 279-283.

Coppel, H.C. and Mertins, J.W. (1977). Biological Insect Pest Suppression. Advanced series in Agricultural Sciences 4. Springer-Verlag. Berlin, Heidelberg, New York.

Cutright, C.R. (1923). Life history of *Micromus posticus* Walker.
J. Econ. Ent. 16: 448-456.

DeBach, P. (ed.) (1964). Biological control of insect pests and weeds. London : Chapman and Hall.

Dietrick, E.J., Schlinger, E.I. and van den Bosch, A. (1959). A new method for sampling arthropods using a suction collecting machine and modified Berlese funnel separator.
J. Econ. Ent. 52: 1085-1091.

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.

Dixon, A.F.G. (1970). Factors limiting the effectiveness of the coccinellid beetle *Adalia bipunctata* (L.) as a predator of the sycamore aphid *Drepanosiphum platanoides* Schr.).
J. Anim. Ecol. 39: 739-751.

Dunbier, M.W. (1979). Lucerne cultivars - wide choice for 1979 sowings.
N.Z. J. Agr. 139 (3): 27-28.

Dunn, J.A. (1952). The effect of temperature on the pea aphid - ladybird relationship.
Rep. Nat. Veg. Res. Sta.: 1951: 21-23.

Dunn, J.A. (1954). *Micromus variegatus* (Fab) (Neuroptera) as a predator of the pea aphid.
Proc. R. Ent. Soc. Lond. A, 29: 76-80.

Edwards, C.A., Sunderland, K.D. and George, K.S. (1979). Studies on Polyphagous predators of cereal aphids.
J. Appl. Ecol. 16: 811-823.

Eubank, W.P., Atmar, J.W. and Ellington, J.J. (1973). The significance and thermodynamics of fluctuating versus static thermal environments on *Heliothis zea* egg development rates.
Environ. Entomol. 2: 491-496.

Evans, H.F. (1976a). The role of predator-prey size ratio in determining the efficiency of capture by *Anthocoris nemorum* and the escape reactions of its prey, *Acyrthosiphon pisum*. Ecol. Ento. 1: 85-90.

Evans, H.F. (1976b). Mutual interference between predatory anthocorids. Ecol. Ento. 1: 283-286.

Eveleigh, E.S. and Chant, D.A. (1981). Experimental studies on acarine predator-prey interactions : effects of predator age and feeding history on prey consumption and the functional response (Acarina : Phytoseiidae). Can. J. Zool. 59: 1387-1406.

Farrell, J.A. and Stufkens, M.W. (1981). Field evaluation of lucerne cultivars for resistance to blue green lucerne aphid and pea aphid (*Acyrthosiphon* spp.) in New Zealand. N.Z. J. Agr. Res. 24: 217-220.

Fleschner, C.A. (1950). Studies on searching capacity of the larvae of three predators of the citrus red mite. Hilgardia 20: 233-265.

Fox, L.R. and Murdoch, W.W. (1978). Effects of feeding history on short-term and long-term functional response in *Notonecta hoffmanni*. J. Anim. Ecol. 47: 945-959.

Frazer, B.D., Gilbert, N. (1976). Coccinellids and aphids : a quantitative study of the impact of adult ladybirds (Col. Coccinellidae) preying on a field population of pea aphids (Homoptera : Aphididae). J. Ento. Soc. of British Columbia 37: 33-56.

French, R.A. (1966). The biology and ecology of *Coccinella undecimpunctata* L. Unpublished M.Agr.Sc. Thesis, Lincoln College, University of Canterbury, New Zealand.

Getz, W.M. and Gutierrez, A.P. (1982). A perspective on systems analysis in crop production and insect pest management. Ann. Rev. Ent. 27: 447-466.

Gilbert, N., Gutierrez, A.P., Frazer, B.D. and Jones, R.E. (1976). Ecological Relationships. 157 pp. Freeman, N.Y.

Glen, D.M. (1975). Searching behaviour and prey density requirements of *Blepharidopterus angulatus* Fall. (Heteroptera : Miridae) as a predator of the lime aphid *Eucallipterus tiliae* L. and the leafhopper *Alnetoidea alneti* Dahlbom.
J. Anim. Ecol. 44: 85-114.

Gregg, P. (1982). A simulation model of the development of *Chortoicetes terminifera* (Orthoptera : Acarididae) under fluctuating temperatures.
pp. 117-125. In Lee, K.E. (ed.) Proc. 3rd Australasian Conf. Grassl. Invert. Ecol. Adelaide 30 Nov - 4 Dec. 1981. Govt. Printer, Adelaide.

Griffiths, E. (1982). The carabid *Agonum dorsale* as a predator in cereals.
Ann. Appl. Biol. 101: 152-154.

Gurney, B. and Hussey, N.W. (1970). Evaluation of some coccinellid species for the biological control of aphids in protected cropping.
Ann. Appl. Biol. 65: 451-458.

Gutierrez, A.P., Baumgaertner, J.U. and Summers, C.G. (1984). Multitrophic models of predator-prey energetics.
Can. Ent. 116: 923-963.

Hagen, K.S. and Bishop, G.W. (1979). Use of supplemental foods and behavioral chemicals to increase the effectiveness of natural enemies.
In Davis, D.W. *et al.*, (eds.). Biological control and insect pest management. Berkeley : Div. agric. Sci., Univ. Calif. Publ. 4D96: 102 pp.

Hagen, K.S., Sawell, E.F. Jr. and Tassan, R.L. (1970). The use of food sprays to increase effectiveness of entomophagous insects.
Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage., Tallahassee, Fla (1970) 2: 59-81.

Hagan, K.S. and van den Bosch, R. (1968). Impact of pathogens, parasites and predators on aphids.
Ann. Rev. Ent. 13: 325-384.

Hagstrum, D.W. and Hagstrum, W.R. (1970). A simple device for producing fluctuating temperatures, with an evaluation of the ecological significance of fluctuating temperatures.
Ann. Ent. Soc. of America 63 (5): 1385-1389.

Halfhill, J.E. and Featherston, P.E. (1973). Inundative releases of *Aphidius smithi* against *Acyrthosiphon pisum.*
Environ. Entomol. 2 (3): 469-472.

Harris, B.M. (1980). Insects associated with the lupin (*Lupinus angustifolius*) cultivars Fes and Uniharvest. Unpublished M.Appl.Sci. Thesis, University of Canterbury, New Zealand.

Hassell, M.P., Lawton, J.H. and Beddington, J.R. (1976). The components of arthropod predation I. The prey death-rate.
J. Anim. Ecol. 45: 135-164.

Heathcote, G.D. (1972). Evaluating aphid populations on plants. Chapter 3. Invan Emden (ed.). Aphid Technology. Academic Press. London.

Henderson, N.C. (1979). Studies on the predators, a parasite, and an entomophthorous fungus affecting *Acyrthosiphon kondoi* (Hemiptera : Aphididae) in the Manawatu, New Zealand. pp. 278-82. In Crosby, T.K. and Pottinger, R.P. (eds.). Proc. 2nd Australasian Conf. Grassl. Invert. Ecol. Government Printer, Wellington.

Hilbert, D.W. and Logan, J.A. (1983). Empirical model of nymphal development for the migratory grasshopper, *Melanoplus anguinipes* (Orthoptera : Acrididae).
Environ. Entomol. 12: 1-5.

Hilson, R.J.D. (1964). The ecology of *Micromus tasmaniae* Walker. Unpubl. M.Sc. Thesis, University of Canterbury.

Hodek, I. (1957). The influence of *Aphis sambusi* L. as food for *Coccinella 7-punctata* L.
Acta Soc. ent. Bohem. 54: 1-8.

Hodek, I. (1970). Coccinellids and the modern pest management.
Bio Science 20 (9): 543-552.

Hodek, I. (1973). Biology of Coccinellidae. Academia, Prague.

Hodek, I., Hagen, K.S. and van Emden, H.F. (1972). Methods for studying effectiveness of natural enemies.
Chapter 4. In van Emden (ed.). Aphid Technology. Academic Press, London.

Hogg, D.B. (1985). Potato leafhopper (Homoptera : Cicadellidae) immature development, life tables, and population dynamics under fluctuating temperature regimes.
Environ. Entomol. 14: 349-355.

Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism.
Can. Ent. 91: 385-398.

Holling, C.S. (1961). Principles of insect predation.
Ann. Rev. Ent. 6: 163-182.

Holling, C.S. (1966). The functional response of invertebrate predators to prey density.
Mem. Ent. Soc. Can. 48: 1-86.

Houck, M.A. and Strauss, R.E. (1985). The comparative study of functional responses : Experimental design and statistical interpretation.
Can. Ent. 117: 617-629.

Huffaker, C.B. and Kennett, C.E. (1969). Some aspects of assessing efficiency of natural enemies.
Can. Ent. 101: 425-447.

Hughes, R.D. (1955). The influence of the prevailing weather on the numbers of *Meromyza variegata* Meigen (Diptera, Chloropidae) caught with a sweep net.
J. Anim. Ecol. 24: 324-35.

Hughes, R.D. (1963). Population dynamics of the cabbage aphid *Brevicoryne brassicae* (L.).
J. Anim. Ecol. 32: 393-424.

Hukusima, S. and Kamei, M. (1970). Effects of various species of aphids as food on development fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera : Coccinellidae). Res. Bull. Fac. Agr. Gifu. Univ. 29: 53-66.

Hull, L.A., Asquith, D. and Mowery, P.D. (1977). The functional response of *Stethorus punctum* to densities of the European red mite. Environ. Entomol. 6: 85-90.

Hutchison, W.D. and Hogg, D.B. (1984). Demographic statistics for the Pea aphid (Homoptera : Aphididae) in Wisconsin and a comparison with other populations. Environ. Entomol. 13: 1173-1181.

Ishaaya, I. and Casida, J.E. (1981). Pyrethroid esterase(s) may contribute to natural pyrethroid tolerance of larvae of the common green lacewing. Environ. Entomol. 10: 681-684.

Ives, P.M. (1981). Estimation of coccinellid numbers and movement in the field. Can. Ent. 113: 981-997.

Ives, P.M. (1981). Feeding and egg production of two species of coccinellids in the laboratory. Can. Ent. 113: 999-1005.

Kain, W.M., Esson, M.J., Holland T.V. and Atkinson, D.S. (1976). Preliminary studies of chemical control of blue green lucerne aphid. Proc. 29th N.Z. Weed and Pest Control Conf.: 23-30.

Kain, W.M., Atkinson, D.S., Marsden, R.S., Oliver, M.J. and Holland, T.V. (1977). Blue green lucerne aphid damage in lucerne crops within southern North Island. Proc. 30th N.Z. Weed and Pest Control Conf.: 177-181.

Kain, W.M., Atkinson, D.S., Oliver, M.J. and Stiefel, W. (1979). Pest assessment studies of blue green lucerne and pea aphids in the Southern North Island region of New Zealand. Proc. 32nd N.Z. Weed and Pest Control Conf.: 171-179.

Kain, W.M., Atkinson, D.S. and Oliver, M.J. (1979). Seasonality of blue green lucerne and pea aphids in the Southern North Island of New Zealand.
Proc. 32nd N.Z. Weed and Pest Control Conf.: 180-185.

Kiritani, K. and Dempster, J.P. (1973). Different approaches to the quantitative evaluation of natural enemies.
J. Appl. Ecol. 10: 323-330.

Kuenen, D.J. (1947). On the ecological significance of two predators of *Metatetranychus ulmi.*
Tijdschr. Ent. 88: 303-312.

Lawrence, P.O., Kerr, S.H. and Whitcomb, W.H. (1973). *Chrysopa rufilabris* : effect of selected pesticides on duration of third larval stadium, pupal stage, and adult survival.
Environ. Entomol. 2: 477-480.

Leathwick, D.M. and Winterbourn, M.J. (1984). Arthropod predation on aphids in a lucerne crop.
N.Z. Entomologist 8: 75-80.

Leslie, P.H. (1945). On the use of matrices in certain population mathematics.
Biometrika 33: 183-212.

Livdahl, T.P. and Stiven, A.E. (1983). Statistical difficulties in the analysis of predator functional response data.
Can. Ent. 115: 1365-1370.

MacFarlane, R.P. (1970). A preliminary study of the fauna associated with lucerne *Medicago sativa* variety Wairau in New Zealand, with special reference to pests, sampling methods and lucerne seed production. M.Agr.Sc. Thesis, Lincoln College, University of Canterbury, New Zealand.

Maelzer, D.A. (1978). The growth and voracity of larvae of *Leis conformis* (Boisd) (Coleoptera : Coccinellidae) fed on the rose aphid *Macrosiphum rosae* (L.) (Homoptera : Aphididae) in the laboratory.
Aust. J. Zool. 26: 293-304.

Messenger, P.S. and Flitters, N.E. (1959). Effect of variable temperature environments on egg development of three species of fruit flies.
Ann. Ent. Soc. of America 52: 191-204.

Miermont, Y. and M. Canard (1975). The biology of the aphidophagous predator *Eumicromus angulatus* (Neur. : Hemerobiidae) : Studies in the laboratory and observations in the south-west of France.
Entomophaga 20 (2): 179-191.

Miller, G.L. and Cave, R.D. (1987). Bionomics of *Micromus posticus* (Walker) (Neuroptera : Hemerobiidae) with descriptions of the immature stages.
Proc. Ent. Soc. Wash. 89 (4): 776-789.

Mills, N.J. (1981). Some aspects of the rate of increase of a coccinellid.
Ecol. Ent. 6: 293-299.

Mills, N.J. (1982). Satiation and the functional response : a test of a new model.
Ecol. Ent. 7: 305-315.

Milne, W.M. and Bishop, A.L. (1987). The role of predators and parasites in the natural regulation of lucerne aphids in eastern Australia.
J. Appl. Ecol. 24: 893-905.

Murdoch, W.W. (1973). The functional response of predators.
J. Appl. Ecol. 10: 335-341.

McDonald, S. and Harper, A.M. (1978). Laboratory evaluation of insecticides for control of *Acyrthosiphon pisum* (Hemiptera : Aphididae) in alfalfa.
Can. Ent. 110: 213-216.

Neutwig, W. (1988). Augmentation of beneficial arthropods by strip-management 1. Succession of predaceous arthropods and long-term change in the ratio of phytophagous and predaceous arthropods in a meadow.
Oecologia 76: 597-606.

Neuenschwander, P. (1975). Influence of temperature and humidity on the immature stages of *Hemerobius pacificus*.
Environ. Entomol. 4: 215-220.

Neuenschwander, P., Hagen, K.S. and Smith, R.F. (1975). Predation on aphids in California's alfalfa fields.
Hilgardia 43: 53-78.

Neuenschwander, P. (1976). Biology of the adult *Hemerobius pacificus*.
Environ. Entomol. 5: 96-100.

New, T.R. (1975). The biology of Chrysopidae and Hemerobiidae (Neuroptera) with reference to their use as biological control agents.
Trans. R. Ent. Soc. of Lond. 127: 115-140.

New, T.R. (1984). Chrysopidae : ecology on field crops.
pp. 160-167. In Canard, M., Semeria, Y. and New, T.R. Biology of Chrysopidae. Dr W. Junk Publishers.

Nowierski, R.M., Gutierrez, A.P. and Yanninek J.S. (1983). Estimation of thermal threshold and age-specific life table parameters for the Walnut Aphid (Homoptera : Aphididae) under field conditions.
Environ. Entomol. 12: 680-686.

Penman, D.R., Rohitha, B.H., White, J.G.H. and Smallfield, B.M. (1979). Control of blue-green lucerne aphid by grazing management.
Proc. 32nd N.Z. Weed and Pest Cont. Conf.: 186-191.

Pienkowski, R.L. (1965). The incidence and effect of egg cannibalism in first instar *Coleomegilla maculata lengi*.
Ann. Ent. Soc. Amer. 58: 150-153.

Pinter, P.J., Hadley, N.F. and Lindsay, J.H. (1975). Alfalfa crop micrometeorology and its relation to insect pest biology and control.
Environ. Entomol. 4 (1): 153-162.

Potts, G.R. and Vickerman, G.P. (1974). Studies on the cereal ecosystem.
Adv. Ecol. Res. 8: 107-197.

Principi, M.M. and Canard, M. (1984). Feeding Habits.
pp. 76-92. In Canard, M., Semeria, Y. and New, T.R. Biology of Chrysopidae. Dr W. Junk Publishers.

Propp, G.D. (1982). Functional response of *Nabis americoferus* to two of its prey, *Spodoptera exigua* and *Lygus hesperus*.
Environ. Entomol. 11: 670-674.

Pruess, K.P., Lal Saxena, K.M. and Koinzan, S. (1977). Quantitative estimation of alfalfa insect populations by removal sweeping.
Environ. Entomol. 6: 705-708.

Raychaudhuri, D.N., Ghosh, D., Poddar, S.C. and Ghosh, S.K. (1981). Notes on an aphidiphagous insect, *Micromus timidus* Hagen (Neuroptera : Hemerobiidae).
Science and Culture 47 (6): 223-224.

Readshaw, J.L. (1973). The numerical response of predators to prey density.
J. Appl. Ecol. 10: 342-351.

Ridgway, R.L. and Murphy, W.L. (1984). Biological control in the field.
pp. 220-228. In Canard, M., Semeria, Y. and New, T.R. Biology of Chrysopidae. Dr W. Junk Publishers.

Rogers, D.J. (1972). Random search and insect population models.
J. Anim. Ecol. 41: 369-383.

Rohitha, B.H. (1979). Some aspects of the biology, damage, population dynamics and flight of *Acyrthosiphon kondoi* Shinji (Homoptera : Aphididae) in Canterbury, New Zealand.
Unpublished Ph.D. Thesis, Lincoln College, University of Canterbury, New Zealand.

Rohitha, B.H. and Penman, D.R. (1981). A comparison of sampling methods for bluegreen lucerne aphid (*Acyrthosiphon kondoi*) in Canterbury, N.Z.
N.Z. J. of Zool. 8: 539-542.

Rohitha, B.H. and Penman, D.R. (1983). Effect of temperature on the biology of bluegreen lucerne aphid, *Acyrthosiphon kondoi*.
N.Z. J. of Zool. 10: 299-308.

Rohitha, B.H., Pottinger, R.P. and Firth, A.C. (1985). Population monitoring studies of lucerne aphids and their predators in the Waikato.
Proc. 38th N.Z. Weed and Pest Control Conf.: 31-34.

Royama, T. (1971). A comparative study of models for predation and parasitism.
Res. Popul. Ecol. Suppl. No. 1.

Russel, R.J. (1970). the effectiveness of *Anthocoris nemorum* and *A. confusus* (Hemiptera : Anthocoridae) as predators of the sycamore aphid, *Drepanosiphum platanoides*. I. The number of aphids consumed during development.
Ent. Exp. Appl. 13: 194-207.

Samson, P.R. and Blood, P.R.B. (1979). Biology and temperature relationships of *Chrysopa* sp., *Micromus tasmaniae* and *Nabis capsiformis*.
Ent. Exp. Appl. 25 (3): 253-259.

Samson, P.R. and P.R.B. Blood (1980). Voracity and searching ability of *Chrysopa signata* (Neuroptera : Chrysopidae), *Micromus tasmaniae* (Neuroptera : Hemerobiidae), *Tropiconabis capsiformis* (Hemiptera : Nabidae).
Aust. J. Zool. 28: 575-580.

Sandness, J.N. and McMurtry, J.A. (1972). Prey consumption behaviour of *Amblyseius largoensis* in relation to hunger.
Can. Ent. 104: 461-470.

Santos, M.A. (1975). Functional and numerical responses of the predatory mite, *Amblyseius fallacis*, to prey density.
Environ. Entomol. 4: 989-992.

Saugstad, E.S., Bram, R.A. and Nyquist, W.E. (1967). Factors influencing sweep-net sampling of alfalfa.
J. Econ. Ent. 60: 521-426.

Schlinger, E.I. and Dietrick, E.J. (1960). Biological control of insect pests aided by strip-farming alfalfa in experimental program.
California Agriculture 14: 7-8, 15.

Siddique, M.A.B> (1985). Biology and predation of pacific damsel bug, *Nabis kingbergii* Reuter, (Hemiptera : Nabidae). Unpublished Ph.D. Thesis, University of Canterbury, New Zealand.

Siddique, A.B. and Chapman, R.B. (1987a). Effect of prey type and quantity on the reproduction, development and survival of Pacific damsel bug, *Nabis kinbergii* Reuter (Hemiptera : Nabidae).
N.Z. J. of Zool. 14: 343-349.

Siddique, A.B. and Chapman, R.B. (1987b). Functional response of pacific damsel bug, *Nabis kinbergii* (Hemiptera : Nabidae).
Entomophaga 32 (3): 303-309.

Siddiqui, W.H., Barlow, C.A, and Randolph, P.A. (1973). Effects of some constant and alternating temperatures on the population growth of the pea aphid *Acyrthosiphon pisum* (Homoptera : Aphididae).
Can. Ent. 105: 145-156.

Simpson, R.G. and Burkhardt, C.C. (1960). Biology and evaluation of certain predators of *Therioaphis maculata* (Buckton).
J. Econ. Ent. 53: 89-94.

Smith, B.C. (1965). Effects of food on some aphidophagous Coccinellidae.
In: Hodek, I. (ed.). Ecology of aphidophagous insects. Dr W. Jurek Pub., The Hague.

Smith, B.D. (1966). Effects of parasites and predators on a natural population of the aphid *Acyrthosiphon spartii* (Koch) on broom (*Sarothamnus scoparius* L.).
J. Anim. Ecol. 35: 255-267.

Solomon, M.E. (1949). The natural control of animal populations.
J. Anim. Ecol. 18: 1-35.

Southwood, T.R.E. (1978). Ecological Methods. Methuen, London.

Stern, V.M. and van den Bosch, R. (1959). Field experiments on the effects of insecticides.
Hilgarida 29: 103-130.

Summers, C.G. (1976). Population fluctuations of selected arthropods in alfalfa : influence of two harvesting practices.
Environ. Entomol. 5 : 103-110.

Sundby, R.A. (1966). A comparative study of the efficiency of three predatory insects *Coccinella septempunctata* L. (Coleoptera : Coccinellidae), *Chrysopa carnea* St. (Neuroptera : Chrysopidae) and *Syrphus ribesii* L. (Diptera : Syrphidae) at two different temperatures.
Entomophaga 11 (4): 395-404.

Sunderland, K.D. and Vickerman, G.P. (1980). Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields.
J. Appl. Ecol. 17: 389-396.

Syrett, P. and Penman, D.R. (1980). Studies of insecticide toxicity to lucerne aphids and their predators.
N.Z. J. of Agr. Res. 23: 575-580.

Syrett, P. and Penman, D.R. (1981). Development threshold temperatures for the brown lacewing, *Micromus tasmaniae* (Neuroptera : Hemerobiidae).
N.Z. J. of Zool. 8: 281-283.

Tamaki, G. and Long, G.E. (1978). Predator complex of the green peach aphid on sugarbeets : Expansion of the predator power and efficacy model.
Environ. Entomol. 7: 835-842.

Tamaki, G. and Weeks, R.E. (1972). Efficiency of three predators *Geocoris bullatus, Nabis americoferus* and *Coccinella transversoguttata*, used alone or in combination against 3 insect prey species, *Myzus persicae, Ceramica picta*, and *Mamestra configurata.* Environ. Entomol. 1: 258-263.

Taylor, F. (1982). Sensitivity of physiological time in arthropods to variation of its parameters. Environ. Entomol. 11: 573-577.

Thomas, W.P. (1977). Biological control of the blue green lucerne aphid. The Canterbury situation.
Proc. 30th N.Z. Weed and Pest Control Conf.: 182-187.

Ting, T.H., Swincer, D.E. and Walden, K.J. (1978). Laboratory studies on the native predators of the spotted alfalfa aphid in South Australia.
Proc. Lucerne Aphid Workshop, Tamworth 1978, 84-98.

Turner, J.W. and Teakle, R.E. (1979). Manipulation of beneficial organisms.
Aust. Appl. Ent. Res. Conf.

Valentine, E.W. (1967). A list of the hosts of entomophagous insects of New Zealand.
N.Z. J. of Science. 10: 1100-1210.

van den Bosch, R., Messenger, P.S. and Gutierrez, A.P. (1982). An introduction to biological control. Plenum Press. New York and London.

van den Bosch, R. and Stern, V.M. (1969). The effect of harvesting practices on insect populations in alfalfa.
Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage. 1: 47-54.

Van Emden, H.F. (1966). The effectiveness of aphidophagous insects in reducing aphid populations.
In Hodek, I. (ed.). Ecology of aphidophagous insects.

Varley, G.C., Gradwell, G.R. and Hassell, M.P. (1983). Insect population ecology : an analytical approach. Blackwell, Oxford, London.

Vickerman, G.P. and Sunderland, K.D. (1975). Arthropods in cereal crops : Nocturnal activity, vertical distribution and aphid predation.
J. Appl. Ecol. 12: 755-766.

Walpole, R.E. (1974). Introduction to statistics. MacMillan Publishing Co., New York.

Waterhouse, D.F. (1979). Pasture pests and biological control in Australia.
pp. 12-16 In Crosby, T.K. and Pottinger, R.P. (eds.). Proc. 2nd Australasian Conf. Grassl. Invert. Ecol. N.Z. Govt. Printer, Wellington.

Wheeler, A.G. (1977). Studies on the arthropod fauna of alfalfa. VII. Predaceous insects.
Can. Ent. 109: 432-428.

Wightman, J.A. and Whitford, D.N.J. (1982). Integrated control of pests of legume seed crops. 1. Insecticides for mirid and aphid control.
N.Z. J. of Exp. Agr.: 209-215.

Williams, F.M. and Juliano, S.A. (1985). Further difficulties in the analysis of functional response experiments and resolution.
Can. Ent. 117: 631-640.

Wise, K.A.J. (1963). A list of the Neuroptera of New Zealand.
Pacif. Insects. 5: 53-58.

Wratten, S.D. and Pearson, J. (1982). Predation of sugar beet aphids in New Zealand.
Ann. Appl. Biol. 101: 178-181.

ACKNOWLEDGEMENTS

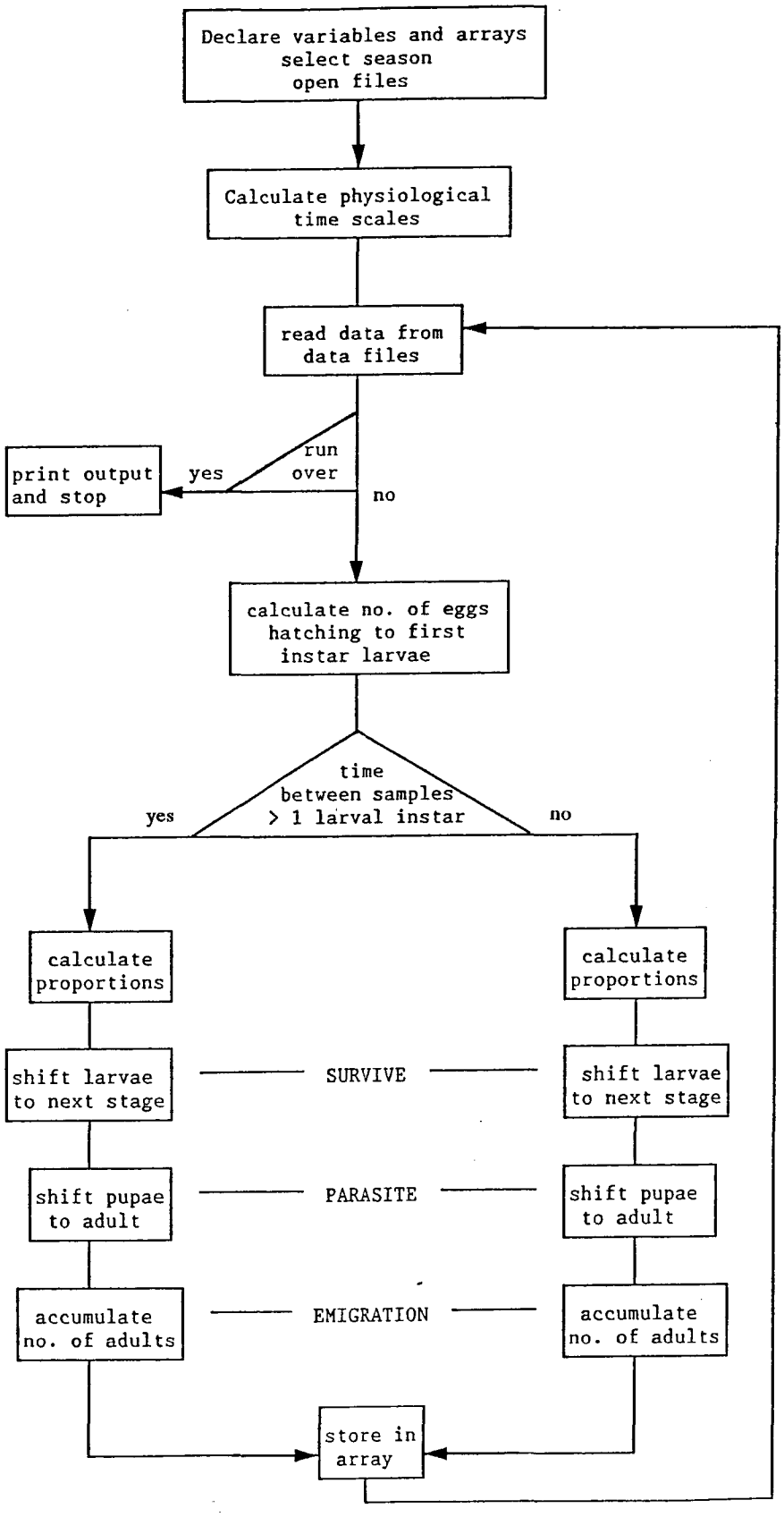
I would like to thank my supervisors, Prof. D.R. Penman and Dr. R.M. Emberson of the Entomology Department, Lincoln College and Dr. J.A. Wightman and Dr. O.R.W. Sutherland of Entomology Division, D.S.I.R. for their guidance and encouragement throughout the project. Thanks must also go to Entomology Division, D.S.I.R. for funding the project.

Many people gave assistance along the way. Megan Brown, Jane Lindsay and Sue Appleby helped with the collection and sorting of samples. Dan Pearson (D.S.I.R.) kindly loaned his electrobalance. Kathy Macken and Ruth Frampton (Lincoln College) gave advice on statistical matters. Nigel Barlow and Steve Goldson (M.A.F.Tech) gave valuable comments on the thesis.

The staff and fellow students of the Entomology Department, Lincoln College created a pleasant environment to work in. I am grateful for advice and encouragement given freely by the various members of staff and fellow students. In particular Mike Bowie who shared his room with me, Mike Butcher who was always willing to discuss ideas, and Sue Trotter and Marnie Barrell who gave invaluable assistance with preparation of the thesis.

Family and friends gave support and encouragement which was always appreciated.

APPENDIX: Flow chart and Fortran 77 listing for lacewing development model.



```
c
c
      PROGRAM MODEL
c
c     This program is a simple transitional model written to simulate
c     development of the juvenile stages of the hemerobiid lacewing
c     Micromus tasmaniae.
c     Designed expressly for comparison with field populations, the model
c     is 'fed' egg densities, aphid densities and hourly temperatures from
c     field data from which it produces stage-frequency predictions.
c
c     THE MODEL IS WRITEN IN 5 SECTIONS
c     PHASE 1:-Arrays are declared and files opened.
c     PHASE 2:-Hourly temperature data from the field are converted to
c              day-degrees and stored in an array STORE for accessing in
c              phase 4
c     PHASE 3:-This section inputs the data from the first field sample
c              into an array STAGE so that it can be used as the starting
c              point for the model in phase 4
c     PHASE 4:-This section reads date, egg and aphid #s from a file
c              DATA.DAT and stores the egg # directly into array STAGE.
c              The days-degrees corresponding to the date are read from
c              array STORE and stored in STAGE.  The day-degrees between
c              samples is then divided by the time (in day-degrees
c              required for the full development of each stadium.  This
c              proportion is then used to partition the individuals in
c              each stadium into those which pass on to the next stadium
c              and those which remain the same.  Various mortalities are
c              applied to 'tune' the model to the field data.
c     PHASE 5:-Output phase; a file named MODEL.OUT is created in the
c              users directory and the data accumulated in array STAGE
c              is printed to it.
c
c     MORTALITIES: Mortalities unassociated with specific causes are
c              built into the model.  These are based on the survial of
c              lacewings reared individually in the insectary.
c              Mortalities are allocated as follows;
c              SURVIVAL: EGG-FIRST INSTAR=88.61%
c              SURVIVAL: FIRST-SECOND INSTAR=97.14%
c              SURVIVAL: SECOND-THIRD INSTAR=97.79%
c              SURVIVAL: THIRD INSTAR-PUPA=100%
c              SURVIVAL: PUPA-ADULT=98.50%
c
c              Mortality due to the parasite Anacharis zealandica was
c              measured in the field and is allocated as follows;
c              SPRING 85:  2.8%
c              AUTUMN 86: 86.0%
c              SPRING 86: 11.8%
c
c              Survival of larvae was linked to the availability of aphid
c              prey.  A variable SURVIVE was calculated using the formula;
c
c              SURVIVE = aphid no. / 10 * total no. of larvae
c
c              with the constraints that survival cannot be greater than
c              100% or less than some minimun value.  As long as there
c              are more than 10 aphids per lacewing larvae all larvae
c              survive.  As the ratio falls below 10:1 so too does larval
c              survival, until it reaches the lower limit.  The lower
c              limits were set to make the model fit the field data and
c              allow for larval survival through cannibalism and
c              alternative food sources.
c
c              Two unexplained mortalities were necessary to 'tune' the
c              model to the field data in the autumn run.  The first of
c              these GONE1 coincides with a period of bad weather, and
```

```
c             involves a 70% mortality on the larval stages.  The second
c             GONE2 is completely unexplained and involves an 85%
c             mortality to the pupal and adult stages.
c
c
c
c                                PHASE 1
c                                =======
c             DECLARATION OF ARRAYS AND VARIABLES, OPEN FILES
c             ===============================================
c
c
      REAL I0
      REAL I1
      REAL I2
      REAL I3
      REAL I4
      REAL S1
      REAL S2
      REAL S3
      REAL EMERGE
      REAL APHIDS
      REAL MORT
      REAL SURVIVE
      REAL ADD11
      REAL ADD12
      REAL ADD21
      REAL ADD22
      REAL ADD31
      REAL ADD32
c
      DIMENSION STORE1(100,24)    !real 2 dimensional arrays
      DIMENSION STORE2(100,24)    !used in calculating day-
      DIMENSION STORE3(100,24)    !degrees.
c
      DIMENSION STAGE(30,7)
c
      DIMENSION FIRSTS(30,4)
c
      DIMENSION T(24)
c
      DIMENSION Q(5)
c
      DIMENSION EGGS(30)
c
      REAL INT(30)
c
c
      TYPE *,'WHICH SEASON DO YOU WISH TO RUN?:'
      TYPE *,'INPUT;  1 FOR SPRING 1985'
      TYPE *,'        2 FOR AUTUMN 1986'
      TYPE *,'        3 FOR SPRING 1986'
      TYPE *,'    '
      ACCEPT *,P
c
      IF(P.EQ.1)THEN
      OPEN(UNIT=1,FILE='TEMP01.DAT',STATUS='OLD')    !sequential access
      ELSE IF(P.EQ.2)THEN                            !    by default
      OPEN(UNIT=2,FILE='TEMP02.DAT',STATUS='OLD')
      ELSE IF(P.EQ.3)THEN
      OPEN(UNIT=3,FILE='TEMP03.DAT',STATUS='OLD')
      ENDIF
c
      IF(P.EQ.1)THEN
         OPEN(UNIT=10,FILE='DATA1.DAT',STATUS='OLD')
      ELSE IF(P.EQ.2)THEN
```

```
         OPEN(UNIT=20,FILE='DATA2.DAT',STATUS='OLD')
      ELSE IF(P.EQ.3)THEN
         OPEN(UNIT=30,FILE='DATA3.DAT',STATUS='OLD')
      ENDIF
c
c
c
c                     PHASE 2
c                     =======
c              CALCULATION OF DAY-DEGREES
c              ==========================
c
c     Three files are created (STORE1-3)and accumulated day-degrees
c     for 3 different developmental threshold temperatures produced
c     and stored.  Day-degrees are calculated on hourly temperature
c     summations above the threshold.
c
c     DT1= developmental threshold for egg development
      DT1=4.40
c     DT2= developmental threshold for larval development
      DT2=3.82
c     DT3= developmental threshold for pupal development
      DT3=4.68
c
      DAYDEG1=0
      DAYDEG2=0
      DAYDEG3=0
      D=1
      H=1
c
c     read temperature from file
c
 200  IF(P.EQ.1)THEN
         READ(1,*)(T(I),I=1,24)
      ELSE IF(P.EQ.2)THEN
         READ(2,*)(T(I),I=1,24)
      ELSE IF(P.EQ.3)THEN
         READ(3,*)(T(I),I=1,24)
      ENDIF
c
c     calculate day-degrees and store
c
      DO J=1,24
           IF(T(J).EQ.99)GO TO 300
c          ----------------------------------
           IF(T(J).LT.DT1)GO TO 210
           DAYDEG1=DAYDEG1+(0.041667*(T(J)-DT1))
 210       STORE1(D,H)=DAYDEG1
c          ----------------------------------
           IF(T(J).LT.DT2)GO TO 220
           DAYDEG2=DAYDEG2+(0.041667*(T(J)-DT2))
 220       STORE2(D,H)=DAYDEG2
c          ----------------------------------
           IF(T(J).LT.DT3)GO TO 230
           DAYDEG3=DAYDEG3+(0.041667*(T(J)-DT3))
 230       STORE3(D,H)=DAYDEG3
c          ----------------------------------
           H=H+1
      ENDDO
c
c
      D=D+1
      H=1
      GO TO 200
c
c
```

```
c                    PHASE 3
c                    =======
c          SET PARAMETERS FOR MODELLING PHASE
c          ==================================
c
c
 300  IF(P.EQ.1)THEN              !spring '85
        STAGE(1,1)=1.0
        STAGE(1,2)=27.4
        STAGE(1,3)=8.0
        STAGE(1,4)=3.8
        STAGE(1,5)=1.4
        STAGE(1,6)=0.0
        STAGE(1,7)=0.5
        EGGS(1)=27.4
        MORT=2.8
        APHIDS=1317
c
      ELSE IF(P.EQ.2)THEN         !autumn '86
        STAGE(1,1)=1.0
        STAGE(1,2)=53.3
        STAGE(1,3)=3.5
        STAGE(1,4)=1.4
        STAGE(1,5)=3.8
        STAGE(1,6)=0.0
        STAGE(1,7)=2.4
        EGGS(1)=53.3
        MORT=95.0
        APHIDS=21890
c
      ELSE IF(P.EQ.3)THEN          !spring '86
        STAGE(1,1)=1.0
        STAGE(1,2)=75.0
        STAGE(1,3)=15.2
        STAGE(1,4)=14.5
        STAGE(1,5)=4.9
        STAGE(1,6)=0.0
        STAGE(1,7)=0.2
        EGGS(1)=75.0
        MORT=11.8
        APHIDS=232
c
      ENDIF
c
c     Set duration of each stadium
c
      I0=93.5      ! day-degrees for egg development
      I1=44.6      ! day-degrees for first instar larval development
      I2=38.0      ! day-degrees for second instar larval development
      I3=43.2      ! day-degrees for third instar larval development
      I4=198.4     ! day-degrees for pupal development
c
c
c
c                     PHASE 4
c                     =======
c                   MODEL PHASE
c                   ===========
c
c
      D=1                              ! set counters
      D1=2                             ! set counters
      ADD11=0                          ! set counters
      ADD21=0
      ADD31=0
c
```

```
c      read date,egg # and aphid density from file DATA.DAT
c
 400   IF(P.EQ.1)THEN
          READ(10,*)(Q(I),I=1,4)        ! read data from DATA.DAT
       ELSE IF(P.EQ.2)THEN              ! read data from DATA.DAT
          READ(20,*)(Q(I),I=1,4)        ! read data from DATA.DAT
       ELSE IF(P.EQ.3)THEN
          READ(30,*)(Q(I),I=1,4)
       ENDIF
c
       DAY=Q(1)
       IF(DAY.EQ.99)GO TO 500           !run finished-output phase
       HOUR=Q(2)
       ADD12=STORE1(DAY,HOUR)
       ADD22=STORE2(DAY,HOUR)
       ADD32=STORE3(DAY,HOUR)
c
       STAGE(D1,1)=DAY                 !input day into array STAGE
       STAGE(D1,2)=Q(3)                !input # of eggs into array STAGE
c
c
c
c      Here we position the unexplained variables GONE1 and GONE2
c      for the autumn run only
c
       IF(P .EQ. 2)THEN
             IF(Q(1) .EQ. 11)THEN
                 GONE1=0.3                 ! GONE1 = 70% mortality
             ELSE                          ! applied at day 11
                 GONE1=1.0
             ENDIF
c
             IF(Q(1) .EQ. 31)THEN
                 GONE2=0.15                ! GONE2 = 85% mortality
             ELSE                          ! applied at day 31
                 GONE2=1.0
             ENDIF
       ELSE
             GONE1=1.0
             GONE2=1.0
       ENDIF
c
c
c      This section of the program calculates the # of eggs hatching to
c      first instar larvae in the interval ADD12-ADD11 and stores the
c      components in an array FIRSTS.
c
       INT(D1)=(ADD12-ADD11)/I0
c      ---------------------------
       FIRSTS(D1,1)=EGGS(D)*INT(D1)
c      ---------------------------
       IF((D-1).LT.1.0)THEN
          FIRSTS(D1,2)=0
       ELSE
          IF((INT(D1)+INT(D)).GT.1.0)THEN
              FIRSTS(D1,2)=EGGS(D-1)-FIRSTS(D,1)
          ELSE
              FIRSTS(D1,2)=EGGS(D-1)*(INT(D1)+INT(D))-EGGS(D-1)*INT(D)
          ENDIF
       ENDIF
c      ---------------------------
       IF((D-2).LT.1.0)THEN
           FIRSTS(D1,3)=0
       ELSE
          IF((INT(D1)+INT(D)+INT(D-1)).GT.1.0)THEN
             FIRSTS(D1,3)=EGGS(D-2)-(FIRSTS(D-1,1)+FIRSTS(D,2))
```

```
         ELSE
            FIRSTS(D1,3)=(EGGS(D-2)*(INT(D1)+INT(D)+INT(D-1)))-
     1                          (EGGS(D-2)*(INT(D)+INT(D-1)))
         ENDIF
       ENDIF
c      ---------------------------
       IF((D-3).LT.1.0)THEN
          FIRSTS(D1,4)=0
       ELSE
          TOT=FIRSTS(D-2,1)+FIRSTS(D-1,2)+FIRSTS(D,3)
          FIRSTS(D1,4)=EGGS(D-3)-TOT
       ENDIF
c      ---------------------------
       SUM=FIRSTS(D1,1)+FIRSTS(D1,2)+FIRSTS(D1,3)+FIRSTS(D1,4)
c      ---------------------------
c
c      This section of the program calculates the # of larvae and pupae
c      passing to higher stadia, and stores the components in STAGE.
c      The model splits into two sections depending on whether the
c      physiological time between samples (which equals the step of
c      the model) is greater or smaller than one larval instar period.
c
c
       IF((ADD22-ADD21).GE.41.3 .AND. (ADD22-ADD21).LE.44.6)THEN
         ADD22=ADD22 + 3.3
       ELSE IF((ADD22-ADD21).GE.38.0 .AND. (ADD22-ADD21).LT. 41.3)
      1THEN
         ADD22=ADD22 - 3.3
       ELSE IF((ADD22-ADD21).GT.44.6 .OR. (ADD22-ADD21).LT. 38.0)
      1THEN
         CONTINUE
       ENDIF
c
c
c      ====================================
       IF((ADD22-ADD21) .LT. 38.0)GO TO 401
c      ====================================
c                 SECTION 1
c                 SECTION 1
c
c      Time between samples is greater than one larval instar period
c
       PN1=I1/(ADD22-ADD21)                    ! calculate proportions
       PN2=I2/(ADD22-ADD21)                    ! calculate proportions
       PN3=I3/(ADD22-ADD21)                    ! calculate proportions
c      ----------------------
       PN4=(ADD32-ADD31)/I4
c      ----------------------
c
c      This section calculates the no. of larvae which would survive
c      given an excess of aphid prey i.e., S1-S3 and then calculates
c      the ratio SURVIVE to correct for any food shortage-see notes
c      above.
c
       S1=(SUM-(SUM*(1-PN1)))*0.8861
c
       S2=((STAGE(D,3)*PN2)+(SUM*(1-PN1)))*0.9714
c
       S3=((STAGE(D,4)*PN3)+(STAGE(D,3)*(1-PN2)))*0.9779
c
       SURVIVE=Q(4)/(10*(S1+S2+S3))              ! calculate SURVIVE
c                                                ! calculate SURVIVE
       IF(SURVIVE .GT. 1.0) SURVIVE=1.0          ! calculate SURVIVE
c
       IF(P.EQ.1)THEN
          IF(Q(1).LE.50)THEN
```

```
          IF(SURVIVE.LT.0.4)SURVIVE=0.4
        ELSE IF(Q(1).GT.50)THEN
          IF(SURVIVE .LT. 0.1) SURVIVE=0.1
        ENDIF
      ELSE IF(P.EQ.2)THEN
        IF(SURVIVE .LT. 0.2) SURVIVE=0.2
      ELSE IF(P.EQ.3)THEN
        IF(Q(1).LE.50)THEN
          IF(SURVIVE.LT.0.7)SURVIVE=0.7
        ELSE IF(Q(1).GT.50)THEN
          IF(SURVIVE.LT.0.4)SURVIVE=0.4
        ENDIF
      ENDIF
c
      STAGE(D1,3)=SURVIVE * S1 * GONE1
c
      STAGE(D1,4)=SURVIVE * S2 * GONE1
c
      STAGE(D1,5)=SURVIVE * S3 * GONE1
c
c
c     This section calculates the no. of larvae progressing to pupal
c     and adult stages.
c
      IF(ADD22.GT.150)THEN
c
      STAGE(D1,6)=(STAGE(D,5)+(STAGE(D,6)*(1-PN4))+(STAGE(D,4)*(1-PN3)))
     1 *GONE2
c
      STAGE(D1,7)=(((STAGE(D,6)*PN4)*((100-MORT)/100)*0.985
c
      ELSE
c
      STAGE(D1,6)=(STAGE(D,4)*(1-PN3))+STAGE(D,5)+STAGE(D,6)
c
      STAGE(D1,7)=STAGE(D,7)
c
      ENDIF
c     ----------------------------------
      IF(S1 .GT. STAGE(D1,2))THEN
          EGGS(D1)=0
      ELSE
          EGGS(D1)=STAGE(D1,2)-S1
      ENDIF
c     ----------------------------------
c
      GO TO 402
c
c                 SECTION 2
c                 SECTION 2
c
c     Time between samples is less than one larval instar period
c
c
 401  PN1=(ADD22-ADD21)/I1                  ! calculate proportions
      PN2=(ADD22-ADD21)/I2                  ! calculate proportions
      PN3=(ADD22-ADD21)/I3                  ! calculate proportions
c     ----------------------
      PN4=(ADD32-ADD31)/I4
c     ----------------------
c
c     This section calculates the no. of larvae which would survive
c     given an excess of aphid prey i.e., S1-S3 and then calculates
c     the ratio SURVIVE to correct for any food shortage.
c
      S1=(SUM+(STAGE(D,3)*(1-PN1)))*0.8861
```

```
c
      S2=((STAGE(D,3)*PN1)+(STAGE(D,4)*(1-PN2)))*0.9714
c
      S3=((STAGE(D,4)*PN2)+(STAGE(D,5)*(1-PN3)))*0.9779
c
      SURVIVE=Q(4)/(10*(S1+S2+S3))              ! calculate SURVIVE
c                                               ! calculate SURVIVE
      IF(SURVIVE .GT. 1.0) SURVIVE=1.0          ! calculate SURVIVE
c
      IF(P.EQ.1)THEN
        IF(Q(1).LE.50)THEN
           IF(SURVIVE.LT.0.4)SURVIVE=0.4
        ELSE IF(Q(1).GT.50)THEN
           IF(SURVIVE.LT.0.1)SURVIVE=0.1
        ENDIF
      ELSE IF(P.EQ.2)THEN
        IF(SURVIVE.LT.0.2)SURVIVE=0.2
      ELSE IF(P.EQ.3)THEN
        IF(Q(1).LE.50)THEN
           IF(SURVIVE.LT.0.7)SURVIVE=0.7
        ELSE IF(Q(1).GT.50)THEN
           IF(SURVIVE.LT.0.4)SURVIVE=0.4
        ENDIF
      ENDIF
c
      IF(SURVIVE .LT. 0.2) SURVIVE=0.2
c
      STAGE(D1,3)=SURVIVE * S1 * GONE1
c
      STAGE(D1,4)=SURVIVE * S2 * GONE1
c
      STAGE(D1,5)=SURVIVE * S3 * GONE1
c
c     ----------------------
c
c     This section calculates the no. of larvae progressing to pupal
c     and adult stages.
c
      IF(ADD22.GT.150)THEN
c
      STAGE(D1,6)=((STAGE(D,5)*PN3)+(STAGE(D,6)*(1-PN4)))*GONE2
c
      STAGE(D1,7)=(((STAGE(D,6)*PN4)*((100-MORT)/100)*0.985))
c
      ELSE
c
      STAGE(D1,6)=(STAGE(D,5)*PN3)+STAGE(D,6)
c
      STAGE(D1,7)=STAGE(D,7)
c
      ENDIF
c     ------------------------------------
      IF( S1 .GT. STAGE(D1,2) ) THEN
          EGGS(D1)=0
      ELSE
          EGGS(D1)=STAGE(D1,2)-S1
      ENDIF
c     ------------------------------------
c
 402  D=D1
      D1=D1+1                       ! increment counters
      ADD11=ADD12                   ! increment counters
      ADD21=ADD22
      ADD31=ADD32
      APHIDS=Q(4)
```

```
C
      GO TO 400
C
C
C
C                    PHASE 5
C                    =======
C                  OUTPUT PHASE
C                  ============
C
 500  OPEN(UNIT=3,FILE='MODEL.OUT',STATUS='NEW',CARRIAGECONTROL='LIST')

      WRITE(3,*) '     ========================'
      WRITE(3,*) '     OUTPUT FROM PROGRAM MODEL'
      WRITE(3,*) '     ========================'
      WRITE(3,*) '           '
C
      IF(P.EQ.1)THEN
         WRITE(3,*) '           SPRING 1985  '
      ELSE IF(P.EQ.2)THEN
         WRITE(3,*) '           AUTUMN 1986 '
      ELSE IF(P.EQ.3)THEN
         WRITE(3,*) '           SPRING 1986'
      END IF
C
      WRITE(3,*) '              '
      WRITE(3,*) 'DEVELOPMENTAL THRESHOLD USED;'
      WRITE(3,*) 'FOR EGGS=  ',DT1
      WRITE(3,*) 'FOR LARVAE=',DT2
      WRITE(3,*) 'FOR PUPAE= ',DT3
      WRITE(3,*) '       '
      WRITE(3,*) 'MORTATILITY DUE TO PARASITE=',MORT,' %'
      WRITE(3,*) '     '
      WRITE(3,*) 'LIMIT=',LIMIT
      WRITE(3,*) '   '
      WRITE(3,*)'          NO.      NO.LARVAE-INSTARS        NO.       NO.'
      WRITE(3,*)' DAY    EGGS      1       2       3       PUPAE   ADULTS'
      WRITE(3,*)' ===    ====    ==================      =====   ======'
C
      DO J=1,D
        WRITE(3,501)STAGE(J,1),STAGE(J,2),STAGE(J,3),STAGE(J,4),
     1STAGE(J,5),STAGE(J,6),STAGE(J,7)
 501    FORMAT(F5.1,3X,F5.1,3X,F5.1,3X,F5.1,3X,F5.1,3X,F5.1,3X,F5.1)
        WRITE(3,*)'    '
      ENDDO
      CLOSE(UNIT=3)
C
      TYPE *,'   THE CALCULATIONS ARE NOW COMPLETE'
      TYPE *,'   ================================'
      TYPE *,'          '
      TYPE *,'a file named MODEL.OUT has been created and the output'
      TYPE *,'from the model stored in it.--HAVE A NICE DAY--'
C
      STOP
      END
```